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Cover: Brown Bullhead, Ictalurus nebulosus, Ottawa River specimens photographed by Peter J. Rubec. See Article by Rubec and Qadri page 6.
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Home Range, Daily Movements, and Reproductive Biology of Brown Bear in Southcentral Alaska

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Twenty-three radio-collared adult Brown/Grizzly Bears (Ursus arctos) were studied in the Nelchina Basin of southcentral Alaska during 1978 and 1979. Radio-collared bears were seen on 85.4% of 644 radio locations. Home ranges of adult females averaged 408 km², while those of adult males averaged 769 km². Daily movement of males averaged 7.7 km/d, while females averaged 7.0 km/d. Most bears entered dens in late October and emerged between 9 April and 12 May and therefore were active for half of the year. Most females became reproductively mature at 4.5 y; in three cases females successfully bred at 3.5 y. A reproductive interval of 2 y was reported in one case following loss of a yearling offspring. Typical breeding intervals were 3 y. Average size of 17 cub and yearling litters was 1.9; high rates of cub loss were observed. Breeding activity was concentrated in May and June. Relative to most other North American Brown Bear populations, Brown Bears in Interior Alaska had larger home ranges, females reached sexual maturity at younger ages, and weaning of litters occurred earlier.

Key Words: Brown Bear, Ursus arctos, home range, daily movements, denning, sexual maturity, reproductive interval, litter size, cub mortality, breeding season.

Alaskan Brown (Grizzly) Bear ecology has been investigated on the Alaska Peninsula (Glenn 1976), Kodiak Island (Hensel et al. 1969), the Brooks Range (Reynolds 1976, 1980) and in southeastern Alaska (Klein 1958; Wood 1976), all coastal or arctic populations. Although a few studies have been conducted on subarctic populations (notably Pearson 1975), no studies have been conducted on Interior Alaskan Brown Bear populations. In recent years these populations have been subject to increasing levels of hunting and destruction of habitat resulting from expanded resource development and increased human populations. Furthermore, outside of Alaska and portions of Canada, North American, European and Asian Brown Bear populations have typically been eliminated or greatly reduced in areas of former abundance (Cowan 1972). Baseline biological studies of relatively abundant and unexploited populations such as those in Interior Alaska provide insights into the biology of Brown Bears that are important in understanding and reestablishing populations in areas where the species has been eliminated or greatly reduced. This paper presents information on home range size, daily movements, and several reproductive parameters of a previously unstudied subarctic Brown Bear population.

Study Area

The study was conducted in the Nelchina and upper Susitna River Basins of southcentral Alaska, an area of 61595 km² of which 18798 km² is above 1200 m in elevation. Topography, geology, vegetation, and climate of the area have been thoroughly described (Skog 1968; Rausch 1969; Bishop and Rausch 1974; Ballard 1982). The bears reported on here did not utilize salmon (Oncorhynchus spp.) for food during the period of investigation. Bear food habits were reported elsewhere (Ballard et al. 1981).

Procedures

Between 9 April and 23 June 1978, 23 adult Brown Bears were captured, equipped with radio collars (Telonics, Mesa, AZ), ear tagged with red plastic rototags (Dalton Supplies Limited, Nettlebed, England), weighed, measured, and had both lower premolars extracted for age determination by methods similar to those described by Stoneberg and Jonkel (1966).

Radio-collared bears were observed twice daily for the first 2 w of study, once daily through the remainder of June 1978, and once per week subsequently. Bears were radio-located from fixed-wing aircraft according to methods described by Mech (1974) and radio-locations were plotted on 1:250,000

1
scale maps. This portion of the study was terminated in summer 1979.

Home ranges of individual bears were calculated by connecting the outer-most radio-locations, thereby providing a minimum estimate of home range (Mohr 1947). The area of the resulting polygon was determined with a Numonics Model 1224 electronic digitizer. Daily movements were determined by measuring straight-line distance moved between observations on consecutive days.

Reproductive data collected in 1978 studies were supplemented by captures of 48 Brown Bears in 1979 and 28 in 1980. These captures were in the same or adjacent areas to the 1978 home range study area.

Results and Discussion

Radio-collared bears were observed on 85.4% of the occasions they were radio-located (n = 644). Absence of observation was often associated with den site observations or with hazardous terrain which precluded more thorough searches. Observability of individual bears varied from 59.3% to 97.2%. For bears occurring on relatively flat terrain, where thorough searches were possible, a radioed female with three newborn cubs was the least frequently observed (84.0%). Relative to other adult bears, females with newborn cubs appeared more secretive in behavior, frequently hiding in dense bushes.

Home Range

Home ranges of radio-collared female bears averaged 407.7 km² (range 193.5-733.5 km²) significantly smaller (P<0.05) than male home ranges which averaged 768.7 km² (range 281.5 to 1381.5 km²) [Table 1]. Combining sexes yielded an average home range of 571.9 km². Home range of females accompanied by young (≤2.5 y), averaged 451.2 km² and did not differ significantly (P>0.05) from home ranges of single females (364.4 km²). Generally, older bears (≥6 y) appeared to have larger home ranges than younger bears, but differences were not significant (P>0.05). These trends were similar to those reported by Pearson (1975) in southwestern Yukon Territory, except that Yukon females with cubs had smaller

### Table 1. Summary of sex, age and radio-location data for 23 Brown (Grizzly) Bears studied in the Nelchina Basin study area of southcentral Alaska during 1978 and 1979.

<table>
<thead>
<tr>
<th>Bear No.</th>
<th>Sex-age</th>
<th>Reproductive status</th>
<th>No. of Radio-locations</th>
<th>Home Range</th>
<th>Daily movements — 1978</th>
<th>Denning dates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>1978</td>
<td>1979</td>
<td>km²</td>
<td>Period X (km)</td>
</tr>
<tr>
<td>209</td>
<td>f - 4</td>
<td>alone</td>
<td>25</td>
<td>1</td>
<td>241.4</td>
<td>5/28-6/22</td>
</tr>
<tr>
<td>219</td>
<td>f - 4</td>
<td>estrus</td>
<td>20</td>
<td>0</td>
<td>305.1</td>
<td>5/30-6/9</td>
</tr>
<tr>
<td>220</td>
<td>f - 5</td>
<td>w/1-1.5 y</td>
<td>39</td>
<td>7</td>
<td>580.7</td>
<td>6/2-6/24</td>
</tr>
<tr>
<td>202</td>
<td>f - 8</td>
<td>estrus, w/male</td>
<td>37</td>
<td>0</td>
<td>439.0</td>
<td>5/29-6/21</td>
</tr>
<tr>
<td>204</td>
<td>f - 7</td>
<td>w/2-2.5 y</td>
<td>28</td>
<td>0</td>
<td>523.4</td>
<td>5/29-6/20</td>
</tr>
<tr>
<td>221</td>
<td>f - 8</td>
<td>w/2.1.5 y</td>
<td>34</td>
<td>2</td>
<td>859.9</td>
<td>6/4-6/21</td>
</tr>
<tr>
<td>212</td>
<td>f - 10</td>
<td>estrus</td>
<td>21</td>
<td>0</td>
<td>222.2</td>
<td>5/29-6/21</td>
</tr>
<tr>
<td>213</td>
<td>f - 3</td>
<td>w/1-1.5 y</td>
<td>23</td>
<td>1</td>
<td>193.5</td>
<td>5/29-6/22</td>
</tr>
<tr>
<td>207</td>
<td>f - 11</td>
<td>w/3-0.5 y</td>
<td>43</td>
<td>7</td>
<td>307.4</td>
<td>5/28-6/24</td>
</tr>
<tr>
<td>208</td>
<td>f - 12</td>
<td>alone</td>
<td>46</td>
<td>1</td>
<td>733.5</td>
<td>5/28-6/20</td>
</tr>
<tr>
<td>231</td>
<td>f - 12</td>
<td>estrus, w/male</td>
<td>20</td>
<td>16</td>
<td>262.9</td>
<td>6/11-6/21</td>
</tr>
<tr>
<td>206</td>
<td>f - 13</td>
<td>estrus, w/male</td>
<td>45</td>
<td>4</td>
<td>223.3</td>
<td>5/28-6/23</td>
</tr>
<tr>
<td>234</td>
<td>f - 5</td>
<td>w/2-1.5 y</td>
<td>6</td>
<td>0</td>
<td>*</td>
<td>—</td>
</tr>
<tr>
<td>217</td>
<td>m - 3</td>
<td>alone</td>
<td>19</td>
<td>0</td>
<td>281.5</td>
<td>6/5-6/25</td>
</tr>
<tr>
<td>205</td>
<td>m - 4</td>
<td>w/female</td>
<td>41</td>
<td>0</td>
<td>798.0</td>
<td>5/27-6/28</td>
</tr>
<tr>
<td>211</td>
<td>m - 4</td>
<td>w/female</td>
<td>19</td>
<td>1</td>
<td>472.2</td>
<td>5/29-6/21</td>
</tr>
<tr>
<td>225</td>
<td>m - 4</td>
<td>alone</td>
<td>28</td>
<td>5</td>
<td>1038.1</td>
<td>6/4-6/21</td>
</tr>
<tr>
<td>200</td>
<td>m - 7</td>
<td>alone</td>
<td>6</td>
<td>4</td>
<td>312.9</td>
<td>—</td>
</tr>
<tr>
<td>228</td>
<td>m - 7</td>
<td>w/female</td>
<td>14</td>
<td>0</td>
<td>1252.0</td>
<td>6/15-6/20</td>
</tr>
<tr>
<td>227</td>
<td>m - 9</td>
<td>w/female</td>
<td>13</td>
<td>0</td>
<td>495.5</td>
<td>6/13-6/17</td>
</tr>
<tr>
<td>201</td>
<td>m - 10</td>
<td>w/female</td>
<td>24</td>
<td>2</td>
<td>1381.5</td>
<td>5/29-6/19</td>
</tr>
<tr>
<td>216</td>
<td>m - 10</td>
<td>alone</td>
<td>14</td>
<td>1</td>
<td>586.1</td>
<td>5/29-6/3</td>
</tr>
<tr>
<td>222</td>
<td>m - 11</td>
<td>alone</td>
<td>25</td>
<td>2</td>
<td>1069.7</td>
<td>6/5-6/21</td>
</tr>
</tbody>
</table>

*Home range size not determined.
home ranges than females accompanied by older young (1.5 and 2.5 y old). This may be the case for Nelchina bears as well, but it could not be shown with available data. In the western Brooks Range, Reynolds (1980) determined that home range size declined successively as follows: breeding males, breeding females, sub-adult females, and females with offspring. As has been reported elsewhere in North America (Mundy and Flook 1973; Pearson 1975; Reynolds 1980), the home ranges of Nelchina Basin bears were not exclusive, and overlap existed in the home ranges of all sex and age groups.

Average home range sizes of Nelchina Basin bears were compared with those reported elsewhere in North America (Table 2). Except for unpublished data on male bears in northwestern Alaska, Nelchina bears had larger home ranges than reported elsewhere in North America. Geographic differences in home range sizes probably reflect food availability.

**Daily Movement Rates**

Average daily movements of the 23 radio-collared brown bears ranged from 2.9 to 27.2 km/d during late May and June, 1978 (Table 1). Males averaged 7.7 km/d, while females averaged 7.0 km/d, a non-significant difference \( (P>0.05) \). Individual bear movements ranged from a minimum of 0.0 to 8.0 km/d for male No. 216 (10 y) to a maximum of 17.6 to 37.6 km/d for male No 228. Pearson (1975) stated that the daily activities and movements of bears were associated with food gathering throughout the year except, possibly, during the breeding season when male movements were influenced by the movement of females. Movements presented here reflect both activities. We were unable to detect significant \( (P>0.05) \) differences in daily movements associated with sex, age, family status, or predation frequency of individual bears.

**Denning Dates**

Bears began visiting den sites in early October and entered dens between 17 and 27 October 1978. Bear emmergence in spring 1979 ranged from 9 April to 12 May. Females accompanied by young generally remained at den sites longer than single adults, one bear as late as 31 May. Our observations are similar to data from elsewhere in North America (Murie 1944, Craighead and Craighead 1972, Pearson 1975 and others).

**Age of Reproductive Maturity**

One Nelchina Basin female was in estrus at 3.5 y. Females may successfully breed at this age as evidenced by the capture of three 5.5 y females accompanied by yearling offspring. All females captured at 4.5 y \((n = 5)\) were in estrus, successful breeding at this age was verified by the capture of two females, with offspring, that must have successfully bred at 4.5 y. Successful breeding by one female at 5.5 y was similarly verified. It appeared that most Brown Bears in the Nelchina Basin first become reproductively mature at 4.5 y with fewer females becoming mature at 3.5 or 5.5 y. This is younger than has been reported in the Yukon Territory (Pearson 1975) or in Yellowstone National Park (Craighead et al. 1969).

**Breeding Interval**

Available data suggest that the breeding interval for Nelchina Basin Brown Bears was 3 y. However, it is

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**Table 2. Comparison of reported home range sizes of Brown (Grizzly) Bears in North America**

<table>
<thead>
<tr>
<th>Area</th>
<th>Sex</th>
<th>Sample Size</th>
<th>Average home range km²</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alaska Peninsula</td>
<td>m</td>
<td>4</td>
<td>262</td>
<td>Glenn and Miller 1980</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>30</td>
<td>293</td>
<td></td>
</tr>
<tr>
<td>Yellowstone National Park</td>
<td>m</td>
<td>6</td>
<td>161</td>
<td>Craighead 1976</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>14</td>
<td>73</td>
<td></td>
</tr>
<tr>
<td>Southwestern Yukon</td>
<td>m</td>
<td>5</td>
<td>287</td>
<td>Pearson 1975</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>8</td>
<td>86</td>
<td></td>
</tr>
<tr>
<td>Kodiak Island, Alaska</td>
<td>m</td>
<td>7</td>
<td>24</td>
<td>Berns et al. 1980</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>23</td>
<td>12</td>
<td></td>
</tr>
<tr>
<td>Northern Yukon</td>
<td>m</td>
<td>9</td>
<td>414</td>
<td>Pearson 1976</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>12</td>
<td>73</td>
<td></td>
</tr>
<tr>
<td>Western Montana</td>
<td>m</td>
<td>3</td>
<td>513</td>
<td>Rockwell et al. 1978</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>1</td>
<td>104</td>
<td>This study</td>
</tr>
<tr>
<td>Nelchina Basin</td>
<td>m</td>
<td>10</td>
<td>769</td>
<td>Reynolds 1980</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>12</td>
<td>408</td>
<td></td>
</tr>
<tr>
<td>Northwestern Alaska</td>
<td>m</td>
<td>8</td>
<td>1350</td>
<td>Reynolds 1980</td>
</tr>
<tr>
<td></td>
<td>f</td>
<td>18</td>
<td>344</td>
<td></td>
</tr>
</tbody>
</table>
noteworthy that one female (10.5 y) accompanied by a yearling (age was determined visually), lost its offspring and had newborn cubs the following spring, a reproductive interval of 2 y. It appeared that offspring in the Nelchina Basin are commonly weaned soon after they emerge from their dens as 2 y-old bears, this was observed for five litters with separation occurring from mid-May to early June. No weaning of yearling litters was observed and no females entered dens with offspring of 2 y or older. Subsequent to weaning, four females were observed involved in breeding activity. If this breeding was successful (not determined) these bears would have had a reproductive interval of 3 y.

**Litter Size**

The average litter size for 4 litters of newborn cubs was 2.8 (2-3), for 13 litters of yearlings it was 1.7 (1-2), and for 4 litters of 2 y-offspring it was 1.5 (1-2). The low sample of litters with newborn cubs probably reflected capture biases against these particular family groups caused by their more secretive behavior (Ballard et al. 1980).

Although the sample size for litters with newborn cubs was small, the decline in average litter size between newborn and yearling litters was verified by observations of cub losses. In two cases, 2 of 3 cubs in undisturbed litters were lost prior to emergence from their winter dens as yearlings. Another litter of 2 cubs was lost following the successful transplant of cubs and mother to another location (Miller and Ballard unpubl. data). Causes of cub losses were not determined, however, predation by adult males may be significant as suggested by Reynolds (1980). In one case a sow and the single cub survivor of a litter of 3 were observed running from a single adult bear.

**Breeding Season**

Brown Bear breeding activity was in progress in late May and continued through the end of June. Of 112 visual observations of radio-collared bears accompanied by other adult bears in 1978; 96% occurred during May and June; only 80% of all observations were in this period, a significant difference from expected values (Chi-square test, $P<0.001$). Fifteen of the 17 radio-collared bears (excluding six females accompanied by offspring) were observed with other bears in May and June. Females accompanied by cubs or yearlings were not observed in association with other bears. Copulations were observed on 7 and 12 June 1978. This breeding peak corresponds with that observed in Mt. McKinley National Park (Murie 1944).

**Acknowledgments**

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**Literature cited**


*Available on request to the Alaska Department of Fish and Game, Division of Game, P.O. Box 3-2000, Juneau, AK 99802.

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Comparative Age, Growth, and Condition of Brown Bullhead, *Ictalurus nebulosus*, in Sections of the Ottawa River, Canada

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The abundance, age, growth and condition of six populations of Brown Bullhead, *Ictalurus nebulosus* from three sections of the Ottawa River have been compared. Gill netting indicated bullheads were more abundant below industrial and municipal effluents. The species was most abundant and formed a larger percentage of the catch of all species below Hawkesbury. Significantly slower growth and poorer condition of Brown Bullhead were found at stations in the lotic lower river section, below Ottawa, where wood-fiber blankets much of the substrate. Better growth and condition of bullheads occurred in the lake-like Hawkesbury and upper river sections where wood-fiber is scarce or absent. Growth in length appeared related to physical conditions applicable to an entire section of river, rather than to localized factors at stations below industrial and municipal effluents. Previous age and growth estimates from pectoral spines have generally underestimated age by one year and hence seriously overestimated growth at “age 1”.

Key Words: Brown Bullhead, *Ictalurus nebulosus*, growth, ecology, population dynamics, pollution, catfish, Canada.

The Brown Bullhead (*Ictalurus nebulosus*) is an important commercial and sport fish widely distributed in North America and introduced elsewhere (Scott and Crossman 1973; Wheeler 1978). Despite this, the only published studies of its age and growth are from Czechoslovakia (Frank 1955; Hensel 1966). Carlander (1969) summarized some data on the growth of the species. This study was undertaken to compare the age, growth and condition of Brown Bullhead from three sections of the Ottawa River, near Ottawa and Hawkesbury, Canada, subject to industrial and municipal pollution.

The Brown Bullhead was chosen for study because it is very tolerant of adverse conditions of temperature, oxygen, and pollutants (Brett 1956; Marvin and Heath 1968; Loeb and Starkey 1968). Scott and Crossman (1973) noted that in many heavily polluted streams near Montreal they were the only species present. A creel census below Ottawa by Levere (1969) indicated that the Brown Bullhead was the most abundant commercial species and the fish most sought after by anglers on the Ottawa River. A gill net survey of the part of the river below Hawkesbury indicated bullheads were very abundant comprising 96% of the catch (Le Sauteur 1965).

An extensive study of the chemical and physical characteristics of the Ottawa River was conducted in 1968 by the Ontario Water Resources Commission* and Quebec Water Board (OWRC-QWB 1971). The part of the river extending from the Chaudière Falls to the Carillon Dam (Figure 1) was shown to be grossly contaminated by six paper mills and the urban centers of Ottawa and Hull. Local municipalities were sources of nutrient enrichment and bacterial contamination while the pulp and paper industry was noted to contribute 90% of the dissolved organic wastes and 99% of the suspended solids entering the river. Adverse conditions caused by pulp and paper mills included: extensive bottom sludge deposits and floating sludge mats; high concentrations of suspended wood-fiber with reduced water transparency; reduced assimilative capacity indicated by elevated 5-day biological oxygen demands, ammonia and conductivity, excessive slime growth; odors; and significant mercury contamination of sediments and tissues of fish species. Dissolved oxygen conditions of 5.0-5.5 mg/L were common at several points and during July decreased to 4.3 mg/L at the Carillon Dam. The composition of bottom fauna communities was adversely altered throughout most of the river between Ottawa and the Carillon Dam, particularly in areas of sludge (wood chip and fiber) deposition. Little information was presented concerning how effluents from industries and municipalities affect the fish fauna of the Ottawa River.

Description of Study Area

The upper river section within Lac Déschènes above Ottawa extends from the YMCA Camp 4 km west of Ottawa to the Déschènes Rapids in Ottawa (Figure 1). The lower river section below Ottawa extends from the Chaudière Falls in Ottawa to Hiawatha Park, just east of Ottawa. The Hawkesbury section extends 4.8 km above and below the town of

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*Presently Ontario Ministry of Environment.
Hawkesbury about 140 km downstream of Ottawa.

Lac Déschênes is a lake-like expanse of river characterized by gently sloping shorelines, slow currents and relatively good water quality (OWRC-QWB 1971). The lower river is a less homogeneous habitat with steep shorelines, moderate to fast currents and moderately polluted conditions. The water quality is not directly hazardous to fish and invertebrates except in certain localized areas below industrial and municipal effluents (Stobo 1971; Mackie and Qadri 1973).

The current and morphometry of the lower river allow the rapid oxygenation of much of the chemical and dissolved organic wastes entering the section. Wood-fiber from the two local paper mills (Figure 1) is widespread, but it is carried downstream before it can settle long enough to exert any significant influence on oxygen demand in the water column. Below Hawkesbury, the Carillon Dam completed in 1964 (Munro 1967), has created a slow flowing environment which does not adequately assimilate the wastes from the
pulp and paper mill at Hawkesbury (Le Sauter 1965; OWRC-QWB 1971).

Most bullheads in the upper river were collected in Shireys Bay (Station 1). This area receives the secondary effluent from the Watts Creek sewage treatment plant. Concern over the eutrophication of the plant prompted the construction of a causeway across most of the mouth of Shireys Bay in 1971 in order to divert the effluent away from the shoreline. Nevertheless, rising coliform counts forced the closure of Britannia Beach 4 km downstream in 1972.

In the lower river bullheads were collected from Hay Bay (2), Governor's Bay (3) and the top of Upper Duck Island (4) stations (Figure 1). Station 2 is below the mouth of Brewery Creek, a side channel of the Ottawa River, which until recently received most of the untreated municipal effluent from Hull, Quebec. Station 3, on the Ontario shore below the confluence with the Rideau River, was chosen as a control. Station 4 is situated below the pulp and paper mill at Gatineau as well as being influenced by municipal and industrial effluents upstream.

At Hawkesbury, bullheads were collected at a control station (5) on the Ontario shore 4.8 km above the Perley Bridge. Another station (6) was chosen in the area influenced by the pulp and paper mill, 4.8 km downstream of the bridge.

Materials and Methods

Water sampling was conducted monthly at the six stations between May and September 1970 and 1971. Water samples were taken 0.3 m from the surface and bottom with a 4 L Van Dorn water sampler. The pH, carbon dioxide, and dissolved oxygen were determined on site with an AL-36B Hach test kit. Measurements of alkalinity, chloride, calcium and total hardness, nitrite nitrogen, orthophosphate, sulphate, and turbidity were made in the laboratory with a Hach DR-EL Water Test Laboratory. The measurements were found comparable to samples sent to the Ontario Water Resources Commission (Mackie 1971).

The bullheads used for age and growth determinations were mostly collected at stations (1-6) utilizing a 1.8-m trap net with 5.1-cm stretched mesh during June, July, and August 1971. Gill nets with four 15.2-m gangs consisting of 3.8, 5.1, 7.6, and 10.2-cm stretched mesh were used to catch a wider size range of bullheads. Biweekly, overnight gill net sets were used during the 1968-1972 summer seasons, to assess relative abundance of bullheads at locations (A-H) in the upper and lower river (Figure 1). Since a gill net survey had been conducted below Hawkesbury (Le Sauter 1965), with gangs of identical mesh size (omitting 7.6 cm), less effort was expended to assess abundance in the Hawkesbury section. A 0.65-cm square mesh was used to collect young-of-year bullheads in the upper and lower river sections at two locations (Figure 1). The scarcity of suitable locations in the lower river and Hawkesbury sections inhibited seining in these areas. It was possible to collect young-of-year bullheads over the 1972 season, at Britannia Bay in the upper river.

Lengths and weights were taken from 803 specimens collected during 1971 and frozen for 4-6 months. Losses in length and weight due to freezing were assessed by taking data from 30 specimens while alive and after 4 months of being frozen (Rubec 1975). The bullheads had lost 1.4% of their total length (TL) and 8.7% of their original weight. The data were corrected accordingly.

The bullheads were aged from pectoral spine sections. The spines were air dried, fixed in 10% non-buffered formalin and then placed in decaalcifying fluid (Scholl 1968). A single-edged razor blade was used to cut sections 0.1-0.2 mm thick from the distal end of the basal groove (Sneed 1951). The sections were stored in one dram vials containing 10% glycerine with a few crystals of thymol to prevent mold growth.

Annuli were drawn along the anterior radius of the sections, at 100X magnification, with the aid of a camera lucida mounted on a binocular dissecting microscope. Because the centre of the lumen is difficult to determine, measurements were made from the edge of the lumen to the anterior edge of the spine. Thirty spine sections were measured to the center of the lumen to obtain a correction factor (1.32) by which the sections, measured from the edge of the lumen, were multiplied to obtain the spine radius.

Spine sections were examined at least twice before an age was assigned. To check the validity of ages derived from spines, we examined the fifth vertebral centrum behind the Weberian apparatus of 30 bullheads from station 2. The number of annuli noted on the vertebra appeared to be comparable with spine readings from the same fish.

Due to the large variation in lengths for a given spine radius it was difficult to determine the body-spine relationship empirically. Because age I and II bullheads were inadequately sampled at most stations, body-spine regressions at these stations yielded unrealistic Y intercepts. By including young-of-year bullheads it was possible to determine the linear regression formulae at stations 1 and 2. Shireys Bay L = 39.55 + 1.4167S, r = 0.930, n = 178 Hay Bay L = 43.84 + 1.6102S, r = 0.883, n = 181

where L = TL (mm). S = spine radius (mm) at 100X magnification, r = correlation coefficient, n = number of fish.

To ascertain more accurately the body-spine rela-
tionship at stations 1 and 2, we made logarithmic regressions for log TL on log S and then plotted these data on an arithmetic scale (Figure 2). While the plotted points depart slightly from linearity at station 1, both lines are effectively straight lines. The logarithmic regressions pass through the zero coordinates. However, a straight line drawn through the points at station 1 (black circles) and extrapolated (dashed line) yields an intercept closer to 15 mm than the 40 mm predicted from the linear regressions.

Back-calculations were made with the age and growth program of Voigtlander and Roohvarg (1967) utilizing the modification of the direct-proportionality formula proposed by Frazer (Tesch 1971). Computations were made for each sex as well as sexes combined at each of the six stations. Calculations were also made for the pooled lower river stations and the pooled Hawkesbury stations.

A common intercept for all six stations was chosen for substitution into the Frazer formula. This assumes that newly free-swimming bullheads should be close to the same size at all stations. An intercept of 13 mm was used since this was the size of newly free-swimming fry which hatched in an aquarium. The mean size of schooling fry collected in the field was 16.3 mm at station 1 and 15.4 mm at station 2. These fish had probably grown a little after becoming free-swimming.

Linear weight-length relationships were derived by regressing log W on log TL (Tesch 1971). A one-way analysis of covariance computer program (National Research Council of Canada) was used to compare weight-length regressions for the sexes separately and combined at all stations. The same program was used to compare Walford plots derived from back-calculations (Ricker 1958). Utilizing the procedure outlined by Ricker, von Bertalanffy equations were then derived from the data.

Comparing weight-length regressions between stations, differences in elevation due to weight were determined through a test of adjusted means (Snedecor 1956: 395). The ratio of adjusted means was used to determine the percentage greater weight at any given length between stations having similar slopes.

**Results**

Water chemistry at the six stations was generally within the acceptable criteria established by the OWRC-QWB (1971). Turbidity measurements below the paper mill near Gatineau (Station 4) exceeded the criterion of 25 Jackson Turbidity Units (JTU's) with a mean of 29.4 ± 4.9 JTU's, N = 15 bottom and surface samples. Average turbidity measurements below municipal effluents (stations 1 and 2) and below the paper mill at Hawkesbury (6) ranged from 21-24.6 JTU's, while three control stations (3 and 5 plus one above the Gatineau paper mill) had mean values from 16-17 JTU's. Low dissolved oxygen values (3 mg/L) were noted at station 6 in surface and bottom samples during July and August 1970. Mean carbon dioxide values were higher (10-15 mg/L) below municipal and paper mill effluents (stations 2, 4 and 6) but these conditions were quite localized.

The relative abundance of bullheads at various locations is indicated by catch-per-unit-effort (C/E) data in Table 1. Although the C/E varied between locations depending on the type of habitat sampled, bullheads tended to become more prevalent in the gill net catch going downstream. Localities with sand and rock substrates had low catches. Turbid localities with soft mud substrates yielded higher catches of bullheads.

Young-of-year from Britannia Bay grew most...
rapidly during July (Figure 3). A large variation in growth between individuals was evident, and it became greater as the summer progressed (Table 2). The average length of bullheads from the September sample was 62.5 mm and the maximum length was 83 mm. The growth over the summer was similar to that of young Brown Bullhead collected in New York State by Raney and Webster (1940).

**Back-Calculations**

The back-calculated lengths for each age group at stations in the Ottawa River were tabulated (Rubec 1975) and the weighted mean lengths for each age are summarized in Table 3. Back-calculated lengths of males at each annulus were slightly higher than those of females from the same station. Length gains were highest among bullheads from station 1 in the upper river. The younger year classes (ages II and III) at the Hawkesbury stations (5 and 6) exhibited better length gains that those from station 1, but the growth of adults was intermediate to that of the upper and lower river stations (Figure 4).

Covariance analysis indicated no significant difference in growth between the sexes at the six individual stations, nor between sexes for the lower river stations combined (2, 3, and 4) or Hawkesbury combined (5 and 6). Consequently, the data of both sexes was pooled to compare the growth of bullheads between stations. No significant difference was found in the growth of the sexes combined between stations 2, 3 and 4 and between stations 5 and 6. Significant differences ($P \leq 0.01$) were observed in the growth between stations.

![Figure 3](image-url)  
**Figure 3.** Seasonal growth of young-of-year Brown Bullhead from Britannia Bay of the Ottawa River compared with those collected by Raney and Webster (1940) from Cayuga Lake. The range in total length is given by vertical lines, the points depict the means.
stations in the upper river, lower river, and near Hawkesbury.

The back-calculated lengths at each annulus varied between different year classes of the same population as well as between the six stations. The growth was highest the first year followed by smaller increments in succeeding years.

The back-calculations from the three sections of the Ottawa River have been compared to studies elsewhere (Table 4). The growth of Brown Bullhead in the lower Ottawa River was similar to acid polluted environments in the Monongahela River, West Virginia (Redd 1970). The growth in the upper river and near Hawkesbury was generally higher than that observed in the United States and Czechoslovakia (Tables 4 and 5). Growth of Brown Bullhead in the upper Ottawa River was similar to those from Lake Washington (Table 4). However, L∞ calculations (Table 5) indicate that Washington State fish (Imamura 1975) have the potential to attain a larger size. The growth of youth bullheads in Oklahoma was very high (Table 4) but the L∞ value calculated (Table 5) is probably too high due to the lack of older fish in the sample (Finnell et al. 1956). Bullheads from Rivière du Nord (Phaneuf 1974), a tributary of the Ottawa River, exhibited a lower growth rate than those in the Ottawa River.

Bullheads within any age group exhibited a large range in size indicating that the population consisted of both fast and slow growing individuals (Table 6). The large overlap in lengths of bullheads of different ages made the determination of age groups from length frequency distributions impractical. However, the fact that the mean lengths of the sampled bull-

![Figure 4](image_url)

**Figure 4.** Back-calculated average length at each annulus of Brown Bullhead sexes combined, from the upper Ottawa River, lower river and near Hawkesbury during 1971. Vertical lines represent 95% confidence limits about the means. The number of fish at each annulus is given in parentheses. Age 1 based on measurements of specimens.
Table 1. Catch-per-unit-effort of Brown Bullhead taken by gill nets in the Ottawa River.

<table>
<thead>
<tr>
<th>Location</th>
<th>Catch (C)</th>
<th>Effort (E)</th>
<th>C/E</th>
<th>Range of catch</th>
<th>% Total catch of all species</th>
<th>Substrate type</th>
<th>Surface current m/sec</th>
</tr>
</thead>
<tbody>
<tr>
<td>UPPER RIVER</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A Shirleys Bay</td>
<td>24</td>
<td>10</td>
<td>2.40</td>
<td>0-10</td>
<td>12.83</td>
<td>rock &amp; mud</td>
<td>0.1-0.4</td>
</tr>
<tr>
<td>B Britannia Bay</td>
<td>34</td>
<td>58</td>
<td>0.17</td>
<td>0-2</td>
<td>4.83</td>
<td>sand</td>
<td>0.1-0.4</td>
</tr>
<tr>
<td>Total Section</td>
<td>34</td>
<td>68</td>
<td>0.50</td>
<td>0-10</td>
<td>8.83</td>
<td>sand</td>
<td>0.1-0.4</td>
</tr>
<tr>
<td>LOWER RIVER</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C Brewery Creek</td>
<td>244</td>
<td>18</td>
<td>13.55</td>
<td>1-64</td>
<td>20.68</td>
<td>mud &amp; detritus</td>
<td>0.1-2.1</td>
</tr>
<tr>
<td>D Governor’s Bay</td>
<td>12</td>
<td>5</td>
<td>2.40</td>
<td>0-9</td>
<td>9.84</td>
<td>rock &amp; clay</td>
<td>0.1-2.0</td>
</tr>
<tr>
<td>E Mouth Gatineau R.</td>
<td>7</td>
<td>17</td>
<td>0.41</td>
<td>0-4</td>
<td>2.46</td>
<td>sand</td>
<td>0.5-1.5</td>
</tr>
<tr>
<td>F New Edinburgh</td>
<td>118</td>
<td>21</td>
<td>5.62</td>
<td>0-53</td>
<td>21.18</td>
<td>sludge</td>
<td>0.6-2.0</td>
</tr>
<tr>
<td>G Above Gatineau</td>
<td>39</td>
<td>17</td>
<td>2.29</td>
<td>0-27</td>
<td>14.61</td>
<td>sand</td>
<td>0.6-3.8</td>
</tr>
<tr>
<td>H Below Gatineau</td>
<td>16</td>
<td>16</td>
<td>1.00</td>
<td>0-4</td>
<td>24.62</td>
<td>wood-fiber</td>
<td>0.6-3.8</td>
</tr>
<tr>
<td>Total Section</td>
<td>436</td>
<td>94</td>
<td>4.64</td>
<td>0-64</td>
<td>15.57</td>
<td>mostly wood-fiber</td>
<td>0.1-3.8</td>
</tr>
<tr>
<td>HAWKESBURY</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Above Hawkesbury (5)</td>
<td>22</td>
<td>3</td>
<td>7.33</td>
<td>0-17</td>
<td>19.64</td>
<td>sand &amp; clay</td>
<td>0.1-1.5</td>
</tr>
<tr>
<td>Below Hawkesbury (6)</td>
<td>199</td>
<td>5</td>
<td>39.80</td>
<td>0-105</td>
<td>64.19</td>
<td>sand &amp; clay</td>
<td>0.1-1.0</td>
</tr>
<tr>
<td>(Le Sauteur 1965)</td>
<td>5385</td>
<td>45</td>
<td>119.70</td>
<td></td>
<td>95.3</td>
<td>mixed bottom</td>
<td>0.1-1.0</td>
</tr>
<tr>
<td>Total Section</td>
<td>5606</td>
<td>53</td>
<td>105.77</td>
<td>0-105</td>
<td>59.71</td>
<td>mixed bottom</td>
<td>0.1-1.5</td>
</tr>
</tbody>
</table>

Table 2. Growth of young-of-year Brown Bullhead taken in Britannia Bay from the upper Ottawa River.

<table>
<thead>
<tr>
<th>Date collected</th>
<th>Number measured</th>
<th>Total Length (mm)</th>
<th>Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Range</td>
<td>Mean</td>
<td>Range</td>
</tr>
<tr>
<td>5 July 1971</td>
<td>15</td>
<td>14-18</td>
<td>16.3</td>
</tr>
<tr>
<td>15 July 1971</td>
<td>30</td>
<td>18-24</td>
<td>21.8</td>
</tr>
<tr>
<td>17 July 1972</td>
<td>50</td>
<td>15-26</td>
<td>22.7</td>
</tr>
<tr>
<td>29 July 1969</td>
<td>20</td>
<td>31-46</td>
<td>39.0</td>
</tr>
<tr>
<td>6 Aug. 1969</td>
<td>20</td>
<td>32-52</td>
<td>39.9</td>
</tr>
<tr>
<td>8 Aug. 1969</td>
<td>46</td>
<td>40-56</td>
<td>47.8</td>
</tr>
<tr>
<td>7 Sept. 1972</td>
<td>48</td>
<td>48-69</td>
<td>57.9</td>
</tr>
<tr>
<td>22 Sept. 1972</td>
<td>31</td>
<td>49-83</td>
<td>62.5</td>
</tr>
<tr>
<td>30 Oct. 1972</td>
<td>6</td>
<td>49-75</td>
<td>61.9</td>
</tr>
</tbody>
</table>

Weight-Length Relationships

No significant difference in slopes or intercepts was found utilizing covariance analysis to compare weight-length regressions according to sex at each station. Consequently, the data were pooled and the stations compared with the sexes combined. The regressions are given in Table 7.

Fish from station 5 did not differ significantly from station 6 indicating that a common weight-length regression could apply to them. Stations 1, 2, 3, 4, and 5, 6 combined were significantly different (P ≤ 0.01) from one another. All stations, with the exception of station 4, had similar slopes indicating that the differences between them were due to significant differences in their intercepts. The ratios of adjusted means indicated that bullheads from stations 1, 3 and 5, 6 combined were respectively, 5%, 2% and 8% heavier than those from station 2. The difference in intercepts between stations 2 and 3 may have resulted from more bullheads being sampled from the former station in July while more fish from the latter station were taken in June. The other stations, sampled in early August, are believed to be comparable. The bullheads from station 4 were in the poorest condition having the lowest intercept and slope in comparison to the other stations.

In addition to live specimens, data were taken from live specimens in the lower river during August 1972 (Table 7). The regression based on field data
TABLE 3. Weighted mean back-calculated total lengths of Brown Bullhead from various stations in the Ottawa River during 1971.

<table>
<thead>
<tr>
<th>Station</th>
<th>No. of fish</th>
<th>Sex</th>
<th>Calculated total length (mm) at each annulus</th>
<th>Age assigned to each annulus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>I</td>
<td>II</td>
</tr>
<tr>
<td>UPPER RIVER</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1. Shirleys Bay</td>
<td>75</td>
<td>M</td>
<td>142</td>
<td>199</td>
</tr>
<tr>
<td></td>
<td>88</td>
<td>F</td>
<td>131</td>
<td>177</td>
</tr>
<tr>
<td></td>
<td>136</td>
<td>M&amp;F</td>
<td>136</td>
<td>187</td>
</tr>
<tr>
<td>LOWER RIVER</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2. Hay Bay</td>
<td>101</td>
<td>M</td>
<td>128</td>
<td>168</td>
</tr>
<tr>
<td></td>
<td>67</td>
<td>F</td>
<td>118</td>
<td>155</td>
</tr>
<tr>
<td></td>
<td>168</td>
<td>M&amp;F</td>
<td>124</td>
<td>163</td>
</tr>
<tr>
<td>3. Governor's Bay</td>
<td>114</td>
<td>M</td>
<td>127</td>
<td>162</td>
</tr>
<tr>
<td></td>
<td>65</td>
<td>F</td>
<td>126</td>
<td>160</td>
</tr>
<tr>
<td></td>
<td>179</td>
<td>M&amp;F</td>
<td>127</td>
<td>161</td>
</tr>
<tr>
<td>4. Top Upper Duck Island</td>
<td>46</td>
<td>M</td>
<td>121</td>
<td>156</td>
</tr>
<tr>
<td></td>
<td>38</td>
<td>F</td>
<td>121</td>
<td>155</td>
</tr>
<tr>
<td></td>
<td>84</td>
<td>M&amp;F</td>
<td>120</td>
<td>155</td>
</tr>
<tr>
<td>Lower River stations</td>
<td>261</td>
<td>M</td>
<td>126</td>
<td>163</td>
</tr>
<tr>
<td>combined 2,3,4</td>
<td>170</td>
<td>F</td>
<td>122</td>
<td>157</td>
</tr>
<tr>
<td></td>
<td>431</td>
<td>M&amp;F</td>
<td>125</td>
<td>161</td>
</tr>
<tr>
<td>HAWKESBURY</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5. Above Hawkesbury</td>
<td>50</td>
<td>M</td>
<td>154</td>
<td>198</td>
</tr>
<tr>
<td></td>
<td>62</td>
<td>F</td>
<td>142</td>
<td>180</td>
</tr>
<tr>
<td></td>
<td>112</td>
<td>M&amp;F</td>
<td>148</td>
<td>188</td>
</tr>
<tr>
<td>6. Below Hawkesbury</td>
<td>50</td>
<td>M</td>
<td>149</td>
<td>194</td>
</tr>
<tr>
<td></td>
<td>47</td>
<td>F</td>
<td>141</td>
<td>184</td>
</tr>
<tr>
<td></td>
<td>97</td>
<td>M&amp;F</td>
<td>145</td>
<td>189</td>
</tr>
<tr>
<td>Hawkesbury stations</td>
<td>100</td>
<td>M</td>
<td>152</td>
<td>196</td>
</tr>
<tr>
<td>combined 5,6</td>
<td>109</td>
<td>F</td>
<td>142</td>
<td>182</td>
</tr>
<tr>
<td></td>
<td>209</td>
<td>M&amp;F</td>
<td>147</td>
<td>188</td>
</tr>
</tbody>
</table>

from Hay Bay (2) shows close agreement with that derived from frozen specimens from the same station. The regressions for Kettle Island Bay (7), the top of Lower Duck Island (8) as well as the Upper Duck Island station (4) all had slopes less than three indicating that bullheads in the vicinity of the paper mill at Gatineau were in poor condition.

Discussion

Brown Bullhead is the most abundant fish species in the Ottawa River downstream from Ottawa. Extensive trap netting indicated they comprise 42% of the catch in the upper river and 86% in the lower river (Rubec 1975). Gill net (C/E) data show that the relative abundance of bullheads increases in the lower river (Table 1). While our gill netting near Hawkesbury is insufficient, we believe Courtemanche’s data (Le Sauteur 1965) are comparable to our own. Since both surveys utilized the same 3.8 and 5.1-cm mesh gangs, in which most of our bullheads were taken, the selectivity of the gear were similar. The combined data indicate that bullheads were 22.8 times more abundant near Hawkesbury than in the lower river. The C/E noted by Le Sauteur (1965) may reflect the highly productive environment created by a new impoundment.

The construction of the Carillon Dam impounded water as far upstream as Ottawa, flooding many areas and creating an extensive backwater marsh habitat (Munro 1967). This alteration appears to have created a more favorable habitat for bullheads below Ottawa. This could have allowed Brown Bullhead to become more abundant in relation to other fish species. While back-calculations (Table 3) were made to the 1963 year class, no trend according to age classes, such as Lee’s phenomenon, was discernable to indicate a decline or improvement of bullhead growth occurred from 1963 to 1971. Bullheads taken before the con-
Table 4. Comparison of back-calculated weighted mean total lengths of Brown Bullhead sexes combined, from various localities.

<table>
<thead>
<tr>
<th>Location</th>
<th>No. of specimens</th>
<th>Mean calculated length (mm) at each annulus</th>
<th>Citation</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>1   2    3    4    5    6    7    8    9</td>
<td></td>
</tr>
<tr>
<td><strong>CANADA</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper Ottawa River</td>
<td>163</td>
<td>136</td>
<td>187</td>
</tr>
<tr>
<td>Lower Ottawa River</td>
<td>431</td>
<td>125</td>
<td>161</td>
</tr>
<tr>
<td>Hawkesbury</td>
<td>209</td>
<td>147</td>
<td>188</td>
</tr>
<tr>
<td>Du Nord River, Quebec</td>
<td>945</td>
<td>95</td>
<td>144</td>
</tr>
<tr>
<td><strong>CZECHOSLOVAKIA</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pond Zehun</td>
<td>63</td>
<td>93</td>
<td>145</td>
</tr>
<tr>
<td>Poltruba, Elbe River</td>
<td>159</td>
<td>75</td>
<td>116</td>
</tr>
<tr>
<td>Poltruba, Elbe River</td>
<td>107</td>
<td>98</td>
<td>132</td>
</tr>
<tr>
<td>Prochaskova, Elbe River</td>
<td>46</td>
<td>101</td>
<td>142</td>
</tr>
<tr>
<td><strong>UNITED STATES</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Washington, Washington State</td>
<td>452</td>
<td>70</td>
<td>125</td>
</tr>
<tr>
<td>Little River, Oklahoma</td>
<td>41</td>
<td>91</td>
<td>180</td>
</tr>
<tr>
<td>Monongahela River, West Virginia</td>
<td>214</td>
<td>136</td>
<td>158</td>
</tr>
<tr>
<td>Tygart Valley Reservoir, West Virginia</td>
<td>97</td>
<td>183</td>
<td>212</td>
</tr>
</tbody>
</table>

*Unweighted averages
*Cited from Carlander (1969)
*Back-calculations based on annuli readings from pectoral spines.

Table 5. Von Bertalanffy growth parameters of various populations of Brown Bullhead for the sexes combined.

<table>
<thead>
<tr>
<th>Location</th>
<th>L (mm)</th>
<th>K</th>
<th>t₀</th>
<th>Study</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>CANADA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Upper Ottawa River</td>
<td>386.6</td>
<td>0.2839</td>
<td>-0.40</td>
<td>present study</td>
</tr>
<tr>
<td>Lower Ottawa River</td>
<td>325.7</td>
<td>0.2224</td>
<td>-1.16</td>
<td>ibid</td>
</tr>
<tr>
<td>Hawkesbury</td>
<td>371.7</td>
<td>0.2159</td>
<td>-1.36</td>
<td>ibid</td>
</tr>
<tr>
<td>Du Nord River</td>
<td>323.2</td>
<td>0.2771</td>
<td>-0.26</td>
<td>Phaneuf (1974)</td>
</tr>
<tr>
<td><strong>CZECHOSLOVAKIA</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Poltruba, Elbe River</td>
<td>292.1</td>
<td>0.1929</td>
<td>-0.81</td>
<td>Frank (1955)</td>
</tr>
<tr>
<td>Poltruba, Elbe River</td>
<td>253.2</td>
<td>0.2571</td>
<td>-0.91</td>
<td>Hensel (1966)</td>
</tr>
<tr>
<td>Prochaskova, Elbe River</td>
<td>339.3</td>
<td>0.1857</td>
<td>-0.90</td>
<td>Hensel (1966)</td>
</tr>
<tr>
<td><strong>UNITED STATES</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lake Washington, Washington</td>
<td>413.9</td>
<td>0.2505</td>
<td>+0.26</td>
<td>Imamura (1975)</td>
</tr>
<tr>
<td>Little River, Oklahoma</td>
<td>552.4</td>
<td>0.2197</td>
<td>+0.18</td>
<td>Finnel et al. (1956)</td>
</tr>
<tr>
<td>Monongahela River, West Virginia</td>
<td>327.7</td>
<td>0.2342</td>
<td>-0.67</td>
<td>Redd (1970)</td>
</tr>
<tr>
<td>Tygart Valley Reservoir, West Virginia</td>
<td>283.8</td>
<td>0.3507</td>
<td>-1.95</td>
<td>Redd (1970)</td>
</tr>
</tbody>
</table>
Table 6. Mean total lengths (mm), ranges and numbers of Brown Bullhead sampled in the upper river, lower river and Hawkesbury sections of the Ottawa River in 1971.

<table>
<thead>
<tr>
<th>Age group</th>
<th>Mean Upper River</th>
<th>Range</th>
<th>No.</th>
<th>Mean Lower River</th>
<th>Range</th>
<th>No.</th>
<th>Mean Hawkesbury</th>
<th>Range</th>
<th>No.</th>
</tr>
</thead>
<tbody>
<tr>
<td>I</td>
<td>* 63</td>
<td>49-83</td>
<td>48</td>
<td>* 61</td>
<td>52-70</td>
<td>68</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>II</td>
<td>145</td>
<td>125-159</td>
<td>4</td>
<td>* 92</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>III</td>
<td>259</td>
<td>197-306</td>
<td>5</td>
<td>203</td>
<td>166-230</td>
<td>13</td>
<td>202</td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>IV</td>
<td>292</td>
<td>218-330</td>
<td>50</td>
<td>227</td>
<td>187-285</td>
<td>73</td>
<td>270</td>
<td>211-318</td>
<td>26</td>
</tr>
<tr>
<td>V</td>
<td>305</td>
<td>261-351</td>
<td>75</td>
<td>252</td>
<td>203-311</td>
<td>123</td>
<td>283</td>
<td>232-344</td>
<td>31</td>
</tr>
<tr>
<td>VI</td>
<td>313</td>
<td>274-333</td>
<td>23</td>
<td>265</td>
<td>201-340</td>
<td>142</td>
<td>300</td>
<td>210-360</td>
<td>79</td>
</tr>
<tr>
<td>VII</td>
<td>331</td>
<td>288-362</td>
<td>4</td>
<td>274</td>
<td>208-334</td>
<td>61</td>
<td>316</td>
<td>216-361</td>
<td>48</td>
</tr>
<tr>
<td>VIII</td>
<td>354</td>
<td></td>
<td>1</td>
<td>276</td>
<td>233-355</td>
<td>13</td>
<td>319</td>
<td>281-349</td>
<td>18</td>
</tr>
<tr>
<td>IX</td>
<td>343</td>
<td></td>
<td>1</td>
<td>280</td>
<td>254-311</td>
<td>6</td>
<td>327</td>
<td>294-345</td>
<td>6</td>
</tr>
</tbody>
</table>

*Based on measurements of 0+ fish at end of 1972 growing season.
Based on fish collected in Kettle Island Bay in 1980.

Table 7. Weight-length regressions of Brown Bullhead from various stations in the Ottawa River during 1971. W = weight (g), TL = total length (mm).

<table>
<thead>
<tr>
<th>Station</th>
<th>Regression Equation</th>
<th>r</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Shirley’s Bay</td>
<td>log W = -5.503 + 3.260 log TL</td>
<td>0.922</td>
<td>163</td>
</tr>
<tr>
<td>Hay Bay</td>
<td>log W = -5.306 + 3.159 log TL</td>
<td>0.962</td>
<td>169</td>
</tr>
<tr>
<td>Governor’s Bay</td>
<td>log W = -5.145 + 3.100 log TL</td>
<td>0.943</td>
<td>181</td>
</tr>
<tr>
<td>Upper Duck Island</td>
<td>log W = -3.062 + 2.222 log TL</td>
<td>0.870</td>
<td>85</td>
</tr>
<tr>
<td>Above Hawkesbury</td>
<td>log W = -4.930 + 3.042 log TL</td>
<td>0.938</td>
<td>113</td>
</tr>
<tr>
<td>Below Hawkesbury</td>
<td>log W = -5.229 + 3.191 log TL</td>
<td>0.961</td>
<td>98</td>
</tr>
<tr>
<td>Above and Below Hawkesbury</td>
<td>log W = -5.115 + 3.116 log TL</td>
<td>0.948</td>
<td>211</td>
</tr>
</tbody>
</table>

Weight-length regressions during 1972

<table>
<thead>
<tr>
<th>Station</th>
<th>Regression Equation</th>
<th>r</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hay Bay</td>
<td>log W = -5.210 + 3.121 log TL</td>
<td>0.963</td>
<td>100</td>
</tr>
<tr>
<td>Kettle Island Bay</td>
<td>log W = -4.093 + 2.654 log TL</td>
<td>0.962</td>
<td>100</td>
</tr>
<tr>
<td>Lower Duck Island</td>
<td>log W = -4.893 + 2.983 log TL</td>
<td>0.899</td>
<td>100</td>
</tr>
</tbody>
</table>

The observed growth of young-of-year from the upper river (Table 2) did not match back-calculated lengths at the first annulus (Table 3). This was originally believed to be due either to net selection or over-wintering growth. The cause of the discrepancy became apparent from seining conducted in Kettle Island Bay of the lower river on 11 June 1980. Age I bullheads were collected ranging from 52-70 mm TL (Table 6). Apparently, the first annulus representing Age I bullheads was not present in the spine sections used for back-calculations in the present study. Marzolf (1955) found a similar situation with Channel Catfish (I. punctatus). The basal-groove extends distally as the fish grows, obliterating the first annulus of the spine in older fish. Consequently, no back-calculations for Age I fish were available in the present study. This error accounts for unreasonably high estimates of the length at Age I in other studies where lengths were calculated from spines (Table 4.) Similarly the first annulus of vertebrae is indistinct (Imamura 1975).

Layher (1981) confirmed the inherent error in pectoral spines by finding higher annuli counts in dorsal spines of Flathead Catfish (Pylodictis olivaris). Ashley and Garling (1980) have presented methods for decalcification and staining spine sections which facilitate the interpretation of annuli.

The similarity of the back-calculations at stations in the lower river and near Hawkesbury respectively (Table 3) indicates that conditions affecting growth within each section were similar. The significant differences between the upper river, lower river, and Hawkesbury sections indicate that growth in length is more dependent on conditions which apply to an entire section, rather than to localized conditions within a section.

Carlander (1969) noted that most bullhead growth studies have been on overcrowded and stunted populations. This has led to efforts to thin bullhead populations in order to attain better growth and hence a
greater proportion of marketable sized fish (Grice 1957). Such programs have been found to have little effect on other species in the community. This indicates that slow growth and poor condition are the result of intraspecific competition at high density, rather than interspecific competition for a limiting food supply. Carlander pointed out that there is no absolute population density of fish which has such a dominant effect on growth, but it is the population density in relation to the carrying capacity of the body of water.

This interpretation has been used to explain the deterioration in growth and short lifespan of bullheads in the Polderba backwater of the Elbe River, Czechoslovakia (Frank 1955; Hensel 1966). Similarly, one can consider the slower growth and poorer condition of bullheads in the lower Ottawa River indicative of an environment less suitable for the species than were the upper river and Hawkesbury sections. Within the lower river, poor condition of bullheads (Table 7) below the paper mill at Gatineau (4) tends to indicate that this area is less favorable than stations (2 and 3) upstream.

Within the Ottawa River, one can interpret the faster growth rates and condition of bullheads in the upper river and near Hawkesbury to indicate that the species has not exceeded the carrying capacity of these areas. Bullheads in the upper river were not abundant but exhibited the best growth of the three sections. Fish from the Hawkesbury section, though having a somewhat slower growth rate, exhibited the best condition. The C/E of bullheads implies a high population density near Hawkesbury; their better growth rate also indicates a very high carrying capacity for this section. Overpopulation of bullheads in the lower river was indicated by their having significantly slower growth rates and worse condition than those from the other two sections.

It has not been possible to relate the growth of bullheads to localized sources of pollution, temperature, water levels or any particular aspect of water chemistry. Most of the water chemistry was within the criteria established by the OWRC-QWB (1971). While factors such as low dissolved oxygen or high carbon dioxide may have affected the abundance of bullheads (Table 1), they did not appear to be directly related to their growth at the stations examined. The similarity of growth between stations within a section and the marked differences between sections points to the influence of physical factors.

The decomposition of wood-fiber in areas of the Ottawa River where there is little current can create anoxic water conditions lethal to fish (Knight 1907a, b). In the lower river, the mixing of the water column by the current generally prevents this. The water column did not appear to be toxic to invertebrates, because many pollution sensitive forms readily colonized rock-filled wire baskets set below the paper mill at station 4 (OWRC-QWB 1971). However, even where the water column is well mixed, poor water quality can exist in wood-fiber sludge deposits which can be toxic to invertebrates, fish eggs and fry (Colby and Smith 1967).

Sludge deposits blanket much of the lower river and form localized pockets in the Hawkesbury section (OWRC-QWB 1971). Wood-fiber deposits have been traced downstream as much as 48 km from their source and in some places are 8.5 m thick (eg. at the Macdonald Cartier Bridge in the lower river). Consequently the problem of its dispersal, decomposition, and effect on the benthos is widespread below Ottawa. The paper mill at Hawkesbury has a lagoon which prevents most of the wood-fiber from entering the river allowing larger standing crops of pollution tolerant invertebrates in the Hawkesbury section (OWRC-QWB 1971).

The deep fast flowing environments of the lower river are less productive than the Hawkesbury and upper river sections. The lower river has a lower diversity and biomass of aquatic invertebrates than the upper river (Mackie 1971). Most of the benthos (0.25-2.16 g/m², dry weight) is restricted to a narrow littoral zone while the deeper areas support small standing crops (0.07 g/m²) of invertebrates (Qadri et al. 1977). Invertebrates were scarce in areas where the substrate consisted of wood-fiber. The scarcity of invertebrates in the substrate is reflected by the food habits of bullheads in the lower river (Rubec 1975; Gunn 1976).

The widespread physical smothering of the substrate by wood-fiber from local paper mills limits the abundance of benthic invertebrates and restricts the area suitable for foraging by bullheads in the lower Ottawa River. The high standing crops of benthic invertebrates is reflected in the significantly better growth of bullheads (Tables 3, 4, and 5) in the upper river and Hawkesbury sections where sludge deposits are absent. The presence of wood-fiber deposits appears to be the most important factor limiting invertebrate productivity in the lower river. The scarcity of benthic invertebrates near Gatineau appears to be the cause of the poor condition of bullheads indicated by weight-length relationships (Table 7).

Brown Bullhead in the lower river make feeding excursions over a wide area (Rubec 1975; Gunn 1975). These fish must expend more energy swimming against the current than those bullheads foraging in the more quiescent upper river and Hawkesbury sections. It is difficult to separate the effects of morphology and current from the effects of wood-fiber on the benthos in the lower river. It seems likely that
the lower river would produce a greater, more diverse, food supply if wood-fiber was not present. But, to what degree wood-fiber rather than current limits invertebrate abundance in the lower river cannot be determined from this study.

The abundance of Brown Bullhead over other species in the lower river and Hawkesbury sections may be due to their ability to localize food by taste (Atema 1971). The highly turbid environments created by industrial and municipal effluents favors Brown Bullhead over other species which are more dependent on vision for food localization. Low oxygen conditions below Hawkesbury may be detrimental to less tolerant species; favoring bullheads due to the lack of competition with other species (Le Sauter 1965).

Bullheads are exploited commercially in the Hawkesbury section, but not in the upper and lower rivers. The better growth of bullheads near Hawkesbury may be in part because they are exploited. An improvement in growth would probably occur if bullheads were exploited in the lower river.

The logarithmic body-spine regressions for stations 1 and 2 (Figure 2) have slopes close to one. Further analyses indicate that the logarithmic body-spine regression for all stations combined has a slope of 0.997 (D.P. Scott, personal communication 1981). A logarithmic regression with a slope of one demonstrates direct-proportionality of the body-spine relationship (Smith 1955). The original data set is being further analyzed to elucidate the statistical justification for various back-calculation methods.

Since this study was undertaken, efforts have been made to reduce pollution of the Ottawa River. The Canadian government has encouraged the relocation of the paper mill near the Chaudière Falls. The paper mill near Gatineau has installed a new process for digesting wood pulp that is purported to reduce its effluent by 80%1. A collector sewer and regional sewage treatment plant is nearly completed to service communities on the Quebec side of the Ottawa River near Ottawa. Studies are needed to assess whether these measures have been effective in improving the environmental quality as reflected by changes in the aquatic biota of the lower Ottawa River.

Acknowledgments

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Literature Cited


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Snowshoe Hare Distribution and Habitat Use in Wisconsin

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Snowshoe Hares (Lepus americanus) are restricted to the northern half of Wisconsin, whereas Cottontail Rabbits (Sylvilagus floridanus) are found statewide. The southern limit of snowshoe distribution in Wisconsin was mapped by field-checking 287 2.56-km² sites along the approximate range boundary during winter 1978–79 and 1979–80. Hares occurred in six vegetative types, but were most abundant in the two types with low-growing conifer cover. Two major areas of range extension since 1944 were found in central and northwestern Wisconsin, and two areas of range loss in eastern and west-central Wisconsin. The absence of cyclic fluctuations along the snowshoe's southern geographic limit is likely attributable to a combination of fragmented habitat and relatively stationary and diverse predator populations. A habitat-predator interaction is also proposed as the major factor limiting hare distribution in Wisconsin. Within the snowshoe's current range, its occurrence and abundance are inversely related to that of cottontails, suggesting interspecific competition.

Key Words: Snowshoe Hare, Lepus americanus, distribution, habitat, competition, Cottontail Rabbit, Sylvilagus floridanus, Wisconsin.

The Snowshoe Hare (Lepus americanus) is hunted in Wisconsin by an estimated 57,000 small-game hunters, and is an important prey base for a diversity of resident predators (Les 1979).

Distribution and abundance of snowshoes probably changed markedly as the pristine forests of northern and central Wisconsin were logged, burned, and cleared for agriculture. Logging peaked in the late 1800's (Hoveland 1948), and the last great wildfires occurred in the 1930's (Grange 1949). Land in central Wisconsin was drained and farmed in the early 1900's, then abandoned during the 1930's (Catenhusen 1950). Reforestation efforts have continued, but on a smaller scale than during the 1930's and 40's. Such perturbations by man, and the natural regeneration and succession of forest cover, have created a mosaic of potential habitat for Snowshoe Hares.

The present study was undertaken to determine the current geographic distribution of snowshoes in Wisconsin, and to identify its major environmental correlates. Information on Cottontail Rabbit (Sylvilagus floridanus) distribution and abundance was obtained concomitantly, on the assumption that the two species might interact.

**Study Area**

This study was conducted in a belt of 21 counties through central Wisconsin (Figure 1), coinciding closely with a vegetational tension zone separating the northern hardwood-coniferous province from the southern prairie-forest province (Curtis and McIntosh 1951). Tension-zone vegetation is a mixture of northern and southern species.

North of the zone, summers are short and cool, winters are long and cold with continuous snow cover. South of the zone, summers are warmer and drier with variable precipitation, and winters are more moderate, sometimes lacking continuous snow cover (Curtis 1959).

Study-area topography varies from ridges and lowlands in the east to sand plains in central and western parts (Martin 1965). The soils in eastern Wisconsin consist of clays over clayey glacial till, and loams over

![Figure 1. Region of Wisconsin field-checked in the winters of 1978–79 and 1979–80 to determine the southern limit of Snowshoe Hare distribution.](imageURL)
Methods

The present geographic distribution of snowshoes and cottontails was first broadly outlined by interviewing Wisconsin Department of Natural Resources field personnel, hunters, and trappers. The southern limit of snowshoe distribution was then mapped by field-checking 287 sites during periods of suitable snow cover in the winters of 1978–79 and 1979–80.

At least one 2.56-km² site was field-checked per township along the approximate southern limit of hare distribution as determined from the interviews. Subsequent sites were selected in townships immediately north and south to further delimit the boundary. Selected sites had the greatest amount of continuous forest cover in the township, minimal human development, and were accessible by road; none had less than 10 hectares (4%) forest cover.

Forest and brush covered areas of each 2.56-km² site were systematically searched along a series of parallel transect lines for snowshoe and cottontail tracks, pellets, and clippings. Only tracks were used to distinguish snowshoes from cottontails, the hind foot of the snowshoe being about 50% longer and wider than that of the cottontail. Snowshoe and cottontail track counts were recorded over a 1-hour search interval. Individual sets of tracks were assigned a value of 1, runways a value of 2 (very light use) to 5 (very heavy use). A maximum value of 5 was given to runways because trails used more frequently were impossible to differentiate from those used only five times. The recorded track count equalled the sum of all single-track and runway values. Track counts were standardized for recency of snowfall by dividing the count by the number of nights since the last snowfall ≥ 2.5-cm. Such periods averaged four days, the longest being 13 days. A log transformation was made of all track count data to stabilize variance. We used analyses of variance only on track-counts from winter 1978–79 to avoid the problem of between-year differences in abundance. Occurrence data from both winters was used to determine distribution.

The main trees and shrubs were noted on each site, and the vegetation classified accordingly into seven habitat types; we attempted no within-type partitioning by stand age or density.

Jackpine-Hill’s Oak xeric forest (Pinus banksiana-Quercus ellipsoidalis)

alder-willow shrub communities (Alnus rugosa-Salix)

Black Spruce-White Cedar-Tamarack lowland forest (Picea mariana-Thuja occidentalis-Larix laricina)

Conifer plantations (Pinus-Picea)

aspen-birch forest (Populus tremuloides-Betula papyrifera)

pine-maple dry mesic forest (Pinus strobus-Pinus resinosa-Acer rubrum)

maple-basswood mesic forest (Acer saccharum-Tilia americana)

When more than one of these types was present, separate track counts were made within each and the total one hour search partitioned accordingly. All such counts were extrapolated to hypothetical one-hour search intervals. Topographic characteristics (lowland, intermediate, or upland) were recorded for each site and habitat type.

The forested area of each 2.56-km² site was estimated from Wisconsin Land Economic Inventory maps (scale 1/64,000). These maps were also used to estimate the total area of each habitat type within counties along the snowshoe’s southern limit. Because the land inventory maps were based on 1933–55 surveys, they were compared with 1968–78 aerial photos (scale 1/42,000 and 1/21,000) to determine changes in forest cover that occurred since the former were conducted. Ratios of change in amounts of forested land within randomly-selected, 2.56-km² sites of field-checked townships were used to correct initial estimates of forest cover and hare habitat.

Results

Geographic Distributions

Snowshoes were present in 117 of the 287 field-checked sites (Figure 2). These data were used to map the snowshoe’s current, geographic limit of distribution (Figure 3B).

Cottontails were reported statewide by Wisconsin Department of Natural Resources field personnel (Figure 4). In the north, however, cottontails apparently occur only in brushy areas near towns, villages, and farmsteads; and not within the extensive forests.

Habitat Use

Snowshoes were found in six of seven major vegetative types which were thus designated hare habitat. The seventh, maple-basswood forest, had no snowshoes in any of the 25 sites checked. Frequency of occurrence within the geographic distribution of snowshoes did not differ (P = 0.42) among the six habitats, ranging from 60% in pine-maple to 84% in conifer plantations and Jackpine-Hill’s Oak.

Mean snowshoe track counts in occupied sites only, an index to relative abundance (Hartman 1960), differed (P < 0.01) among all habitats (Figure 5). Conifer lowland forests had greater mean counts than Jackpine-Hill’s Oak (P < 0.001), alder-willow (P < 0.0001), aspen-birch (P < 0.03), and pine-maple (P < 0.03) habitats. Conifer plantations had greater...
mean counts than Jackpine-Hill's Oak (P < 0.015), alder-willow (P < 0.01), aspen-birch (P < 0.09), and pine-maple (P < 0.06). Conifer lowland forests and conifer plantations were consequently classified as optimal habitat.

Neither frequency of occurrence nor mean track counts of snowshoes within suitable habitat changed (P = 0.26) with topography. Frequencies were 71% in uplands, 76% in lowlands, and 85% in intermediate sites. Track counts averaged 9.9/hr searched in uplands, 14.0/hr in lowlands, and 11.4/hr on intermediate sites.

Frequency of occurrence of snowshoes on 2.56-km² sites was compared with amounts of habitat (Table 1) and total forest cover (including nonhabitat) (Table 2). Sites with more than 160 ha of total forest cover were most often (P < 0.05) occupied by snowshoes; mean frequencies were 75% (≤ 160 ha) and 88% (> 160 ha). Sites with more than 160 ha of habitat were most often (P < 0.05) occupied; mean frequencies were 68% (≤ 160 ha) and 86% (> 160 ha).

Frequency of occurrence of snowshoes on 2.56-km² sites with less than 160 ha of habitat was compared among the six major habitat types. No difference (P = 0.85) in occurrence was found except for aspen-birch habitat where only five sites were examined. Comparison of snowshoe occurrence among the six habitats also showed no difference on sites having more than 160 ha of habitat (P = 0.78), less than

**Figure 2.** Southern limit of Snowshoe Hare distribution in Wisconsin based on field-checking of 287 sites in winters of 1978-79 and 1979-80.

**Figure 3.** Snowshoe Hare distribution in 1944 (Leopold 1945) and 1980, and major areas of range extension and loss over the 1944-80 period.
Figure 4. Distribution of the Cottontail Rabbit in Wisconsin based on interviews with Wisconsin Department of Natural Resources personnel in 1978–79.

Figure 5. Mean snowshoe track count per 1 hour search interval in different habitat types. Means of log transformed data were compared (P < 0.01).

Table 1. Snowshoe Hare frequency of occurrence and mean track count on 2.56-km² sites having different amounts of snowshoe habitat. Number of sites given in parentheses.

| Habitats of | % occurrence of snowshoesc | Mean snowshoe track count/hr searchedd |
| habitat     |                           |                                      |
| ≤ 40        | 73 (67)                   | 10.9 (49)                             |
| 41-80       | 71 (21)                   | 14.6 (15)                             |
| 81-120      | 73 (22)                   | 10.4 (16)                             |
| 121-160     | 73 (15)                   | 13.6 (11)                             |
| 161-200     | 86 (14)                   | P > 0.05                              |
| 201-240     | 86 (14)                   | 25.3 (12)                             |
| > 240       | 91 (14)                   | 18.2 (12)                             |

1Suitable habitat described in text.
2Level of significance determined by Chi-square.
3Level of significance determined by t-test.

160 ha of total forest cover (P = 0.43), and more than 160 ha of total forest cover (P = 0.65).

Mean track counts were not greater (P > 0.15) on sites with more than 160 ha of habitat (Table 1); but did tend to be greater (P < 0.10) when total forest cover exceeded 120 ha (Table 2).

Snowshoe-Cottontail Interaction

We compared frequency of occurrence of snowshoes on sites with and without cottontails and vice versa (Figure 3). Snowshoe frequency was greater when cottontails were absent in Jackpine-Hill's Oak (P < 0.07), alder-willow (P < 0.01), conifer lowlands (P < 0.02), and all habitats combined (P < 0.001). Similarly, cottontail frequency was greater when snowshoes were absent in these same habitats (Table 3).

Mean track counts of snowshoes on occupied sites were compared with and without cottontails. Because of small sample sizes, data from conifer lowlands and conifer plantations (optimal snowshoe habitats, Fig-

Table 2. Snowshoe Hare frequency of occurrence and mean track count on 2.56-km² sites having different amounts of forest cover. Number of sites given in parentheses.

<table>
<thead>
<tr>
<th>Forest cover</th>
<th>% occurrence of snowshoesc</th>
<th>Mean snowshoe track count/hr searchedd</th>
</tr>
</thead>
<tbody>
<tr>
<td>≤ 40</td>
<td>50 (4)</td>
<td>3.3 (2)</td>
</tr>
<tr>
<td>41-80</td>
<td>76 (21)</td>
<td>8.6 (16)</td>
</tr>
<tr>
<td>81-120</td>
<td>70 (23)</td>
<td>9.3 (16)</td>
</tr>
<tr>
<td>121-160</td>
<td>60 (20)</td>
<td>P &lt; 0.05</td>
</tr>
<tr>
<td>161-200</td>
<td>79 (33)</td>
<td>18.5 (12)</td>
</tr>
<tr>
<td>201-240</td>
<td>87 (31)</td>
<td>15.9 (26)</td>
</tr>
<tr>
<td>&gt; 240</td>
<td>91 (44)</td>
<td>13.6 (27)</td>
</tr>
</tbody>
</table>

1Level of significance determined by Chi-square.
2Level of significance determined by t-test.
Table 3. Frequency of occurrence of Cottontail Rabbits within the geographic range of Snowshoe Hares on 2.56-km² sites with and without snowshoes; and frequency of occurrence of snowshoes with and without cottontails. Number of sites given in parentheses.

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>% occurrence of cottontails</th>
<th>% occurrence of snowshoes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Snowshoes present</td>
<td>Snowshoes absent</td>
</tr>
<tr>
<td>White Pine</td>
<td>20 (5)</td>
<td>50 (2)</td>
</tr>
<tr>
<td>Red Pine</td>
<td>33 (6)</td>
<td>40 (5)</td>
</tr>
<tr>
<td>Red Maple</td>
<td>11 (18)</td>
<td>50 (4)</td>
</tr>
<tr>
<td>Aspen birch</td>
<td>20 (49)</td>
<td>70 (10)</td>
</tr>
<tr>
<td>Jackpine</td>
<td>11 (45)</td>
<td>42 (12)</td>
</tr>
<tr>
<td>Hill’s Oak</td>
<td>25 (16)</td>
<td>50 (4)</td>
</tr>
<tr>
<td>Alder willow</td>
<td>17 (139)</td>
<td>51 (37)</td>
</tr>
<tr>
<td>Conifer lowland</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conifer plantations</td>
<td></td>
<td></td>
</tr>
<tr>
<td>All habitats</td>
<td>17 (139)</td>
<td>51 (37)</td>
</tr>
</tbody>
</table>

¹Levels of significance determined by Chi-square; NS indicates P > 0.15.

ure 5) were pooled, as were data from the four suboptimal habitats. Snowshoe track counts were about twice as high (P = 0.07) when cottontails were absent in optimal habitats, but similar (P = 0.27) in suboptimal habitats (Table 4). There were no differences between mean track counts of cottontails on sites with and without snowshoes in either optimal (P = 0.32) or suboptimal (P = 0.37) snowshoe habitats.

Frequency of cottontail occurrence was compared within each of the six snowshoe habitats on sites immediately south of the snowshoe’s current range vs. sites where snowshoes were absent within current range. There were no differences (P > 0.30) between these two regions in the frequency with which cottontails occurred.

Unoccupied Snowshoe Habitat
We estimated that unoccupied habitat in counties along the snowshoe’s southern geographic limit in 1980 totalled about 1737 km², and was comprised of Jackpine-Hill’s Oak (595 km²), conifer plantations (422 km²), alder-willow (245 km²), aspen-birch (222 km²), conifer lowland (155 km²) and pine-maple (98 km²). This was about 7% of the total unoccupied area of these counties. The “sand” counties of central Wisconsin (Adams, Jackson, and Juneau) had the most unoccupied habitat.

Discussion
Changes in Snowshoe and Cottontail Distributions
Snowshoes were historically found throughout

Table 4. Mean track counts of Cottontail Rabbits within the geographic range of Snowshoe Hares on 2.56-km² sites with and without snowshoes; and mean track counts of snowshoes with and without cottontails. Habitat types were pooled because of small sample sizes. Number of sites given in parentheses.

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>Mean cottontail track counts/hr searched</th>
<th>Mean snowshoe track counts/hr searched</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Snowshoes present</td>
<td>Snowshoes absent</td>
</tr>
<tr>
<td>Conifer lowlands</td>
<td>14.0 (8)</td>
<td>16.3 (7)</td>
</tr>
<tr>
<td>conifer plantations</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Jackpine-Hill’s Oak</td>
<td>17.8 (15)</td>
<td>22.0 (12)</td>
</tr>
<tr>
<td>aspen-birch</td>
<td></td>
<td></td>
</tr>
<tr>
<td>alder-willow</td>
<td></td>
<td></td>
</tr>
<tr>
<td>pine-maple</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹Levels of significance determined by t-tests; NS indicates P > 0.15.
northern and central Wisconsin (Cory 1912). They occurred in isolated Tamarack and alder swamps in southeastern Wisconsin (Jackson 1961), and were reported as far south as Chicago, Illinois, in 1824 (Kennicott 1857).

By 1900, snowshoe distribution in the northeastern United States had receded northward as land was cleared for farming (Nelson 1909). Leopold (1945) compiled historic accounts of snowshoes in southern Wisconsin and reported that all but four isolated populations had disappeared by 1944 (Figure 3A). He concluded, however, that farm abandonment in the 1930’s, improved fire control, and subsequent reforestation had stabilized the southern geographic limit of snowshoes. The southern limit of snowshoe distribution has changed since Leopold (1945) mapped it (Figure 3). There are two major areas of range loss in west-central and eastern Wisconsin, and two major areas of range extension in central and northwestern Wisconsin (Figure 3C).

Based on mailed questionnaires, the Wisconsin Department of Natural Resources estimated that 459,000 snowshoes were harvested by about 1/2 million small-game hunters in 1978–79 (0.93 hares/hunter). Harvest rates in Wisconsin ranged from 0.25 to 0.56 hares/hunter between the cyclic low of 1937 and the peak population of 1941 (Keith 1963). Thus, hares may have been more abundant during the present study than during Leopold’s 1935–45 study. The estimated harvest of snowshoes in 1978–79 was the highest since 1933.

Comparison of Wisconsin Economic Land Inventory maps (1933–55 surveys) with 1968–78 aerial photos indicated no interim decrease in total forest cover within the two areas of range loss. We could not measure changes in snowshoe habitat, as such, because forest cover could not be partitioned from aerial photos into habitat and nonhabitat. The latter has probably increased in the absence of extensive fires and logging.

The area of range extension in northwestern Wisconsin (Burnett and Polk counties) had an approximate 7% increase in forest cover during the 35-year period between 1938 and 1973. Such newly forested land consists largely of young Jackpine and aspen, ideal habitat for snowshoes. The extensive pine plantations in St. Croix State Forest were begun during the above period, and may have provided an avenue of dispersal from Burnett to Polk County.

Range extension in central Wisconsin occurred on largely agricultural land with isolated islands of habitat. The area is virtually surrounded by occupied Snowshoe Hare range, and it is possible that this extension is temporary and contingent on the present high population.

Cottontails were abundant on the prairies of southern Wisconsin when white settlers first arrived, and this species spread northward with agricultural clearing of forests (Jackson 1961). Cottontails were first reported in Douglas and Bayfield counties (northwestern Wisconsin) in 1907 and about 1910, respectively (Nelson 1909; Jackson 1920). It is likely that cottontails were found statewide shortly thereafter. Jackson (1961) showed a statewide cottontail distribution, and our interviews with Wisconsin Department of Natural Resources field personnel indicated that this was still true in 1979–80. Distribution probably has varied locally in northern Wisconsin as land-use changes affected habitat associated with towns, villages, and farmsteads.

Snowshoe Hare Habitat

We earlier applied the term habitat to the six major vegetation types within which Snowshoe Hares were sometimes found during our winter surveys. There were marked differences among habitats in both frequency of occurrence and indices of abundance of hares, suggesting a spectrum of favorability. We do not know if snowshoe populations maintained themselves year-round in each of these habitats, or the degree to which net ingress from elsewhere sustained numbers in them. Seasonal shifts in habitat use by snowshoes, evidently linked to changing food and cover, have been recorded in other regions (Adams 1959, Wolff 1980) and probably occur also in Wisconsin.

Throughout the geographic range of the Snowshoe Hare, habitats which tend continuously to support hare populations have one predominant physical attribute in common — the presence of low dense woody vegetation. Along the snowshoe’s southern limits in the midwestern and eastern United States, in eastern Canada, and in the western mountains, young and/or low-growing conifers provide such cover, and appear to be the key local determinent of snowshoe distribution (Table 5). This conifer cover may be lowland or upland, as illustrated in the present Wisconsin study by the equally high use of conifer bogs and plantations (Figure 5). Numbers were much lower in two other habitats, Jackpine-Hill’s Oak and pine-maple, where the conifers on most sites sampled were too large to afford appreciable amounts of low dense cover.

Determination of Southern Range Limit

As already noted, in Wisconsin and elsewhere along the snowshoe’s southern geographic limit, low-growing conifer cover appears to be the key local determinant of distribution. We do not believe that such conifers are an essential food source — the hare eats a great variety of browse (Grange 1932; Adams 1959; Bider 1961; DeVos 1964; Telfer 1972; Pease et
TABLE 5. Reported occurrence of conifer cover as an important habitat component for Snowshoe Hares along the southern geographic limit of distribution.

<table>
<thead>
<tr>
<th>Geographic location</th>
<th>General topography</th>
<th>Conifer cover</th>
<th>Stand type</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>NW Oregon</td>
<td>mountainous</td>
<td>Western Hemlock (<em>Tsuga heterophylla</em>) (Douglas Fir (<em>Pseudotsuga menziesii</em>))</td>
<td>second growth</td>
<td>Black (1965)</td>
</tr>
<tr>
<td>NW Montana</td>
<td>mountainous</td>
<td>Douglas Fir</td>
<td>thickets</td>
<td>Adams (1959)</td>
</tr>
<tr>
<td>Colorado</td>
<td>mountainous</td>
<td>Engleman Spruce (<em>Picea engelmanni</em>) Subalpine Fir (<em>Abies lasiocarpa</em>) Lodgepole Pine (<em>Pinus contorta</em>)</td>
<td>mixed forest</td>
<td>Dolbeer and Clark (1975)</td>
</tr>
<tr>
<td>Utah</td>
<td>mountainous</td>
<td>Engleman Spruce (Subalpine Fir)</td>
<td>forests</td>
<td>Dolbeer and Clark (1975)</td>
</tr>
<tr>
<td>Virginia West Virginia</td>
<td>mountainous</td>
<td>Red Spruce (<em>Picea rubens</em>)</td>
<td>second growth</td>
<td>Brooks (1955)</td>
</tr>
<tr>
<td>Michigan</td>
<td>gently rolling</td>
<td>White Cedar (<em>Thuja occidentalis</em>) Balsam Fir (<em>Abies balsamea</em>)</td>
<td>lowland forest</td>
<td>Conroy et al. (1979)</td>
</tr>
<tr>
<td>SE Ontario</td>
<td>gently rolling</td>
<td>White Cedar Black Spruce (<em>Picea mariana</em>) White Spruce (<em>Picea glauca</em>)</td>
<td>lowland forest</td>
<td>DeVos (1962)</td>
</tr>
</tbody>
</table>

al. 1979) and often exists further north without conifers. We doubt, too, that this hare requires conifers for shelter from the higher summer temperatures — when held outdoors in pens in southern Wisconsin, both Alberta and northern Wisconsin snowshoes survived and reproduced at rates typical for these subspecies in the wild (Keith et al. 1966).

To us, the most plausible explanation for the observed hare-conifer association is that the snowshoe's need for protection from predators increases southward as (1) potential habitats become more scattered, (2) predator populations become more complex and stable, and (3) the hare's seasonal pelage becomes less adaptive as the predictability of snowcover decreases. By providing the best protection from predators, areas of low conifer cover thus become the primary foci of marginal and outlying populations in the south.

We are suggesting that the southern limit of the Snowshoe Hare distribution in Wisconsin, now and historically, has been established mainly by predator-caused mortality which can be significantly moderated by conifer cover and timely snowfalls. Under these circumstances, the most obvious environmental correlate with hare distribution locally will be conifer distribution.
We suspect that much of the predation falls on dispersing individuals. There is likely a critical distance between islands of habitat where the probability of survival for dispersers, and hence of range extension or recolonization, approaches zero. This may largely explain the approximately 1700 km² of unoccupied habitat along the snowshoe's range boundary through central Wisconsin.

**Snowshoe-Cottontail Interaction**

The distribution and abundance of snowshoes and cottontails appear to be interrelated. Snowshoe occurrence was inverse to cottontail occurrence in Jackpine-Hill's Oak, alder-willow, and conifer lowland habitats (Table 3). The other habitat types showed a similar trend, but differences there were not statistically significant with the more limited sampling. Abundance of snowshoes, as indexed by track counts, was lower when cottontails were present in the better habitats (conifer lowland and conifer plantation) (Table 4). Cottontail abundance was likewise lower, but not significantly, when snowshoes were present.

The above inverse relationships imply that there is competition between the two species. Because they coexist over a broad zone through central Wisconsin, neither has a completely competitive advantage. Perhaps at a given time, an island of habitat can support a certain number of rabbits and hares in aggregate; sometimes snowshoes first become established, at other times cottontails. There are numerous reports of interspecific interactions among lagomorphs allegedly affecting distribution and abundance (Rothschild and Marsh 1956; Lind 1963; Bergerud 1967; Braun and Streeter 1968; Flux 1970; Broekhuizen and Kemmers 1976; Hewson 1976; Chapman and Stauffer 1981), but very little field data on the ecological or behavioral mechanisms involved.

**Role of Habitat in Population Fluctuations — A Conceptual Model**

Because low dense woody vegetation seems to be of over-riding importance to Snowshoe Hares, we now examine its role in population dynamics. Three possible benefits of such vegetation to snowshoes are: (1) as a source of browse for winter food, (2) protection from predators through concealment and physical obstruction, and (3) shelter from inclement weather. Our discussion focuses on (1) and (2) because most is known about demographic impacts of food shortages and predation.

Snowshoe Hares are renowned for cyclic fluctuations in abundance averaging about 10 years between peaks, yet not all populations are cyclic (Keith 1963, 67-70). Non-cyclic populations are largely, if not entirely, associated with fragmented or island-like distributions of favorable habitat. Leopold (1933, 64) had earlier sensed this relationship when he stated: “Cycles are more severe on large continuous blocks of range than on small, dispersed or discontinuous blocks.” As Grange (1949, 1965) stressed, only fire can create and maintain large areas of habitat for Snowshoe Hares within the Boreal Forest. It is, of course, brushy cover regenerating post-fire that comprises the most favorable hare habitat. This may be either deciduous or coniferous, depending on a host of edaphic, aspect, and historic factors which locally dictate forest succession.

Cyclic fluctuations, often of high amplitude, characterized Snowshoe Hare populations in Wisconsin from at least the turn of the century until the 1950’s (Keith 1963). These cycles followed extensive logging and burning of the state’s northern forests in the late 1800’s; the last great wildfires occurred in the 1930’s. During the past 40 years, Wisconsin forests matured beyond the stage where brushy cover is extensive; and this vital component of snowshoe habitat is now much reduced and highly fragmented. As might be anticipated, classical fluctuations no longer occur in Wisconsin; recent indices of abundance (McCaffery 1977) have failed completely to track the two peaks and lows that occurred in Canada and Alaska since 1960 (Keith and Winberg 1978; Ernest 1974). The disjunct mountain populations of snowshoes in western Canada and United States have apparently never exhibited 10-year cycles of abundance (Keith 1963; Dolbeer and Clark 1975).

To understand why cyclic fluctuations are not manifested where Snowshoe Hare habitat is fragmented or island-like, one must first grasp how cycles are generated locally in more or less continuous habitat. Field studies in Alberta spanning 16 years indicated that the 10-year cycle is produced intrinsically by successive hare — winter food and hare — predator interactions (Keith 1974; Keith and Winberg 1978). Food shortage initiates a major decline from peak abundance by reducing rates of both reproduction and juvenile survival. This decline, coupled with a lag in the numerical response of hare predators, greatly increases the predator-hare ratio. As a consequence, survival remains low well after the food shortage has ended, thereby extending the period of decline and depressing the hare population still further. Its cyclic increase begins after predator numbers have fallen due to hare scarcity, and hare survival has risen sharply.

Within this broad framework of environmental and demographic change, differences in habitat quality (food and shelter values) play a significant role. In summarizing the general observations of earlier
workers, Keith (1963, 88–89) concluded: “The general pattern that emerges... is clearly one of cyclic species persisting chiefly in restricted islands or foci of favorable habitat during low years, and dispersing into less favorable habitat as numbers begin to increase once again.” Keith (1966) later showed that a cyclic decline in 1962–64 was accompanied by movements of marked individuals from sites affording least brushy cover to sites affording most. This was the main immediate cause of the change from an essentially ubiquitous distribution of hares at the peak to scattered pockets at the low. Keith and Windberg (1978: 41) noted that the next cyclic decline (1971–75) “... was also accompanied by a sharp reduction in habitat utilization. While hares once again no longer utilized open sections of upland and bog, they likewise disappeared from many areas of seemingly good cover as well. Such a situation is common during hare lows, and it appears almost as though chance plays some part in determining where residual populations will be found within a matrix of suitable habitat”. The area of habitat that snowshoes occupied shrank by 72 and 87% during the above population declines.

It is thus clear that a fragmented or insular distribution is typical of cyclic snowshoe populations during their recurrent lows, and of noncyclic populations at all times. The critical question is why then do only the former disperse, increase, and for a time occupy much of the countryside? The answer appears to lie in the greater continuity and extent of favorable habitat where cycles occur. There, dispersers from scattered subpopulations encounter a combination of food and cover affording sufficient nutrition and protection from predators to permit population growth. As Wolff (1981) correctly surmised, onset of the cyclic increase is also importantly facilitated by the scarcity of predators whose numbers have been greatly reduced through dependency on hares (Keith et al. 1977).

Predator species diversity differs little between cyclic and noncyclic hare populations: the Great Horned Owl (Bubo virginianus), Goshawk (Accipiter gentilis), Red-tailed Hawk (Buteo jamaicensis), Broad-winged Hawk (Buteo platypterus), Red Fox (Vulpes vulpes), Coyote (Canis latrans), Marten (Martes americana), and Mink (Mustela vison) are all widely distributed; and such common northern predators as the Lynx (Lynx canadensis) and Fisher (Martes pennanti) may be replaced further south by the Bobcat (Lynx rufus) and Gray Fox (Urocyon cinereoargenteus). On the other hand, where snowshoes are insular and noncyclic, predators are less obligate on single prey species and, individually and collectively, persist as moderate to high density populations. These traits arise jointly from the greater diversity of prey in areas of fragmented (i.e. more diverse) habitats, and the greater stability of the total prey biomass when hare cycles are absent. Such facultative and consistent predation pressure, acting especially on dispersers, is likely sufficient to prevent local hare populations from expanding.

In contrast, the low rates of predation coincident with recovery from cyclic depressions persist throughout the increase phase and peak due to the hare population’s higher potential growth rate and the predator’s lagging numerical and functional responses (Keith et al. 1977). Wolff (1981) applied the term “refugia” to those patches of dense woody cover where remnant snowshoe populations exist during the cyclic low, implying that security from predation was paramount in their utilization. This view was consistent with Keith and Windberg’s (1978, 39) observation that ingress continued at a high rate throughout the cyclic decline on one study area with dense stands of small spruce and a shortage of winter food, but not on four others without such cover or as persistent a food shortage (Pease et al. 1979).

The stabilizing influence of habitat fragmentation per se was shown by Windberg and Keith’s (1978) study of hares in small woodlots created through agricultural clearing of former Boreal Forest. These lay within 25-30 km of largely-forested regions containing cyclic populations that peaked at 17.6 hares per hectare in fall 1970, and fell to 0.5 per ha by May 1974. This 35:1 ratio of change contrasted markedly with the 6:1 in synchronously-fluctuating woodlot populations where peak and low densities were 5.6 and 0.9 per ha. Demographically, the lower peak densities were caused by a much higher rate of juvenile “mortality” (disappearance); environmentally, such losses were evidently caused by higher predation rates. We strongly suspect that predation was disproportionately higher on young dispersing into the surrounding agricultural land. Dolbeer and Clark (1975) had earlier attributed the numerical stability of their Rocky Mountain populations to a density-related dispersal of young from islands of favorable habitat into areas where survival was low. They neither knew nor speculated on the immediate causes of death, however.

To summarize, cyclic fluctuations of Snowshoe Hares are not generated where forest cover may be extensive but where areas of low dense woody vegetation therein are widely separated and island-like. This is because dispersers from these islands of favorable habitat are removed by a relatively stationary and abundant complex of facultative predators, thus effectively negating both expanded distribution and local increases in density. Such hare populations are thereby primarily regulated within comparatively narrow limits by the interaction of habitat, dispersal
Acknowledgments

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Literature Cited


Ernest, J. 1974. Snowshoe Hare studies. Alaska Department of Fish and Game. 46 pp. (mimeographed).


Les, B. L. (Editor). 1979. Fish and wildlife comprehensive plan. Wisconsin Department of Natural Resources. 311 pp. (mimeographed).


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Migration of Juvenile Thick-billed Murres through Hudson Strait in 1980

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Aerial surveys carried out in September 1980 suggested that, after leaving the large colonies at Digges Sound (62°35'N, 77°40'W), Thick-billed Murre Uria lomvia chicks, each with a parent, dispersed slowly during the first 1-2 weeks, but then migrated through Hudson Strait at a rate in excess of 40 km/day1, passing the eastern entrance to the Strait within a month of leaving the colony.

Key Words: Thick-billed Murre Uria lomvia, migration, Hudson Strait.

Banding carried out by the late L. M. Tuck in 1955 showed that Thick-billed Murres (Uria lomvia) from the large colonies at Digges Sound (62°35'N, 77°40'W), at the western end of Hudson Strait, winter off Newfoundland. Young birds leave the colony in August and begin to be recovered in substantial numbers off Newfoundland in October, so the southward movement takes about two months (Gaston 1980). Young Thick-billed Murres leave their colonies while still incapable of sustained flight, at about one-fifth of adult weight, and they probably remain flightless for at least six weeks (Tuck 1961).

To document the timing and speed of migration of the young murres and their parents after leaving Digges Sound, we flew a series of partly overlapping aerial surveys over Hudson Strait in September 1980 using a DeHavilland Twin Otter aircraft equipped with a GNS 500 navigation system. Surveys were flown at 175-220 km.h-1 (mainly 180-200 km.h-1) and 45 m above the sea. Two (or three) observers were used: one in the co-pilot’s seat and the other in the second seat behind the pilot; the third observer, when present, was in the second seat behind the co-pilot. All data presented derive from the first two observers who were the same for all surveys (the author and D. Noble). Sightings of murres and all other birds were recorded on a tape recorder by two-minute periods, so that positions were known within 5.8-7.3 km. Sightings estimated within 200 m of the line of flight were recorded as “on transect”. (For further details of methods see Nettleship and Gaston 1978). Surveys were flown on five days and covered 4112 km (Table 1, Figure 1). Transects parallel to coastlines were flown at 1 km from the shore, cutting across narrow bays and inlets. Where offshore transects started or ended at the coast, the first and/or last 2-minute periods were combined with coastal transects for analysis.

Results and Discussion

Substantial numbers of Thick-billed Murres, including many chicks, were seen on all surveys except 9 September. Most chicks were accompanied by a single adult; less commonly groups of several adults and chicks were encountered. Densities were higher on offshore transects than on coastal transects, except very close to the Digges Sound colonies (Table 1). On 3 and 4 September most chicks and adults were concentrated in an area within 140 km north and east of Digges Sound, well offshore (Figure 2). An extrapolation of observed densities south of Nottingham and Salisbury Islands on transects 5, 23, and 24 on 3 September (mean 3.71 chicks. km-2) to the entire area “A” (11 000 km2, enclosed by the broken line, Figure 2) suggested that approximately 40 000 chicks were present. By 9 September few chicks were seen in West Hudson Strait, but on 13 September a dense concentration was present in a band about 30 km wide along the south coast of the Meta Incognita Peninsula to the east of Lake Harbour (Figure 3). Extrapolation of densities for area B (4000 km2, mean density 2.9 chicks. km-2) suggests that c. 12 000 were present. A concentration along this coast was still apparent on 19 September, when surveys were extended further to the east.

Chicks began to leave the breeding sites at Digges Sound on 10 August and three-quarters of the chicks on the colony had left by 25 August. The total size of the population is approximately 300 000 pairs and in 1980 about 64% of 205 pairs studied reared a chick, so about 190 000 chicks altogether left the colony (unpublished data). Mortality immediately after fledging is probably heavy and this, combined with the tendency of aerial surveys to severely underestimate numbers of birds on the sea (Stott and Olson 1972, Nettleship and Gaston 1978), suggests that the
Table 1. Transects and distances flown and numbers of Thick-billed Murres recorded within 200 m of the line of flight, during 5 surveys in September 1980.

<table>
<thead>
<tr>
<th>Date</th>
<th>Transects</th>
<th>Distance Flown</th>
<th>Unaccompanied Adults</th>
<th>Adult-chick pairs</th>
<th>Density of Adult-chick pairs/km²</th>
</tr>
</thead>
<tbody>
<tr>
<td>3 Sept. coastal</td>
<td>1,4,6,7,22</td>
<td>362</td>
<td>336</td>
<td>36</td>
<td>0.25</td>
</tr>
<tr>
<td>offshore</td>
<td>2,3,5,23,24</td>
<td>538</td>
<td>718</td>
<td>319</td>
<td>1.48</td>
</tr>
<tr>
<td>4 Sept. coastal</td>
<td>11</td>
<td>115</td>
<td>8</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>offshore</td>
<td>25,27,28</td>
<td>363</td>
<td>188</td>
<td>60</td>
<td>0.41</td>
</tr>
<tr>
<td>9 Sept. coastal</td>
<td>8,9,10,19</td>
<td>339</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>offshore</td>
<td>20,21,24,25,26,27</td>
<td>766</td>
<td>34</td>
<td>16</td>
<td>0.05</td>
</tr>
<tr>
<td>13 Sept. coastal</td>
<td>12,18</td>
<td>139</td>
<td>12</td>
<td>5</td>
<td>0.09</td>
</tr>
<tr>
<td>offshore</td>
<td>13,29,30,31,32</td>
<td>632</td>
<td>236</td>
<td>123</td>
<td>0.49</td>
</tr>
<tr>
<td>19 Sept. coastal</td>
<td>16,17</td>
<td>255</td>
<td>4</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>offshore</td>
<td>14,15,32,33,34,35</td>
<td>603</td>
<td>81</td>
<td>43</td>
<td>0.18</td>
</tr>
</tbody>
</table>

Figure 1. Map of aerial surveys conducted over Hudson Strait in September 1980.
Figure 2. Concentrations of Thick-billed Murres observed on transects flown on 3, 4 and 9 September 1980. Upper graph applies to 3 and 4 September only.
Figure 3. Concentrations of Thick-billed Murres observed on transects flown on 13 and 19 September 1980. Left half of upper figure applies to 13 September, right half to 19 September.
The concentration of chicks north and east of Digges Sound on 3 and 4 September may have involved between one-third and one-half of the entire season's production, and probably included some chicks which had fledged at least 10 days previously. If the concentration observed along the south coast of Meta Incognita Peninsula on 13 September included some of the same birds, then the chicks involved covered 400 km in 10 days, averaging about 40 km.day⁻¹.

The large number of chicks still present within 140 km of the colony at least ten days after some had departed the cliffs suggests that movement initially was slow. In Digges Sound adjacent to the murre colony, tidal currents are strong, with the ebb, setting to the north and east at 3-5 km.h⁻¹, being stronger and of longer duration than the flow. Just to the east of Cape Wolstenholme the current inshore sets permanently eastwards at 3-5 km.h⁻¹ (Anonymous 1979). Most chicks moved northeast after fledging, thus avoiding the strong currents along the south shore of Hudson Strait, so they were not carried eastwards immediately. Perhaps adult murres will not commit their chicks to passage through the Straits until they have spent some time feeding.

The direction of surface currents in Hudson Strait is generally westward along the north shore (Anonymous 1979), a pattern confirmed by the position of icebergs on the present surveys. Chicks congregating along the coast to the east of Lake Harbour may have moved into the area against the current, perhaps to take advantage of local opportunities for feeding. The apparent scarcity of murres in central Hudson Strait suggests that that area offers relatively poor feeding, an idea supported by the absence of large seabird colonies between Digges Sound and Ungava Bay although seemingly suitable cliffs exist along the south shore.

Four other Thick-billed Murre colonies exist close to Hudson Strait; two large colonies on Akpatok Island, (both > 100 000 pairs), one on Hantzsch Island, just east of the Meta Incognita Peninsula (50 000 pairs) and one at the northern tip of Coats Island in northern Hudson Bay (15 000 pairs) (Brown et al. 1975). The concentration of chicks in western Hudson Strait on 3-4 September may have included some from Coats Island, whence chicks also migrate to Newfoundland (Tuck 1961), but considering the number involved the majority must have derived from Digges Sound. That chicks seen off the Meta Incognita Peninsula originated from either Hantzsch or Akpatok Islands appears unlikely. Surveys carried out across the eastern entrance of Hudson Strait by MacLaren Marex Inc. in 1978 suggested that chicks from Akpatok Island moved directly eastwards rather than north after leaving the colony (MacLaren Marex Inc., unpublished data). Chicks from Hantzsch Island also would have had to detour a long way from their best course for Newfoundland.

Surveys carried out across eastern Hudson Strait in 1978 suggested that Thick-billed Murre chicks from Digges Sound left Hudson Strait that year in early October (MacLaren Marex, Inc., unpublished data), about three weeks later than in 1980. At the Thick-billed Murre colony on Prince Leopold Island, in Lancaster Sound (74°N, 90°W) also, breeding was approximately three weeks later in 1978 than in the previous three years, a phenomenon probably associated with abnormally low temperatures (Nettleship et al., in prep.). Comparison of the apparent timing of migration suggests that breeding may have been similarly delayed at the Digges Sound colony in 1978.

Acknowledgments

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Literature Cited


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Some Reproductive Traits of Four Shrub Species in the Black Spruce Forest Type of Alaska

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Prickly Rose (Rosa acicularis) has a true rhizome system while Bog Blueberry (Vaccinium uliginosum) and Labrador-tea (Ledum palustre subsp. groenlandicum) have below ground systems developed by layering. Beauverd Spirea (Spirea beauverdiana) reproduced from sprouts formed at or near the root collar. Rose rhizome cuttings produced many more new shoots and roots in vermiculite-perlite than did below-ground stem cuttings of Bog Blueberry and Labrador-tea. Rose seeds exhibited deep dormancy while those of Bog Blueberry, Labrador-tea and Beauverd Spirea exhibited shallow or conditional dormancy. The latter two species required light to germinate.

Key Words: Prickly Rose, Rose acicularis, Bog Blueberry, Vaccinium uliginosum, Labrador-tea, Ledum palustre subsp. groenlandicum, Beauverd Spirea, Spirea beauverdiana, reproductive traits, Black Spruce forest, Alaska.

A knowledge of the reproductive ecology of a species is vital to an understanding of ecosystem recovery following disturbance and essential to understanding a species' natural history. There is a significant amount of information in the form of percent cover and frequency of occurrence for understory shrub occurrence and response to disturbance in the Black Spruce forest type in Alaska (e.g. Viereck and Dyrness 1979; Dyrness and Grigal 1979). However, there is no specific information for Alaska on the nature and extent of shrub clones and the relevance of clone structure to recovery from disturbance and species maintenance in the developing forest. There have been studies of root and rhizome systems of similar species (Kender 1967; Flower-Ellis 1971; Minore 1975) elsewhere in the United States and Europe.

The purpose of this study was to provide specific information on the clone size of four species, Prickly Rose (Rosa acicularis), Bog Blueberry (Vaccinium uliginosum var. alpinum), Labrador-tea (Ledum palustre var. groenlandicum) and Beauverd Spirea (Spirea beauverdiana), the ability of underground parts to produce new shoots and roots, and the seed dormancy pattern and germination requirements. Bog Blueberry and Labrador-tea are two of the most common shrubs in the Black Spruce forest type while Prickly Rose and Beauverd Spirea are less common.

Methods

During the summer and fall of 1975, 6 (3 from each site) complete clones of Prickly Rose, 10 (5 from each site) of Bog Blueberry, and 11 (6 from burn, 5 from Black Spruce stands) of Labrador-tea were hand-excavated at two sites near Fairbanks, Alaska (64° 51'N, 147° 50'W, elevation 130 m); the 1971 Wicker-sham Dome burn and a 70-year-old Black Spruce (Picea mariana) forest. Individuals of Beauverd Spirea were examined at both sites but excavated in the burn only. The substrate of the undisturbed Black Spruce site consists of a 20- to 30-cm moss-organic mat underlain by permafrost-rich minerlal soil. The burned site (formerly a Black Spruce site similar to the undisturbed site) contains patches of unburned moss-organic substrate scattered throughout more intensely burned areas with exposed mineral soil.

In order to obtain an estimate of clone size and the relative importance of sexual and asexual reproduction, all individuals of the three main target species were excavated within a 4-m² area. In all cases, the 4-m² sampling area had to be enlarged to locate all ramets in a selected clone; this was particularly true for Prickly Rose. The dry weight of above- and below-ground materials was determined for clones of each species.

Cuttings of below-ground material from 3-4 clones of Prickly Rose, Bog Blueberry, and Labrador-tea were collected in mid-July, mid-August, and early October to determine the capacity for shoot production. All cuttings were planted in a 1:1 mixture of vermiculite and perlite at 2-cm depth. The mid-July cuttings were placed outside (average maximum air temperature for the period 22.0°C, minimum 8.5°C). The later cuttings were subjected to temperature regimes of 5, 15, 25, and 25/20°C, (12 hours at 25° and 20°C). Four replications of 10 cuttings per container for each of the three species were subjected to each of the temperature regimes, i.e. a total of 40 cuttings/species per temperature regime. The plantings were periodically watered and observed for shoot emergence. Treatments were terminated after 45 days.

35
Shoots were counted, and dry weight determined. Seeds from Labrador-tea, Bog Blueberry, and Beauverd Spirea were collected from open grown plants at the study site in late September and stored in sealed plastic bags at -18°C for about 2 months; stratified and unstratified germination tests were conducted at 5, 10, 15, 20 and 25°C on Kimwipe pads moistened with distilled water in petri dishes. Three replications of 50 seeds were placed at each temperature. Light period was 18 hours. Stratification was for 30 d at 2°C. Tests were terminated after 30 d at 25 and 20°C and 45 to 60 d at 15, 10, and 5°C. A seed was considered germinated if it produced a normal seedling. Dark germination tests were conducted at 25, 20 and 15°C on both stratified and unstratified seeds. Germination is expressed as percent of filled seed (i.e. ungerminated seeds with normal embryos). Filled seed percentage was 88 for Bog Blueberry, 84 for Beauverd Spirea, and 45 for Labrador-tea. Germination of Prickly Rose seeds has been reported earlier (Densmore and Zasada 1977).

Results and Discussion
Vegetative reproduction
Bog Blueberry and Labrador-tea clones covered an area of 5 to 10 m² while Prickly Rose clones covered an area of 10 to 20 m² (Figure 1). The number of ramets per clone varied from 8 to 11 for Prickly Rose, 21 to 25 for Labrador-tea, and 8 to 13 for Bog Blueberry. The ratio of above-(stem and leaves) to below-ground biomass for each species was as follows:

- **Unburned**
  - Prickly Rose: 1:4.8 (± 0.9)*
  - Bog Blueberry: 1:9.7 (± 2.0)
  - Labrador-tea: 1:5.0 (± 1.8)

- **Burned**
  - Prickly Rose: 1:3.1 (± 0.5)
  - Bog Blueberry: 1:3.1 (± 0.5)
  - Labrador-tea: 1:2.5 (± 0.8)

*Standard error of the mean.

Clone development is characterized by the birth and death of ramets and underground parts. Figure 1 and the above data illustrate the architecture and biomass distribution of clones for one point in time. The stability of clone structure over time will depend

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**Figure 1.** Under-ground network of (a) Prickly Rose, (b) Bog Blueberry and (c) Labrador-tea.
on the rate of ramet production and ramet longevity. These variables are affected by biotic and abiotic site factors.

Method of clone expansion differed between Prickly Rose and the ericads. Labrador-tea and Bog Blueberry appeared to expand through growth of above-ground shoots. The decumbent stems were eventually covered by moss growth and organic matter accumulation with rooting occurring along the buried stem. This process is similar to layering in Black Spruce (Staneck 1968). It differs from the type of clone development and rhizome systems reported for Vaccinium angustifolium (Kender 1967), V. myrtillus (Flower-Ellis 1971), and V. membranaceum (Minore 1975) which spread by the elongation of fleshy rhizome tips below the soil surface. Observations made in this study indicated that V. vitis-idaea also spreads vegetatively by rhizomes but no rhizomes were observed on Bog Blueberry or Labrador-tea.

In contrast, Prickly Rose spreads by means of a rhizome. Shoots produced along this horizontal rhizome grow vertically to the soil surface. Figure 2 shows the gross morphological differences between the apices responsible for Bog Blueberry and Prickly Rose clone expansion.

Beauverd Spirea did not exhibit a clonal system similar to the other three species, but rather proved to be a basal-sprouter. It occurred as a multi-stemmed individual with a well-developed fibrous root system.

Depth distribution of the underground system was different between Prickly Rose and the ericads. Prickly Rose rhizomes were predominant in the mineral soil, approximately 20-30 cm below the surface. Labrador-tea and Bog Blueberry generally occurred in the lower half of the organic layer, 15 to 20 cm below the surface; the occurrence of under-ground parts in the mineral soil was uncommon. Figure 3 provides a schematic representation of the relative distribution of the rhizome systems of these species. By having its rhizomes located in the mineral soil, Prickly Rose appears better adapted for re-establishment after disturbance.

Prickly Rose had the highest percentage of cuttings which produced shoots in July, August, and October tests (90 to 100%). Cuttings of Labrador-tea and Bog Blueberry exhibited less shoot production potential than Prickly Rose (Table 1). The weight of shoots produced by rose in the July and October tests was greater than the other species under all temperature regimes (Table 2).

Shoot production at low (5°C) substrate temperatures was greatest in rose. Bog Blueberry and Labrador-tea exhibited reduced or no shoot (percentage cuttings with shoots) production at 5°C.

Time elapsed between planting and shoot emergence above the substrate was recorded in the October study. Prickly Rose shoots appeared after 7 d at 25°C, 19 d at 15°C, and 60 d at 5°C. Bog Blueberry and Labrador-tea appeared after 30 d at 25°C and 40 d at 15°C. Bog Blueberry shoots produced at 5°C did not emerge from the substrate during the 60 d incubation period.

Forty percent of Prickly Rose rhizome cuttings produced roots in addition to shoots. Dense callus was formed at both ends of the rose cuttings subjected to the 15°C temperature regime. No callus was formed on rose cuttings at any of the other temperature regimes. Labrador-tea and Bog Blueberry did not form callus, and new root production was rare.

Distribution of shoots along a cutting segment varied between species. Prickly Rose shoots were solitary. Bog Blueberry formed multiple-stemmed clumps

**Figure 2.** Apices responsible for the expansion of Prickly Rose (a) and Bog Blueberry (b) clones.
Table 1. Mean (± SE) shoot production by rhizome cuttings of Prickly Rose, Bog Blueberry, and Labrador-tea.

<table>
<thead>
<tr>
<th>Treatment (°C)</th>
<th>Collection date</th>
<th>n</th>
<th>% cuttings with shoots</th>
<th>No. shoots per cutting</th>
<th>% cuttings with shoots</th>
<th>No. shoots per cutting</th>
<th>% cuttings with shoots</th>
<th>No. shoots per cutting</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outside</td>
<td>July</td>
<td>4x10</td>
<td>100.0 ± 0.0</td>
<td>4.0 ± 0.4</td>
<td>51.0 ± 9.0</td>
<td>3.3 ± 0.4</td>
<td>77.0 ± 7.1</td>
<td>4.2 ± 0.4</td>
</tr>
<tr>
<td>25</td>
<td>August</td>
<td>4x10</td>
<td>100.0 ± 0.0</td>
<td>2.3 ± 0.2</td>
<td>14.7 ± 9.0</td>
<td>3.2 ± 0.9</td>
<td>33.3 ± 2.6</td>
<td>1.8 ± 0.3</td>
</tr>
<tr>
<td>15</td>
<td>August</td>
<td>4x10</td>
<td>89.0 ± 10.0</td>
<td>2.3 ± 0.2</td>
<td>31.7 ± 7.5</td>
<td>3.1 ± 0.9</td>
<td>7.3 ± 0.6</td>
<td>1.3 ± 0.3</td>
</tr>
<tr>
<td>5</td>
<td>October</td>
<td>4x10</td>
<td>92.5 ± 4.8</td>
<td>3.3 ± 0.3</td>
<td>25.2 ± 11.4</td>
<td>3.2 ± 1.3</td>
<td>21.0 ± 4.0</td>
<td>5.0 ± 1.4</td>
</tr>
<tr>
<td>25/20</td>
<td>August</td>
<td>4x10</td>
<td>95.0 ± 4.0</td>
<td>1.6 ± 0.1</td>
<td>20.0 ± 11.0</td>
<td>2.0 ± 0.9</td>
<td>18.0 ± 13.0</td>
<td>1.8 ± 0.6</td>
</tr>
</tbody>
</table>

Table 2. Mean dry weight (± SE) expressed as grams per shoot produced by Prickly Rose, Bog Blueberry, and Labrador-tea rhizome cuttings after 45 d.

<table>
<thead>
<tr>
<th>Temperature (°C)</th>
<th>Cutting Size</th>
<th>Prickly Rose</th>
<th>Bog Blueberry</th>
<th>Labrador-tea</th>
</tr>
</thead>
<tbody>
<tr>
<td>Outside</td>
<td>0.014 ± 0.002</td>
<td>0.003 ± 0.0004</td>
<td>0.002 ± 0.0003</td>
<td></td>
</tr>
<tr>
<td>25</td>
<td>0.013 ± 0.002</td>
<td>0.002 ± 0.0004</td>
<td>0.0034 ± 0.0005</td>
<td></td>
</tr>
<tr>
<td>15</td>
<td>0.021 ± 0.003</td>
<td>0.002 ± 0.0004</td>
<td>0.002 ± 0.0005</td>
<td></td>
</tr>
<tr>
<td>25/20</td>
<td>0.030 ± 0.007</td>
<td>0.008 ± 0.0003</td>
<td>0.006 ± 0.0001</td>
<td></td>
</tr>
<tr>
<td>10-cm rhizome cutting</td>
<td>0.902 ± 0.144</td>
<td>1.540 ± 0.123</td>
<td>1.5178 ± 0.179</td>
<td></td>
</tr>
</tbody>
</table>

which appeared to originate from the same bud site. Labrador-tea shoots were relatively close together but form distinctly different buds.

Seed Germination

Reproduction from seed is most important where disturbance is relatively severe and most of the underground rhizome and stem material is destroyed. In our study, seedlings were not observed.

Lack of regeneration from seed can be attributed to absence of seed or the absence of "safe-sites" for germination and seedling establishment. There was no seed rain from plants on site as little flowering had occurred at the time this study was conducted; neither the magnitude of the seed rain from off the site or the seed bank were assessed. However, even if seeds were available, the surface condition on the excavated plots, i.e., partially burned organic matter, was a poor environment for germination and seedling establishment. Areas where fire has consumed all of the organic matter exposing mineral soil provide a better environment for regeneration from seed. The objectives of our germination studies were to determine the quality of seed produced on these sites and to evaluate the effect of prechilling on germination response to light and temperature. Germination response to prechilling provides insight to field germination patterns (Densmore 1979).

Bog Blueberry, Labrador-tea, and Beauverd Spirea seeds exhibited shallow or conditional dormancy which contrasted significantly with the deep dormancy pattern that has been shown for Prickly Rose seeds (Densmore and Zasada 1977). A 30-day period of cold stratification enhanced both the rate of germination and total germination for the three species. In contrast, the rose required a period of warm stratification followed by a period of cold stratification before germination occurred (Densmore and Zasada 1977). Bog Blueberry seeds from alpine sites in New Hampshire's White Mountains demonstrated a similar response to cold stratification (Nichols 1934). In our study, Bog Blueberry (both stratified and unstratified) exhibited a sensitivity to colder temperatures with few seeds germinating below 15°C (Table 3). The number of days elapsed before the first germinants appeared varied from 5(25°C) to 19(5°C) d and 6(25°C) to 24 (5°C) d for stratified and unstratified seeds respectively. Germination in the dark decreased between 25 and 15°C and no germination occurred below 15°C. The same general pattern was observed
Labrador-tea and Beauverd Spirea seeds exhibited a marked light requirement for germination (Table 3). Juntila (1972) found that GA₃ (gibberelic acid) treatment of Labrador-tea seeds substituted for the effects of light on germination and enhanced germination percentage and rate at lower temperatures. Cold stratification increased germination percentage at all temperatures for both Labrador-tea and Beauverd Spirea. Time elapsed for the appearance of first germinants varied from 1(25°C) to 8(5°C) days and 3(25°C) to 51(5°C) days for stratified and unstratified Beauverd Spirea seeds respectively and from 4(25°C) to 19(5°C) days and 4(25°C) to 23(5°C) days for stratified and unstratified Labrador-tea seeds respectively. Beauverd Spirea seeds showed a classic response to cold stratification going from no germination of unstratified seeds at 20, 15 and 10°C to nearly 100% germination of the stratified seeds. Stickney (1974) reported that Birchleaf Spirea seeds (S. betulifolia) required no stratification.

One use of laboratory data is to predict the response which may occur in the field. Our data suggested that if temperature was the main factor controlling early germination in these conditionally dormant seeds that Beauverd Spirea would germinate first and be followed by Labrador-tea and then Bog Blueberry. Densmore (1979) observed that Beauverd Spirea germination occurred earlier and at lower spring temperatures than the other two species. Labrador-tea germinated earlier in the field and had a lower threshold temperature than Bog Blueberry.

**Literature cited**
Kender, W. J. 1967. Rhizome development in the lowbush blueberry as influenced by temperature and photoperiod.


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Predation on Seabirds by Red Foxes at Shaiak Island, Alaska

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Two Red Foxes (Vulpes fulva) that invaded Shaiak Island before the 1976 nesting season had a marked impact on the nesting success of five of seven species of seabirds breeding on the island that year. Common Eiders (Somateria mollissima), Glaucous-winged Gulls (Larus glaucescens), and Common Murres (Uria aalge), that nest in areas accessible to foxes, did not raise any young to fledging. Double-crested Cormorants (Phalacrocorax auritus) were only slightly more successful; 13 (4.3%) of 300 pairs raised one or more young to fledging. Evidence suggested that 21 (35.6%) of 62 pairs of Tufted Puffins (Lunda cirrhata) lost eggs or chicks to foxes, and foxes killed at least 13 (8.3%) of 156 adult puffins on ten sample plots. Conversely, Black-Legged Kittiwakes (Rissa tridactyla) and Pelagic Cormorants (Phalacrocorax pelagicus), which nests primarily on cliffs inaccessible to foxes, lost very few nests. There was no apparent change in general nest site selections by seabirds the following year, when foxes were no longer present. Any avoidance by birds of areas vulnerable to fox predation would probably be discernible only after several years of continuous predation.

Key Words: Seabirds, Red Foxes, Vulpes fulva, predation.

The selection of islands for nesting by several groups of seabirds is thought to be in part a result of predation by terrestrial predators on the mainland (for a review see Buckley and Buckley 1980). When foxes are present on islands, they are believed to influence seabirds' choice of nesting habitat (Fay and Cade 1959). Introductions of foxes, for fur farming, on formerly fox-free islands in Alaska are thought to have substantially reduced or eliminated several species of seabirds and waterfowl from those islands (Murie 1959; Jones 1963; Jones and Byrd 1979).

Studies on the impact of foxes on island-nesting gulls (Kadlec 1971; Southern et al. 1979) and shearwaters (Norman 1971) focused on losses of a single species or taxonomic group owing to the presence of foxes. Observations suggest that foxes coexisting with seabird colonies take the birds most readily available (Stephenson 1970). However, the impact of an invasion of foxes to a small island with several species of breeding seabirds has not been documented.

An invasion of mammal-free Shaiak Island, Alaska, by two Red Foxes (Vulpes fulva) before spring 1976 provided an opportunity to evaluate their impact on the reproductive success of Common Eiders (Somateria mollissima), Double-crested Cormorants (Phalacrocorax auritus), Pelagic Cormorants (P. pelagicus), Glaucous-winged Gulls (Larus glaucescens), Black-legged Kittiwakes (Rissa tridactyla), Common Murres (Uria aalge), and Tufted Puffins (Lunda cirrhata).

Study Area and Previous Studies

Shaiak Island (58°33'N, 161°40'W) lies 0.6 km off Cape Peirce, Alaska, and is part of the Togiak National Wildlife Refuge. The island is 0.6 km long, 0.3 km wide, and rises to 132 m. It consists primarily of massive, altered volcanic rocks, siliceous siltstone, and chert (Hoare and Conrad 1961). The island consists primarily of a plateau and gentle slopes covered by sod up to 1.5 m deep, except for a few rock outcroppings and low cliff faces. Vegetation is dominated by Lyme Grass (Elymus arenarius), Bluejoint (Calamagrostis canadensis), and Wormwood ( Artemisia arctica). In some winters (e.g. 1975-76) an ice bridge forms by which foxes may reach the island from the mainland. There is no standing or flowing fresh water on the island after the snow melts in early spring.

Personnel of the U.S. Fish and Wildlife Service (USFWS) and others surveyed the Cape Peirce area during seven breeding seasons between 1963 and 1973. In 1963-65, 1969, 1971, and 1973 observers flew over Shaiak Island, estimated the number of each species there, and documented the presence of Glaucous-winged Gull and Double-crested Cormorant chicks (USFWS, unpublished data). Once between 1963 and 1965, and three times in June and July 1973, observers also landed on the island and photographed the seabirds nesting there. These photographs clearly show the presence of Glaucous-winged Gull chicks on the upper sod slopes (USFWS, unpublished data). Biologists conducting studies at Cape Peirce in 1969, 1970, and 1973 also made detailed observations of seabirds nesting on Shaiak Island by telescope from the mainland. None of the observers reported seeing or suspecting the presence of foxes on Shaiak Island, and the presence of Glaucous-winged Gull and Double-crested Cormorant chicks on accessible sod slopes (USFWS, unpublished data) suggests that no foxes...
inhabited the island during any of those years.

Methods
The density and nesting success of seabirds breeding on Shaiak Island were determined by techniques similar to those described by Nettleship (1976). Details were given by Petersen and Sigman (1977). Depending on species, population estimates were based variously on direct counts of all nests (elders and cormorants) or by quadrat and linear (strip) transect sampling procedures. All accessible nests on study plots were marked with numbered tongue depressors, eggs were marked with indelible ink, and chicks were marked with color bands. The island was visited on nine days (10-18 h/visit) at about weekly intervals as weather permitted from 6 June to 22 August 1976. Numbers of destroyed eggs, dead and partially eaten adults, empty nests, and destroyed burrows on each study plot were recorded during each visit. Dates of initiation of clutches of birds on Shaiak Island and on cliffs at Cape Peirce were determined from observations of incomplete clutches or backdating from hatching dates of eggs. Fledgling dates and success were determined from observations of color-banded young. Additional observations were made at roughly three-day intervals (27 days total) by telescope from the mainland from 2 May to 3 September. During these, the island was scrutinized to determine the number of fledged young of Double-crested Cormorants, Glaucous-winged Gulls, and Black-legged Kittiwakes, and to track the movements of foxes around the island.

During an aerial survey on 21 August 1977, I circled low over Shaiak Island specifically to look for young of Double-crested Cormorants and Glaucous-winged Gulls, both highly visible from the air, and to determine if there were any signs of foxes remaining on the island.

Results
Populations and Nesting Success
About 156 000 seabirds nested on Shaiak Island in 1976 (personal estimate, in Sowls et al. 1978). Glaucous-winged Gulls and Common Murres nested on the sod plateau and gentle sod slopes; most Double-crested Cormorants also nested there, but a few were found on the lower, steeper sod slopes. Black-legged Kittiwakes and Pelagic Cormorants nested primarily on ledges of unvegetated cliffs, although a few kittiwakes used rock outcroppings on the sod slopes. Tufted Puffins nested in all areas with soil suitable for burrowing. Common Eiders and a few Glaucous-winged Gulls nested on the short stretch of beach on the island.

Few birds that nested on the sod slopes, the plateau area, or rock outcrops had eggs hatch or chicks survive until fledging (Figure 1). Few of the estimated 300 pairs of Double-crested Cormorants that nested on the island successfully raised young. Eggs disappeared from all 138 cormorant nests on the plateau sample plots soon after they were laid; all areas on the plateau that had had active nests on 25 June 1973 (USFWS photograph) had only empty nests on 11 June 1976. Thirty-three pairs nested on sod slopes of the island. Eggs and chicks disappeared from these nests until August. The only successful nests on the island were 13 of these 33 that were on extremely steep slopes. These fledglings left the island between 29 August and 3 September (Figure 1).

Although about 100 pairs of Common Eiders attempted to nest on the island, their scrapes either were always found empty or had lost all their eggs between consecutive nest checks. Similarly, eggs from the approximately 50 pairs of Glaucous-winged Gulls which nested on the beach disappeared soon after they were laid. An estimated 2500 Glaucous-winged Gulls nested on the sod slopes. No eggs hatched from 477 nests checked on sample plots (Figure 1), and no young were found on the entire island. Native egg gatherers contributed a minor part to egg loss by taking 25-50 gull eggs.

Only 150 pairs of Black-legged Kittiwakes nested on rock outcroppings. Eggs disappeared from the 23 nests on sample plots soon after they were laid (Figure 1); none of the remaining nests had any eggs survive to hatching. Most of the estimated 10 000 pairs of kittiwakes on the island nested on steep cliff faces, and 44.5% (253 of 568) of the pairs on sample plots raised chicks to fledging. Because these nests were inaccessible and eggs could not be seen, clutch sizes and hatching success could not be determined. However, fledging success was similar to that of kittiwakes on the adjacent mainland (M. R. Petersen, unpublished data).

None of the 10 381 pairs of Common Murres that were present on sample plots on the island in 1976 hatched eggs (Figure 1). Most of the 25 000 pairs nested on the sod-covered plateau and slopes, and their eggs disappeared soon after they were laid. Similar heavy losses were not observed at Cape Peirce where an estimated 20% of the pairs nesting on the mainland cliffs raised young to fledging (M. R. Petersen, unpublished data).

An estimated 79 000 Tufted Puffins nested in shallow burrows on the island. Losses of eggs and young occurred primarily in late July and August when most of the accessible nests of other species had been destroyed (Figure 1). Eggs or young were lost from 21 (34%) of a sample of 62 puffin nests monitored from the start of egg laying. Five of those 21 nests contained...
Figure 1. Nesting success of seabirds on Shaiak Island, Alaska, in 1976. Solid lines — nests with eggs; dashed lines — nests with young; dotted lines — nests with flying young. Sample size in parenthesis represents the number of nests or territorial birds sampled on each visit. Egg laying, hatching, and fledging dates of species are from these data or from studies at Cape Peirce (Petersen and Sigman 1977). DCCO — Double-crested Cormorant; GWGU — Glaucous-winged Gull; BLKI — Black-legged Kittiwake; COMU — Common Murre; TUPU — Tufted Puffin.
eggs or young and were dug out by foxes; eggs disappeared from 11 nests; and 5 eggs were deserted. Additional sample plots were not checked until after incubation had begun; they yielded a total of 80 nests with eggs or chicks. Because early egg or chick loss was not determined on those plots, overall loss was probably more severe than depicted in the figure.

An estimated 50 pairs of Pelagic Cormorants nested on the island, all on extremely inaccessible cliff faces. Each of the three nests which I could check had two or three almost fully-feathered young on 1 August.

**Observations of Foxes and Predation**

I observed two Red Foxes on Shaiaik Island throughout summer 1976. I sighted one or both of them on 2 and 23 May, 10, 17, and 30 July and 22 August 1976. On those and 27 other days I observed anti-predator reactions by seabirds. As foxes walked about the plateau of the island, Glaucous-winged Gulls circled and called over them in a manner similar to that described by Kruuk (1964). Common Murres and Tufted Puffins standing on the plateau and slopes flew from the island en masse whenever a fox neared the area. Double-crested Cormorants and Common Eiders left their nests as foxes approached. Thus, the approximate location of the foxes could usually be determined and their presence on the island verified even when they were obscured from view because of the tall vegetation.

Hundreds of dead adult Tufted Puffins and up to 100 dead adult Glaucous-winged Gulls were found throughout the island. The presence of tooth punctures suggested that the birds were killed by foxes. Between 6 June and 22 August, 13 dead adult puffins were found just on ten 25-m² plots. They represented 8.3% of the 156 puffins nesting on those plots.

Foxes cached eggs all over the island, although they were not the sole predators of eggs. Glaucous-winged Gulls took murre, cormorant, and gull eggs after the incubating adults were flushed from their nests. Layers of smashed shells representing thousands of eggs were found in gull territories, and single eggs that had been eaten by gulls were found scattered over the island.

During the aerial survey the following summer, I detected no sign of the presence of either fox on the island nor of the massive destruction witnessed in 1976. Young Glaucous-winged Gulls and Double-crested Cormorants were dispersed all over the sod slopes in patterns reported and photographed by observers in previous years (USFWS, unpublished data). The foxes may have died or left the island during the intervening winter.

**Discussion**

Although foxes probably took a significant number of eggs from nests of murres, gulls, and cormorants during 1976, their flushing of incubating adults also provided many opportunities for gulls to take eggs. Shell remains scattered throughout nesting areas of gulls indicated that they had contributed substantially to the total loss of eggs. The number of adults, eggs, and young taken by foxes was obviously in excess of their needs. Such surplus killing (Kruuk 1972a; Kruuk 1972b; Patton and Southern 1977) of adult seabirds (especially Tufted Puffins) probably substantially reduced the number of breeding birds that would return to the island in the next few years. If such killing had been sustained by the continued presence of foxes on the island, a dramatic decline in the number of the most susceptible species breeding on the island could have been expected. Possibly the events on islands where nesting seabirds were thought to have been eliminated or reduced following the introduction of foxes for fur farming were similar to those I observed.

Birds were often disturbed by foxes before eggs were laid, yet they persisted in nesting on the island and in areas accessible to foxes. No change was discerned in nesting distribution of even the most susceptible species, either in 1976 or in 1977, after a breeding season of continuous predation. However obvious the effects that foxes or similar mammalian predators may have on the reproductive success of seabirds, studies over a longer period of time are needed to more fully understand predation as an ultimate factor influencing nest site selection of colonial nesting seabirds.

**Acknowledgments**

M. J. Sigman assisted in the field work at Shaiaik Island and Cape Peirce in 1976. I thank J. C. Bartonek for his photographs of Shaiaik Island, and him and M. H. Dick for their observations of the seabirds there. D. V. Derksen, R. L. Garrett, C. M. Handel, C. J. Lensink, J. C. Lewis, N. A. Verbeek, and two anonymous reviewers provided helpful comments on various versions of the manuscript.

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**Literature Cited**


Fay, F. H., and T. J. Cade. 1959. An ecological analysis of


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The Distribution and Status of the Barred Owl in Alberta

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Sightings of Barred Owls (Strix varia) in Alberta from 1912 to 1980 were largely restricted to mixed-wood boreal forest and to montane and foothill forest farther south. Few owls were observed in the aspen parkland, and none in the scattered wooded areas of the prairie. An increase in numbers of this species and its expansion southward through the foothills of western Alberta are suggested, concurrent with recent apparent range expansions in the northwestern United States and British Columbia.

Key Words: Barred Owl Strix varia, Alberta, distribution, status.

The Barred Owl (Strix varia) is a permanent resident across Canada from northern British Columbia to Nova Scotia and southward to Central America (Godfrey 1966). However, the status and biology of this species are well described only in Minnesota (Dunstan and Sample 1972; Nicholls and Warner 1972) and the New England States (Bent 1938).

The Barred Owl is poorly documented in western Canada except for British Columbia (Grant 1966; Campbell 1973). Only a few published records exist for Saskatchewan and Manitoba (e.g. Houston 1959, 1961; Erskine 1972 a and b). In Alberta, the status of the Barred Owl is largely unknown (Oeming 1955; Frye 1976; Salt and Salt 1976). Oeming (1955), during surveys for Great Gray Owls (Strix nebulosa), obtained 11 new records of Barred Owls and documented four earlier sightings. Those 15 records formed the basis of the distribution and status of this species in Alberta as recorded by Salt and Wilk (1966).

Recent range expansions of the Barred Owl have been noted in British Columbia (Grant 1966), Montana (Shea 1974), and Washington and Oregon (Taylor and Forsman 1976). Changes in the numbers and range of Barred Owl may influence other species through competition for food and breeding areas (e.g. Spotted Owl (Strix occidentalis), Taylor and Forsman 1976). In light of the lack of information about Barred Owls in Alberta, we compiled a list of sightings, compared the distribution of earlier records with more recent observations, and related their distribution to broad vegetation regions.

Methods

Records of occurrences of Barred Owls in Alberta were gathered from the literature (Crossa 1914; Preble 1941; Oeming 1955; 1957; Oeming and Jones 1955; Jones 1966; Turner 1966; Hatch 1969; Serr 1979); from unpublished inventory studies by the Canadian Wildlife Service, Alberta Parks and Recreation, and Alberta Fish and Wildlife; and from naturalists throughout the province. We attempted to verify these latter records by obtaining detailed descriptions of plumage and voice from the observer. Doubtful or possible duplicate records were excluded.

These records were assigned to broad vegetation zones of the province (Anonymous 1979; Rowe 1972). We combined the Rocky Mountain and upper and lower foothill forest types because of their predominantly coniferous character, with extensive tracts of Lodgepole Pine (Pinus contorta), White Spruce (Picea glauca), and Black Spruce (Picea mariana); stands of Trembling Aspen, (Populus tremuloides), and Balsam Poplar (Populus balsamifera), are of lesser importance than in the adjacent parkland or mixed-wood boreal forest regions (Rowe 1972). We also considered the “mixed-wood section” of the boreal forest (Rowe 1972) separately from more northern areas. Older stands in the mixed-wood boreal region are composed of White Spruce and Balsam Fir (Abies balsamea) (Rowe 1972), but poplars (Populus spp.) are widespread, particularly in younger stands. The more northern boreal forests are primarily coniferous, with frequent sandy flats, muskegs, and marshes in some areas (Anonymous 1979).

Results

Seventy-nine records of Barred Owls are summarized by 10-year periods (Table 1) and plotted (Figure 1). The species was observed only sporadically up to 1950. The number of observations then increased, and 48 of the 79 observations were made after 1970. Since 1959 the records were most concentrated in the mixed-wood boreal forest northwest of Edmonton (14 observations) and the primarily coniferous foothills and
montane forests west of Calgary and in Jasper National Park (35 observations). Only ten records came from the aspen parkland region and none from the grasslands. The northernmost observation was at the confluence of the Peace and Notikewin Rivers (57°17'N, 117°08'W) and the southermost at Beauvais Lake Provincial Park (49°15'N, 114°06'W). One Barred Owl was reported farther south, about 4 km inside Montana south of Waterton Lakes National Park (T. Hamell, personal communication).

There is some confusion regarding the 1912 Calgary record (Figure 1a), a record which is both early for the province and far south of other early records. Oeming (1955) mentioned a specimen in the Cornell University collection taken at Calgary on 12 February 1912. Salt and Wilk (1966) also mentioned this record, but gave it as near Calgary. Recently W. Bauer at Cornell University (in litt.) could find no record of this specimen in the ornithology collection. This, with the fact that the other pre-1950 observations were in the mixed-wood boreal forest, may cast doubt on the validity of this early record.

Preble's (1941) record for Fort McMurray in 1934 indicated an early presence of the Barred Owl in the mixed-wood boreal forest in Alberta. However, we do not have any data to indicate whether the first appearance of the owl in the province is recent or not. A few recent records are from Fort McMurray or farther north within the mixed-wood region; most of the other recent observations are south of Fort McMurray.

We located eight definite breeding records, six of which were previously unpublished (Table 2). Five were from the coniferous Rocky Mountain and foothills forest regions, and the others from the mixed-wood forest region of the province. Two other records suggested nesting. The record from the Kananaskis area west of Calgary and the most northerly record along the Peace River (Figure 1b) both described pairs of owls restricting their movement to a specific area.

### Table 1. Records of the Barred Owl in Alberta

<table>
<thead>
<tr>
<th>Years</th>
<th>Nearest Locality</th>
<th>Number of owls (% total)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1912-1949</td>
<td>Ft. McMurray, Prairie River, Kvas Creek, Pigeon Lake, Calgary.</td>
<td>5(6)</td>
</tr>
<tr>
<td>1950-1959</td>
<td>Kidney Lake, Calling Lake, Wembly, Flatbush, Fawcett, Tony Creek, Cross Lake, Timeu, Goose Lake (near Ft. Assiniboine), Corbett Creek (2) 1, Edson, Obed Lake (2), Saunders.</td>
<td>15(20)</td>
</tr>
<tr>
<td>1960-1969</td>
<td>Lac La Nonne, Sangudo, Miette River JNP 2, Edmonton (4), Coalspur, Jackfish Lake (near Norburg), Caroline, Calgary.</td>
<td>11(14)</td>
</tr>
<tr>
<td>1980</td>
<td>Jasper, Miette River JNP, Banff, Jumping Pound.</td>
<td>4(5)</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>79(100)</td>
</tr>
</tbody>
</table>

1Numbers in brackets refer to the number of observations at that locality; one bird only if no number given.
2JNP — Jasper National Park; BNP — Banff National Park

### Table 2. Breeding records of the Barred Owl in Alberta

<table>
<thead>
<tr>
<th>Locality</th>
<th>Date</th>
<th>Remarks</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Prairie River</td>
<td>11 July 1949</td>
<td>1 Adult and fledged young</td>
<td>Grant 1966</td>
</tr>
<tr>
<td>Edmonton</td>
<td>28 May 1966</td>
<td>Nest</td>
<td>Jones 1966</td>
</tr>
<tr>
<td>Edmonton</td>
<td>1 April 1968</td>
<td>Nest</td>
<td>E. T. Jones pers. comm.</td>
</tr>
<tr>
<td>Blue Lake</td>
<td>Spring 1976</td>
<td>Nest</td>
<td>J. Salt pers. comm.</td>
</tr>
<tr>
<td>Blue Lake</td>
<td>Spring 1977</td>
<td>Nest</td>
<td>J. Salt pers. comm.</td>
</tr>
<tr>
<td>Miette River JNP</td>
<td>July 1979</td>
<td>1 Adult and fledged young</td>
<td>R. Richards pers. comm.</td>
</tr>
<tr>
<td>Miette River JNP</td>
<td>20 July 1980</td>
<td>1 Adult and fledged young</td>
<td>R. Richards pers. comm.</td>
</tr>
</tbody>
</table>

1Jasper National Park
during the breeding season. In all, 51 observations were made during April through August, and only 19 during fall and winter. The dates of nine observations were not specified.

Discussion

Our data suggest that Barred Owls in Alberta once preferred mixed-wood boreal forest, paralleling their preference for deciduous or mixed transitional forests in eastern North America (Godfrey 1966; Nicholls and Warner 1972; Erskine 1977). In recent times, however, the Alberta birds have apparently adapted to forests of a predominantly coniferous character, as evidenced by the large increase in sightings in the upper foothills and Rocky Mountain regions. There have also been two sightings of Barred Owls in the primarily coniferous northern boreal forest. Rand (1944) observed one bird along the Alaska highway in northern British Columbia, as did A. J. Erskine (personal communication) in 1974.

Our comparison of the early records of this species to records made in the last 20 years shows an increased number of sightings in western Alberta south of Grande Prairie. We suggest this increase and the recent appearance of this species in northern Idaho and northwestern Montana (Shea 1974; Taylor and Forsman 1976) are a related phenomenon, resulting in part from the suggested increased tolerance of conif-

Figure 1. Distribution of sightings of Barred Owls in Alberta in relation to vegetation zones. a. 1912-1959; b. 1960-1980. Heavy stippling represents the coniferous boreal forest region. Diagonal lines depict the montane-foothill region. Fine stippling represents the aspen parkland and vertical lines indicate the grassland region. Unmarked areas indicate mixed-wood boreal forest.
erous forest, and that this phenomenon represents both a range expansion and an increase in numbers within its previous range. Prior to 1960 there was only one record in southwestern Alberta, the unverified record from Calgary.

It is perhaps unusual that we found so few records of this species in the aspen parkland. While this may result in part from extensive agricultural modification of the parkland region in Alberta, it could also be related to the physical characteristics of the parkland aspen forests. Most aspens are appreciably shorter than eastern deciduous hardwoods, and stands of well-developed mature trees are rare. Consequently, few aspen trees provide nest cavities for Barred Owls. In addition, the high density of Great Horned Owls (Bubo virginianus) in the parkland region (Flack 1976) may have a negative effect on Barred Owl populations. Bent (1938) mentioned that Barred Owls are preyed upon by Great Horned Owls.

Our compilation (Table 1) shows a dramatic increase in the frequency of sightings of Barred Owls in the last decade. Salt and Wilk (1966) remarked on the scarcity of records in Alberta, although the bird was believed to breed in small numbers in the forested regions of western and northern Alberta. The first provincial breeding record of the species was not made until 1949 (Grant 1966) and the second not until 1966 (Jones 1966). Salt and Salt (1976) defined the range more precisely, designating the owl as “a scarce nester probably over most of central and western Alberta”. To date only eight definite nestings have been recorded.

We cannot rule out the effect an increased number of observers has had on the number of observations in recent years. However, appreciable ornithological activity occurred prior to 1960 in many areas where the species was previously only sporadically recorded, particularly the foothills and montane areas (cf. Macoun and Macoun 1909; Stansell 1909; Randall 1933; Cowan 1955). In addition, the intensive and well-publicized study of owls in Alberta by Oeming (1955, 1957) did not generate as many Barred Owl records as it did for some other rare species. As Grant (1966: 44) pointed out, many of the early Alberta records were of owls taken in muskrat and weasel traps: “it seems hardly credible that if this species were equally numerous in the preceding century while the fur trade was at its peak not one was known to have been captured in all the scores of thousands of weasel traps set out during that period”.

There seems no question that the Barred Owl is still a rare species throughout most of Alberta. However, in light of the increased number of observations in the forests of the mountains and foothills, we feel this owl is increasing in numbers and distribution within the province.

Acknowledgments
We extend our thanks to T. Hamell, G. Holroyd, E. T. Jones, N. Kondla, J. Podlubny, R. Richards, J. Salt, T. W. Thorin, K. Van Tighem, and the many other naturalists who provided us with their observations. R. Skowronski assisted in searching the literature. C. S. Houston, R. S. Kidd, and C. E. Tull provided helpful comments on the manuscript. This is Natural History Contribution no. 61 from the Provincial Museum of Alberta.

Literature Cited

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Habitats of Sandhill Cranes in the Southern Hudson Bay Lowland, Ontario

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During a 1979 reconnaissance of the southern Hudson Bay Lowland (50° to 52° N, 79° 30' to 86° W), 128 Sandhill Cranes were observed. Based on observations of 10 flightless young, or inference of breeding from adult bird behavior, nine breeding sites are reported. The vegetation at these sites consisted of mixtures of open graminoid, open low shrub and treed low shrub physiognomic groups, in proportions characteristic of the region. In comparison with the habitat occupied by non-breeding cranes, breeding birds appeared to prefer sites with less open graminoid elements, presumably in order to optimize accessible cover for flightless young.

Key Words: Sandhill Crane, Grus canadensis, Hudson Bay Lowland, peatland habitat, breeding records, Ontario.

Sandhill Cranes (Grus canadensis) have been termed "uncommon local summer residents" of the Hudson Bay Lowland and elsewhere in Ontario (James et al. 1976). P. Tebbel (personal communication, 1980, Department of Zoology, University of Western Ontario) reported substantial breeding populations in north central Ontario from Sault Ste. Marie to Spanishola, where they use many wetland types, from large treed bogs and low shrub fens to open cattail marsh, with some preference for secluded, undisturbed bogs and marshes away from the Lake Huron shoreline. Lumsden (1971) reviewed the status of Sandhill Cranes in northern Ontario and reported eight breeding locations, seven of these within the southern Hudson Bay Lowland (Figure 1). Lumsden noted that summer reports of cranes, like Canada Geese, were almost exclusively from areas of postglacial marine submergence or from postglacial lake beds. The maximum limits of the postglacial Tyrrell Sea closely approximate the contact line between the Precambrian Shield and the Paleozoic Lowland (Figure 1; Craig 1968; Sanford et al. 1968).

Methods

A helicopter reconnaissance of the area from 50° to 52° N, and 79° 30' to 86° W, 7-28 July 1979, involved ground-truthing and photography for mapping of surficial geomorphology. This necessitated the development of vegetation mapping units and a wetland classification to describe the vegetation dominating the region. Within this area (1:250 000 mapsheets 42N-P, 42I-K, and parts of 32L and M), approximately 200 sites were visited in order to record data on wetland vegetation. Sites were preselected from aerial photographs to reflect both representative and unusual landscape features. Approximately 16 000 km

were flown, at altitudes generally less than 350 m above ground level. Cranes were actively sought and recorded during this reconnaissance.

The habitats noted at breeding sites were described following the wetland classification of Jeglum et al. (1974, 1977), as modified for the Hudson Bay Lowland. The "formations" mentioned are bogs (peat pH < 5.0) and fens (pH > 5.0), the differences between which are discussed in detail elsewhere (ibid.). The "subformations" are open (< 10% cover by trees > 135 cm tall) or treed (10-40% cover by trees > 135 cm tall). The "physiognomic groups" are graminoid (conspicuous grass/sedge layer > 8% cover, shrubs < 135 cm tall < 10% cover) and low shrub (shrubs < 135 cm tall > 10% cover).

Observations

One hundred and twenty-eight Sandhill Cranes, including 10 flightless young, were recorded from the air or ground (Figure 1). Six breeding sites located were based on observations of flightless young. Three other breeding sites were inferred from the distraction displays by adult birds. (Photos of flightless young at sites A, C, D, G and H have been submitted to the Ontario Nest Records Scheme, Ornithology Department, Royal Ontario Museum.) The habitat descriptions and bird observations at breeding sites proceed from east to west (Figure 1).

A. 50° 10'N, 81° 35'W; east of Coral Rapids (19 July).

Two adults showing distraction display, two flightless young.

Habitat: Open low shrub bog complex; treed low shrub bog 'islands' ca. 10%, and open graminoid bog pools < 5%. Slight 'hummock-hollow' patterning; hummocks with increased low shrub cover and hollows with increased grami-
noid cover. Open low shrub bog (pH 3.9, depth to water 5 to 30 cm, peak depth 3.5 m over silty till) dominated by Sphagnum nemoreum (95% cover), Chamaedaphne calyculata (20%), Erio- phorum spissum (10%), Carex oligosperma (5%), Sphagnum fuscum (5%), Picea mariana (5%), Rubus chamaemorus (3%), Vaccinium oxycoccus (2%). Treed low shrub bog 'islands' in this region predictably consist of: Sphagnum fuscum (80%+), S. magellanicum or S. fallax (< 20%), Chamaedaphne calyculata (25-60%), Picea mariana (15-25%), Kalmia angustifolia (0-15%), Ledum groenlandicum (0-35%); usually with Cladina stellaris and C. rangiferina (0-20%) increasing with the elevation of 'island' above surrounding area.

B. 50° 30'N, 82° 17'W; north of junction of Missinaibi and Rabbit Rivers (15 July). One adult showing distraction display; young assumed.

Habitat: Open bog complex; ca. 15% open graminoid bog 'hollows' (Sphagnum fuscum dominant), ca. 80% open low shrub bog 'hummocks' (S. fuscum – Chamaedaphne calyculata), with some treed graminoid and treed low shrub bog 'islands' and open bog pool patterning.

C. 51° 08'N, 82°15'W; north of junction of Kwataboahegan and Agwasuk Rivers (26 July). Two adults showing distraction display; two flightless young.

Habitat: Open fen complex; ca. 40% treed low shrub fen (Larix laricina > 135 cm 12% cover, shrub layer dominated by Betula pumila var. glandulifera, Rubus acaulis), ca. 50% open graminoid fen (Scirpus cespitosus, Carex exilis), with some treed low shrub bog 'islands'; no patterned pond component.

D. 51° 50'N, 82° 37'W; southeast of Fishing Creek Island (27 July). Two adults; two flightless young.

Habitat: Open graminoid fen and fen pools (Carex limosa, Menyanthes trifoliata dominant) ca. 70% (pools ca. 25%), ribbed with open low shrub fen (25%), and with ca. 5% treed low shrub bog 'islands'.

E. 50° 54'N, 83° 38'W; east end of Pledger Lake (7 July). Two adult cranes showing distraction display; young assumed.

Habitat: Willow-alder-leatherleaf zone along Cheepay River mouth.

F. 50° 52'N, 83° 40'W; south of Pledger Lake (7 July). Two adult cranes showing distraction display; young assumed. Cranes approached within 40 m of ground party, calling rapidly and alternately, with 'cranks' in sets of three. The lighter-coloured (greyish), larger bird (male) led and finished the calls, and the smaller red-brown bird (female) provided the middle 'crank' of each set, at a higher pitch. Approaching each other more closely, their calls came close to unison. Vocalization was part of a distraction display, attempting to lead ground party.

Habitat: Open bog complex; open low shrub bog 'hummocks' (i) ca. 70%, and open graminoid bog 'hollows' (ii) ca. 30%.

i) Open low shrub bog (pH 3.7, depth to water 0 to 30 cm, peak depth 3.5 m over marine silt) dominated by Sphagnum nemoreum (70% cover), S. fuscum (20%), Chamaedaphne calyculata (11%), Picea mariana (10%), Cladina stellaris/rangiferina (6%), Rubus chamaemorus (5%), Scirpus cespitosus (2%).

ii) Open graminoid bog (pH 3.9, depth to water 0 to 10 cm, peak depth 3.5 m over marine silt) dominated by Sphagnum nemoreum (95% cover), Eriothorurn spissum (30%), Chamaedaphne calyculata (6%), Carex oligosperma (5%), Kalmia angustifolia (3%). Bog pool component < 3%.

G. 50° 14'N, 84° 02'W; upper Squirrel River (13 July). One adult showing distraction display; one flightless young.

Habitat: Patterned fen complex; open graminoid fen and fen pools (i) ca. 50%, and treed graminoid fen 'ribs' (ii) ca. 50%.

i) Open graminoid fen and fen pools (pH 5.6, water depth 0 to 40 cm in pools, peak depth > 3.85 m) dominated by Cladopodiella fluitans (80% cover), Scorpidium scorpioides (15%), Scheuchzeria palustris (10%), Carex chordonhiza (8%), Menyanthes trifoliata (4%).

ii) Treed graminoid fen (pH 5.5, depth to water 0 to 40 cm, peak depth 3.8 m over marine silt) dominated by Sphagnum rubellum (30% cover), S. magellanicum (30%), S. fuscum (20%), Larix laricina (15%), Tomentypnum nitens (10%), Drepanocladus sp. (10%), Carex limosa (5%), Chamaedaphne calyculata (5%), Scirpus hudsonianus (5%), S. cespitosus (5%), Smilacina trifolia (3%), Betula pumila var. glandulifera (2%), Ledum groenlandicum (2%); also notable in this rich fen: Aronia prunifolia, Platanthera lacera, Pogonia ophioglossoides, Thelypteris palustris, and 22 other vascular plant species.

H. 50° 06'N, 84° 47'W; northern Rowlandson Twp. (13 July). One adult showing distraction display; one flightless young.

Habitat: Open low shrub fen complex; open low shrub 'hummocks' ca. 50% (dominated by Kalmia angustifolia, Chamaedaphne calyu-
Sandhill Cranes, numbers seen.

Breeding sites, number of flightless young.

Breeding sites reported by Lumsden (1971).

Figure 1. Sandhill Cranes in the southern James Bay Lowland, 1979.
_lata, Betula pumila_ var. _glandulifera, Larix laricina_), and open graminoid fen 'hollows' ca. 50%; minimal pond component.

1. 50°18'N, 84°55'W; north of Pembina Island (12 July). Two adults showing distraction display; two flightless young.

**Habitat:** Patterned open bog complex; open low shrub bog ca. 35%, and open graminoid bog ca. 65%, the latter with bog pools.

**Discussion**

The flightless young were assumed to be four to seven weeks old, based on hatching dates reported by Lumsden (1971) for this area, and the habitats in which they were observed were considered to be their breeding habitats. Previously observed nesting habitats in the southern Lowland (Lumsden 1971) are comparable to those noted above, and no birds, with or without young, were observed in the dominantly treed habitats commonly bounding large wetland systems, where adult birds would have been conspicuous. When flightless young and adult birds were distracted on the ground or by helicopter, the adults invariably showed distraction display, rushing about erratically with spread, drooping wings, while the flightless young ran directly towards shrub cover.

Walkinshaw (1949) reported Sandhill Cranes to be omnivorous, eating cranberries, 'heathberries', blueberries, sedge tubers, mice, lemmings, grasshoppers and other insects. He reported that nesting birds regularly left acid bog nesting areas in northern Michigan to feed in nearby upland sites, including marsh edges, streams and meadows. Omnivory and feeding mobility suggest that diet may not be the critical factor in breeding habitat preference.

There was no apparent preference for either bog or fen systems. The consistent habitat preference was for open systems, with patterning ('ribs', 'hummock-hollows', 'islands', 'pondings') of open graminoid, open low shrub or treed low shrub phases. These systems varied in their percentage composition of particular physiognomic groups but, as homogenous vegetation mapping units, they were never smaller than ca. 100 ha and several were much larger than 1000 ha. They combined open graminoid/pond communities (offering available food, take-off and landing space, and optimal visibility) and treed/low shrub communities (offering accessible cover for flightless young).

Averaging the estimated proportions of physiognomic groups within peatland systems in which breeding activity was observed or inferred suggests a general habitat mix: open graminoid units 42% cover (5–70%), open low shrub units 43% (0–85%), and treed units 14% (0–50%). An open graminoid phase occurred in all sites reported; ponding patterns usually accompanied this phase.

Data on the physiognomic groups making up the peatland systems within which non-breeding cranes were noted were collected for 8 sites in detail, 10 in general, for a total of 18 sites. The averages of physiognomic groups differed from those outlined above: open graminoid units made up 63% cover (20–90%), open low shrub units 18% (10–50%), and treed units 19% (0–80%). These sites differed from breeding sites in that open units tended to lack strong patterning of low shrub phases. These data suggest that areas with more cover (open low shrub and treed) are preferred as breeding habitat.

The preference by non-breeding birds for more open graminoid sites was also suggested by observations of larger groups of non-breeding birds: a) 10 cranes in a very large and unpatterned graminoid bog (Figure 1; 51°37'N, 82°58'W), and b) 9 and 15 cranes in coastal meadows near the mouth of the Moose River.

Cattail marsh, confined basin bogs and other types of open temperate wetlands are rare in the southern Hudson Bay Lowland, but are more common on the Shield to the south and west, where only one crane observation was made (Figure 1). The types of peatland systems described above as breeding habitats dominate the southern Hudson Bay Lowland (Sims et al. 1979; Cowell et al. 1978; Raveling and Lumsden 1977). The breeding habitats are characteristic open peatland systems of this region, with an apparent preference by breeding cranes for sites with vegetation patterns offering accessible cover for flightless young. Sandhill Cranes are regular though uncommon summer residents of the Hudson Bay Lowland, but are locally common in the southern James Bay portion of the Lowland.

**Acknowledgments**

The reconnaissance of this area, of which these notes were a by-product, was part of mapping programmes of the Ontario Centre for Remote Sensing. I particularly thank S. Pala and A. N. Boissonneau for sharing in these observations. I also thank P. Tebbel of University of Western Ontario for his interesting correspondence, and C. Manville of Royal Ontario Museum for assisting in determination of _Sphagnum_ collections. H. G. Lumsden (Ontario Ministry of Natural Resources), R. D. James (Royal Ontario Museum) and R. K. Ross (Canadian Wildlife Service) offered valuable advice on preliminary drafts of this note.

**Literature Cited**


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Populations of Breeding Birds at Alexandra Fjord, Ellesmere Island, Northwest Territories, Compared with Other Arctic Localities

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Populations of breeding birds of a 1200 ha high Arctic oasis at Alexandra Fjord, Ellesmere Island, N.W.T. (78°53'N, 75°55'W) were 153 pairs (12.8 pr/100 ha) in 1980, and 164 pairs (13.7 pr/100 ha) in 1981. An average of 77% of the breeding birds were Snow Buntings (Plectrophenax nivalis); Baird's Sandpipers (Calclus lapponicus), Hoary Redpolls (Carduelis hornemanni), Lapland Longspurs (Calcarius lapponicus), and Arctic Terns (Sterna paradisaea); smaller numbers of five other species made up the rest. The total breeding bird density was similar to those reported for other high Arctic oases, but much lower than for most low Arctic localities, where productivity is higher.

Key Words: Breeding bird population, high Arctic oasis, tundra, Ellesmere Island, Snow Buntings, Plectrophenax nivalis.

There are few quantitative assessments of population densities of Arctic breeding birds. Such data are basic to the understanding of their ecology, and to preservation of their habitats, which may be modified by the activities of man. Many species of high Arctic wildlife occur in relative abundance only in certain localized sites of high primary production and diversity (oases) amidst large regions of unproductive Arctic semi-desert or desert (e.g. Soper 1940; Bliss 1977). The present report describes the breeding populations of birds at a high Arctic oasis on central Ellesmere Island, N.W.T., and compares them with the few other quantitative studies from the Canadian Arctic.

Study Area

The study area, at 78°53'N, 75°55'W, was adjacent to the southern coast of Alexandra Fjord, 154 km SE of Eureka. It comprised the whole of a roughly triangular peri-glacial outwash plain, plus the bases of its adjacent talus slopes, approximately 12 km² in area. This lowland oasis is bordered at the southern apex by two glacial tongues, on the west and east by steep talus slopes or cliffs ca. 500 m in height, and on the north by the fjord. The topography is essentially flat except for frequent erratic boulders, but gently rising from the sea to the glaciers.

This lowland includes four plant communities. The first, ca. 49% of the study area, is a complex of mesic Cassiope tetragona — dominated heath — dwarf shrub — cushion plant communities. The second type, ca. 37%, was xeric lichen — dominated rocky outcrops or talus slopes. Mesic microsites within this community group were dominated by vascular plants. The third type, ca. 9%, was wet to xeric (depending on the time of year) river bed or river outwash plain, dominated by a herbaceous plant community. The fourth community, ca. 5%, was a complex of relatively productive mesic to wet sedge-dominated meadows. Also present, although making up an insignificant fraction of the area, were a number of small freshwater ponds near the coast. The study area was described in more detail in Svoboda and Freedman (1980) and Freedman and Svoboda (1981).

Methods

All 1980 data were gathered between 30 June and 21 July. Intensive coverage up to 12 July comprised some 125 man-hours, with only incidental observations subsequently. The 1981 data were gathered between 20 June and 20 July, with intensive coverage totalling 169 hours. Most censusing occurred between 09:00 and 02:00 EDT, during continuous daylight.

Sub-sections of the study area, defined by river courses and topography, were walked so as to ensure thorough coverage. At least three intensive surveys were made of all sub-sections, with up to six coverages of areas where breeding densities were particularly high. Confirmed pairs were based on nest locations. Probable territories were based on clusters of at least three observations, particularly of singing males, or of defensive posturings. This modification of the spot-map method (Williams 1936; Robbins 1978) is appropriate in open arctic habitats, where birds can be detected at great distances.

Observations and Discussion

The numbers of breeding birds are summarized in Table 1. Snow Buntings were by far the most common species, accounting for some 77% of the breeding pairs.
### Table 1. Bird territories during the breeding seasons of 1980 and 1981 on a 12 km² high Arctic lowland oasis at Alexandra Fjord, Ellesmere Island

<table>
<thead>
<tr>
<th>Species</th>
<th>1980*</th>
<th>1981</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Confirmed Territories</td>
<td>Probable Territories</td>
</tr>
<tr>
<td>Snow Goose (Chen caerulescens)</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Oldsquaw (Clangula hyemalis)</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Rock Ptarmigan (Lagopus mutius)</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Red Knot (Calidris canutus)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Baird's Sandpiper (Calidris bairdii)</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td>Parasitic Jaeger (Stercorarius parasiticus)</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Arctic Tern (Sterna paradisaea)</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Hoary Redpoll (Carduelis hornemanni)</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Lapland Longspur (Calcarius lapponicus)</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Snow Bunting (Plectrophenax nivalis)</td>
<td>47</td>
<td>70</td>
</tr>
<tr>
<td><strong>TOTAL</strong></td>
<td><strong>66</strong></td>
<td><strong>87</strong></td>
</tr>
</tbody>
</table>

*the 1980 census data were previously reported (Freedman and Svoboda 1981).

Fourteen species occurred on the lowland but showed no evidence of breeding: Red-throated Loon (Gavia stellata), Common Eider (Somateria mollissima), King Eider (S. spectabilis), Gyrfalcon (Falco rusticolus), Ringed Plover (Charadrius hiaticula), Ruddy Turnstone (Arenaria interpres), Purple Sandpiper (Calidris maritima), Long-tailed Jaeger (Stercorarius longicaudatus), Glaucous Gull (Larus hyperboreus), Thayer's Gull (L. thayeri), Ivory Gull (Pagophila eburnea), Snowy Owl (Nyctea scandinaca), Horned Lark (Eremophila alpestris), and Common Raven (Corvus corax). Of these, only Common Eider and Glaucous Gull were regular.

The total density of breeding birds at Alexandra Fjord averaged 13.2 pr/100 ha. This was intermediate among densities from five studies in the Canadian high Arctic islands (1.9 to 33 pr/100 ha; sites 11-15 in Table 2). These breeding densities were much lower than in the low Arctic, particularly the western Arctic, where productive plant communities are much more widespread. The mean (± S.D.) breeding density for the Mackenzie Delta, northern Yukon Territory, or Alaska North Slope communities (sites 5–10 in Table 2, all 69°N to 71°N) was 136 ± 52 pr/100 ha, compared with only 13 ± 12 pr/100 ha for the high Arctic sites. These trends are not simply linked to latitude; note the low breeding densities at sites 2 and 3 in Table 2, at 63°N and 64°N respectively. Rather, the breeding densities generally reflect the lushness of vegetation and the primary productivities of the censused habitats, which in turn reflect regional meso- and microclimate, and possibly local topography or hydrology.

Most species had similar breeding densities in both census years. The initiation of the growing season was considerably earlier in 1981 than in 1980. The 1981 snowmelt was ca 90% complete by mid-May, compared to mid-June in 1980. Breeding phenology of some species was somewhat advanced in 1981; the first Snow Bunting fledglings were noted on 6 July, as compared with 15 July in 1980.

Snow Buntings nested throughout the lowland. About half of the nests occurred in the lowland itself. The rest of the Snow Bunting nests were located in the
Table 2. A summary of the literature relevant to total breeding bird populations of North American tundra communities. Censuses are arranged in order of increasing latitude.

<table>
<thead>
<tr>
<th>Latitude °N</th>
<th>Year</th>
<th>Area (ha)</th>
<th>Habitat</th>
<th>Density (pairs/100 ha)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Chesterfield Inlet, N.W.T.</td>
<td>63</td>
<td>1950</td>
<td>1025</td>
<td>Rock, sedge, lichen, heath</td>
<td>60</td>
</tr>
<tr>
<td>3. Foxe Peninsula, N.W.T.</td>
<td>64</td>
<td>1955</td>
<td>5120</td>
<td>Coastal, little vegetation</td>
<td>10</td>
</tr>
<tr>
<td>4. Bowman Bay, N.W.T. a)</td>
<td>65</td>
<td>1929</td>
<td>256</td>
<td>Grass, with rocks</td>
<td>55</td>
</tr>
<tr>
<td>b)</td>
<td>65</td>
<td>1929</td>
<td>320</td>
<td>Grass, with rocks, near river</td>
<td>165</td>
</tr>
<tr>
<td>c)</td>
<td>65</td>
<td>1929</td>
<td>256</td>
<td>Grass, with rocks, near river</td>
<td>77</td>
</tr>
<tr>
<td>b)</td>
<td>69</td>
<td>1973</td>
<td>25</td>
<td>River escarpment with floodplain and upland</td>
<td>207</td>
</tr>
<tr>
<td>c)</td>
<td>69</td>
<td>1973</td>
<td>25</td>
<td>River floodplain with sedge and low willow</td>
<td>119</td>
</tr>
<tr>
<td>b)</td>
<td>69</td>
<td>1972</td>
<td>31.6</td>
<td>Sedge, grass meadows</td>
<td>155</td>
</tr>
<tr>
<td>7. Prudhoe Bay, Alaska</td>
<td>69</td>
<td>1979</td>
<td>100</td>
<td>Inland coastal tundra</td>
<td>72</td>
</tr>
<tr>
<td>13. Isachsen, N.W.T.</td>
<td>79</td>
<td>1960</td>
<td>3800</td>
<td>Largely unvegetated</td>
<td>1.9</td>
</tr>
<tr>
<td>15. Lake Hazen, N.W.T.</td>
<td>82</td>
<td>1962</td>
<td>2227</td>
<td>Largely unvegetated</td>
<td>4.9</td>
</tr>
</tbody>
</table>
lower talus slopes of the cliffs that surround the lowland. Of the 131 nests that were located, 46% were in natural cavities or in old Collared Lemming (Dicrostonyx torquatus) burrows at the bases of erratic boulders or rocky outcrops, 24% in earthen cavities formed by slumping benches along the streams, and 30% in cavities in the rocky talus of the surrounding cliffs. Observations of flight patterns indicated that these latter birds foraged in the lowland plant communities. Very few Snow Bunting or other birds were observed higher on the talus or cliffs, or on the xeric desert plateaus that surround the lowland. Thus, the populations censused in this study were highly discrete, and not typical for the region as a whole. All of the Snow Bunting nests which could be closely examined had obviously been used in previous years. Follow-up studies at this or similar locales could examine both the nest site and lowland philopatry of the Snow Bunting populations, via observations of banded individuals.

The Snow Bunting density (averaging 10.2 pt/100 ha) was higher than generally observed for this species (Table 3). Other species had breeding densities similar to those reported from other high Arctic locations (Table 4). Baird's Sandpipers nested on gravelly raised beach ridges or river terraces, but foraged widely in mesic tundra communities. Hoary Redpolls concentrated their activities on or near talus slopes, and probably also nested there. Lapland Longspur activities were concentrated in mesic dwarf shrub-heath-cushion plant communities, usually near streams or rivers. Arctic Terns nested on shingle beaches along the coast. The Snow Goose nests in 1980 were widely scattered, one on a rocky coastal beach, another in a thermokarst depression along a small stream, and the third in talus at the base of a cliff. The Oldsquaw nests were all within ca. 0.5 km of the coast, and were located in mesic tundra, near coastal ponds or small streams. Although there were

### Table 3. Breeding densities of Snow Bunting in Arctic or Alpine sites

<table>
<thead>
<tr>
<th>Site</th>
<th>Latitude °N</th>
<th>Breeding density (pairs/100 ha)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Finse (Norway, Alpine)</td>
<td>60</td>
<td>3.5</td>
<td>Lien et al. 1970</td>
</tr>
<tr>
<td>Nedal (Norway, Alpine)</td>
<td>63</td>
<td>28</td>
<td>Moksnes 1973</td>
</tr>
<tr>
<td>Frobisher Bay</td>
<td>63</td>
<td>7</td>
<td>McLaren 1965</td>
</tr>
<tr>
<td>Chesterfield Inlet (island)</td>
<td>63</td>
<td>5.8</td>
<td>Höhn 1968</td>
</tr>
<tr>
<td>Chesterfield Inlet (mainland)</td>
<td>63</td>
<td>5</td>
<td>Savile 1951</td>
</tr>
<tr>
<td>Foxe Peninsula</td>
<td>64</td>
<td>1.5</td>
<td>Macpherson and McLaren 1959</td>
</tr>
<tr>
<td>Bowman Bay</td>
<td>65</td>
<td>7</td>
<td>Soper 1949</td>
</tr>
<tr>
<td>Bylot Island</td>
<td>73</td>
<td>3</td>
<td>Van Tyne and Drury 1959</td>
</tr>
<tr>
<td>Truelove Lowland</td>
<td>74</td>
<td>3.9</td>
<td>Patie 1977</td>
</tr>
<tr>
<td>Ellef Ringnes Island</td>
<td>79</td>
<td>1.2</td>
<td>Savile 1961</td>
</tr>
<tr>
<td>Alexandra Fjord</td>
<td>79</td>
<td>9.8</td>
<td>This paper</td>
</tr>
<tr>
<td>1980</td>
<td>79</td>
<td>10.6</td>
<td></td>
</tr>
<tr>
<td>Lake Hazen</td>
<td>82</td>
<td>1.1</td>
<td>Savile and Oliver 1964</td>
</tr>
</tbody>
</table>

### Table 4. Estimate of breeding bird populations at various locations in the Canadian high Arctic. Data concerning several species have been omitted from certain summaries. Data are breeding pairs per 100 hectares

<table>
<thead>
<tr>
<th>Species</th>
<th>Bylot Island</th>
<th>Truelove Lowland</th>
<th>Isachsen</th>
<th>Alexandra Fjord</th>
<th>Lake Hazen</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>73°N</td>
<td>74°N</td>
<td>79°N</td>
<td>79°N</td>
<td>82°N</td>
</tr>
<tr>
<td>Snow Goose</td>
<td>2</td>
<td>0.3</td>
<td>—</td>
<td>0.3</td>
<td>0.05</td>
</tr>
<tr>
<td>Oldsquaw</td>
<td>—</td>
<td>2.7</td>
<td>—</td>
<td>0.3</td>
<td>0.3</td>
</tr>
<tr>
<td>Rock Ptarmigan</td>
<td>—</td>
<td>0.02</td>
<td>0.1</td>
<td>0.1</td>
<td>0.3</td>
</tr>
<tr>
<td>Baird's Sandpiper</td>
<td>10</td>
<td>0.5</td>
<td>0.03</td>
<td>1.0</td>
<td>0.8</td>
</tr>
<tr>
<td>Parasitic Jaeger</td>
<td>—</td>
<td>0.1</td>
<td>—</td>
<td>0.1</td>
<td>—</td>
</tr>
<tr>
<td>Long-tailed Jaeger</td>
<td>—</td>
<td>0.5</td>
<td>0.2</td>
<td>—</td>
<td>0.3</td>
</tr>
<tr>
<td>Arctic Tern</td>
<td>7</td>
<td>0.8</td>
<td>—</td>
<td>0.3</td>
<td>0.6</td>
</tr>
<tr>
<td>Hoary Redpoll</td>
<td>—</td>
<td>—</td>
<td>0.5</td>
<td>0.6</td>
<td>0.5</td>
</tr>
<tr>
<td>Lapland Longspur</td>
<td>10</td>
<td>0.9</td>
<td>—</td>
<td>0.5</td>
<td>0.4</td>
</tr>
<tr>
<td>Snow Bunting</td>
<td>3</td>
<td>3.9</td>
<td>1.2</td>
<td>9.8</td>
<td>1.1</td>
</tr>
</tbody>
</table>

1Van Tyne and Drury 1959.
2Calculated after Patie 1977.
3Savile 1961.
4This paper.
5Savile and Oliver 1964.
several sightings of pairs of Long-tailed Jaegers, no
nesting attempts were observed, likely due to the very
low Collared Lemming abundance in 1980 and 1981
Clutch sizes in 1981 averaged (± S. D.) 5.8 ± 1.1
(n = 55) for Snow Buntings, 6.5 ± 1.1 for two Old-
squaw nests, 8.5 ± 2.5 for two Rock Ptarmigan nests,
4.0 ± 0.0 for four Baird’s Sandpiper nests, 2.0 for one
Parasitic Jaeger nest, and 2.0 ± 0.0 for six Arctic Tern
nests.

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Alexandra Fjord.

Literature cited
Bliss, L. C. 1977. Introduction. pp. 1–12 in: Truelove Low-
land, Devon Island, Canada: A High Arctic Ecosystem.
Edited by L. C. Bliss. University of Alberta Press. Edmon-
ton. 714 pp.
Progress Notes, No. 59. 24 pp.
1974. Disturbance studies of terrestrial breeding bird
populations: Firth River, Yukon Territory, June 1972.
Effects of gas compressor noise simulator disturbance to
 terrestrial breeding birds, Babbage River, Yukon Terri-
 tory, June 1972. Arctic Gas Biological Report Series,
Höhn, E. O. 1968. The birds of the Chesterfield Inlet, Dis-
 trict of Keewatin, N.W.T., Canada. Canadian Field-
Naturalist 82: 244–262.
coastal tundra. American Birds 34: 82.
1970. Quantitative bird surveys in high mountain habi-
tats, Finse, south Norway, 1967–68. Nyt Magasin fur
Macpherson, A. H. and I. A. McLaren. 1959. Notes on
birds of southern Foxe Peninsula, Baffin Island, North-
Field Notes 19: 620–621.
Moksnes, A. 1973. Quantitative surveys of the breeding
bird populations in some subalpine and alpine habitats in
the Nedaral in central Norway (1967–71). Norwegian
Myers, J. P., B. J. McCaffery, S. T. Gellman, F. A. Petelka,
and III. American Birds 34: 82–83.
Owens, R. A. 1974. Environmental Program, McKenzien
Delta, N. W. T., Canada, Volume 4, Birds. Appendix
Oil Ltd., Gulf Oil Canada Ltd., Shell Canada Ltd., Cana-
Pattie, D. L. 1977. Population levels and bioenergetics of
Arctic birds on Truelove Lowland. pp. 413–436 in: True-
love Lowland, Devon Island, Canada: A High Arctic
Ecosystem. Edited by L. C. Bliss. The University of
Richardson, W. J. and M. A. Gollop. 1974. Populations of
birds at Babbage River, Y. T., during the breeding season,
1973: a monitoring and methodological study. Arctic Gas
Erskine (1976).
142–163 in: Management of Southern Forests for Non-
game Birds. USDA Forest Service General Technical
Savile, D. B. O. 1951. Bird observations at Chesterfield
Inlet, Keewatin, in 1950. Canadian Field-Naturalist 65:
Savile, D. B. O. 1961. Bird and mammal observations on
Ellef Ringnes Island in 1960. National History Paper No. 9,
Savile, D. B. O. and D. R. Oliver. 1964. Bird and mammal
observations at Hazen Camp, northern Ellesmere Island,
Soper, J. D. 1940. Local distribution of eastern Canadian
high Arctic lowland oasis. Alexandra Fjord, Ellesmere
of the Departments of Botany, University of Toronto and
Dalhousie University. 109 pp.
Van Tyne, J., and W. H. Drury, Jr. 1959. The birds of
of Zoology, University of Michigan, no. 615. 37 pp.
Williams, A. B. 1936. The composition and dynamics of a
beech-maple climax community. Ecological Monographs
6: 317–408.
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The Dune-Ridge Forest, Delta Marsh, Manitoba: Overstory Vegetation and Soil Patterns

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Overstory composition and structure were determined for a 2-km segment of the dune-ridge forest separating Lake Manitoba from Delta Marsh, Manitoba. The major pattern in the ridge forest was characterized by a decrease in *Acer negundo* and *Fraxinus pennsylvanica* abundances and an increase in *Salix interior* abundance along a slight topographic gradient from lake to marsh (i.e., from north to south). A secondary pattern was related to the pattern of abundance of *Salix amygdaloides*, the quantitative dominant. Canonical correlation and multiple regression analyses of species abundance data and data for a set of soil variables showed significant relationships between the patterns of abundance of *A. negundo*, *F. pennsylvanica*, and *S. interior*, and variation in the soil variables. *Salix amygdaloides* abundance could not be explained by variation in the set of soil variables.

Key Words: Delta Marsh, Manitoba, *Acer negundo*, *Fraxinus pennsylvanica*, *Salix amygdaloides*, *Salix interior*, dune forest, gradient analysis, species-soil relationships, overstory vegetation.

The dune-ridge forest that extends for 25 km along the southern shore of Lake Manitoba, separating the lake from Delta Marsh, is currently the focus of investigations into the ecology of a community of densely nesting passerine bird species (see Goossen 1978; Busby and Sealy 1979; Sealy 1980a, 1980b; MacKenzie and Sealy 1981; MacKenzie, Sealy and Sutherland 1982). The long-term and intensive nature of this research programme, emphasizing bird-habitat relationships, has underlined the necessity to document the composition and structure of the vegetation of the ridge forest, heretofore treated in only a survey fashion (see Löve and Löve 1954; Walker 1959, 1965).

The objectives of the present study are three-fold: 1) to provide a general description of the segment of the ridge forest that constitutes the primary study area; 2) to document the patterns of abundance of the quantitatively important tree species; 3) to relate these patterns to patterns of variation in selected soil variables.

Study Area

The study area is a 2-km segment of the ridge forest that lies approximately 5 km west of the village of Delta (50° 11'N, 98° 19'W) (see Sealy 1980b for a map and photograph of the study area). A 30-year summary (1941-1970) for the Portage La Prairie weather station (49° 58'N, 98° 18'W) gives the following normals: annual mean temperature of 2.7°C, with January averaging -17.7°C and July 20.2°C; average number of frost-free days 177; mean annual precipitation 47 cm, 60% of which occurs from May through August (Environment Canada 1973). Mean July temperature of 20.3°C and precipitation for the period May-August of 23.2 cm on the study area for years 1974-1976 (Goossen 1978) suggest that for the growing season, at least, the Portage La Prairie normals are representative of the climate on the study area. The ridge receives additional moisture in the form of large snow drifts from snow blowing off Lake Manitoba. The lake can also be expected to have some moderating influence on temperature.

The ridge is a remnant of glacial Lake Agassiz, formed by wind, wave, and ice action (Walker 1965; Sproule 1972; see also Teller and Last 1979; Last 1980). It consists of Agassiz soils overlying coarse beach and outwash deposits of limestone and granitic rock origin (Ehrlich et al. 1957, in Walker 1965). In several places no profile development has occurred, and the surface consists of very fine sand to fine sandy loam, with evidence of considerable aeolian action (Fenton 1969). Along the south edge of the ridge, dark gray loamy sands overlie coarser grayish brown sands, and in places, thin muck and peat deposits overlie glacial drift (Walker 1959). The dune formation along the north edge of the ridge averages 2.5 m in height and seldom exceeds 30 m in width, except where the sand extends occasionally to the south edge of the forest. On the study area the ridge forest averages 80 m in width, exceeding 100 m in places. The canopy averages 10 m in height, with few trees exceeding 20 m.

The dune-ridge forest lies in the Aspen-Oak Section (B.16) of the Boreal Forest Region (Rowe 1972), and was considered by Löve and Löve (1954) to be an early
stage of this association. Indeed, the presence of Bur Oak (*Quercus macrocarpa*) on well-drained sites just south of the ridge forest supports this assumption. The dominant tree species on the study area are Peach-leaved Willow (*Salix amygdaloides*), Manitoba Maple (*Acer negundo*), and Green Ash (*Fraxinus pennsylvanica* var. *subintegerrima*). Cottonwood (*Populus deltoides*) occurs less frequently, while American Elm (*Ulmus americana*) and Hackberry (*Celtis occidentalis*) are rare. Delta Marsh is apparently the only location of Hackberry in western Canada (L'ove and L'OVE 1954).

The common shrubs include Sandbar Willow (*Salix interior*), Redberried Elder (*Sambucus pubens*), Redosier Dogwood (*Cornus stolonifera*), Choke Cherry (*Prunus virginiana*), and Pin Cherry (*P. pensylvanica*).

The ridge forest is also characterized by a dense understory of herbs and lianas, the most common of which are Common Nettle (*Urtica dioica* var. *procera*), Great Burdock (*Arctium lappa*), Wild Cucumber (*Echinocystis lobata*), Common Hop (*Humulus lupulus*), Wild Morning-glory (*Convolvulus sepium*), and Virginia Creeper (*Parthenocissus inserta*).

Nomenclature follows Scoggan (1957) for trees and herbs, and Budd and Best (1969) for shrubs. The following exceptions have been made: Green Ash follows Hosie (1969); Redberried Elder, Scoggan (1957); Common Nettle, Budd and Best (1969).

**Methods**

In 1977 the study area was gridded into 20 cells, 100 m × 100 m, using transit and tape. Rectangular plots, 5 × 20 m, were set according to a partial random sampling scheme (Chapman 1976) in which five plots were established randomly within each cell. Each plot was positioned with its long axis perpendicular to the north-south slope of the topographic gradient. Such an orientation of the plots was considered to minimize within-plot variation (LaFrance 1972). Elevation of the north edge of the ridge above lake level was measured at the corner of each cell of the grid with a Haga altimeter.

Only fully established trees, arbitrarily defined as ≥ 5 cm dbh (diameter at breast height), were sampled. In each plot all such stems were identified to species and were recorded in the appropriate diameter size classes (intervals of 5 cm). The conventional Wisconsin school summary statistics (Curtis and McIntosh 1950) were calculated using the entire sample of plots to provide a general description of the overstory vegetation (Table 1).

For statistical analyses, absolute density and absolute dominance (basal area) were calculated for each species in each plot. These absolute values were standardized by converting each value to a percentage of the maximum value attained by that species in a plot. The standardized density and dominance were then summed to give an “Abundance Value” (maximum = 200) for each species in each plot. The Abundance Value thus indicated the performance of each species in a plot in relation to its optimum performance in the entire series of plots (Bray and Curtis 1957).

Soil samples were taken during May and September in plots from half of the cells, selected randomly. All samples were collected on the same day during each sampling period. From the centre of each plot a core, 10 cm in diameter and 15 cm deep, was taken. Because of the lack of soil profile development in the ridge forest, a depth of 15 cm was considered adequate to characterize the topopedaphic gradient.

Soil moisture determinations were made on the samples collected in both periods. Samples were oven-dried to constant weight at 105°C, averaged over the two periods, and expressed as a percentage of soil wet weight. Determinations of soil organic matter, pH, salinity, and texture were made on the September samples by the Manitoba Provincial Soil Testing Laboratory.

**Table 1. Summary statistics for tree species on a segment of the dune-ridge forest, Delta Marsh, Manitoba**

<table>
<thead>
<tr>
<th>Tree species1</th>
<th>Absolute density (stems/ha)</th>
<th>Relative density (%)</th>
<th>Absolute dominance2 (m²/ha)</th>
<th>Relative dominance (%)</th>
<th>Absolute frequency (N = 100)</th>
<th>Relative frequency (%)</th>
<th>Importance value3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manitoba Maple</td>
<td>309</td>
<td>24.6</td>
<td>4.65</td>
<td>23.0</td>
<td>59</td>
<td>31.7</td>
<td>79.3</td>
</tr>
<tr>
<td>Green Ash</td>
<td>212</td>
<td>16.9</td>
<td>3.87</td>
<td>19.1</td>
<td>50</td>
<td>26.9</td>
<td>62.9</td>
</tr>
<tr>
<td>Cottonwood</td>
<td>11</td>
<td>0.9</td>
<td>1.20</td>
<td>5.9</td>
<td>4</td>
<td>2.1</td>
<td>8.9</td>
</tr>
<tr>
<td>Choke and Pin Cherry</td>
<td>28</td>
<td>2.2</td>
<td>0.12</td>
<td>0.6</td>
<td>7</td>
<td>3.8</td>
<td>6.6</td>
</tr>
<tr>
<td>Peach-leaved Willow</td>
<td>322</td>
<td>25.6</td>
<td>8.76</td>
<td>43.2</td>
<td>42</td>
<td>22.6</td>
<td>91.4</td>
</tr>
<tr>
<td>Sandbar Willow</td>
<td>374</td>
<td>29.8</td>
<td>1.66</td>
<td>8.2</td>
<td>24</td>
<td>12.9</td>
<td>50.9</td>
</tr>
<tr>
<td>Total</td>
<td>1256</td>
<td>100.0</td>
<td>20.26</td>
<td>100.0</td>
<td>186</td>
<td>100.0</td>
<td>300.0</td>
</tr>
</tbody>
</table>

1Scientific names given in Study Area section of text
2Basal area at 1.5 m above ground
3Relative density + relative dominance + relative frequency
Laboratory and the Soil Science Department, University of Manitoba, after the moisture determinations had been made. Organic matter was measured using wet combustion (modified Walkley-Black method) because of the presence of moderate amounts of carbonate in the samples. Measurements of pH and salinity (conductivity) were made using a 1:1 soil:water ratio. Texture was determined by mechanical analysis using the pipet method, with pretreatments to remove organic matter and soluble salts. For details concerning these procedures see McKeage (1976).

An attempt was made to quantify the zonal nature of the ridge forest vegetation described qualitatively by Löve and Löve (1954) and M. Levin (personal communication) by dividing the ridge forest arbitrarily into 10 zones of equal width, based on an average forest width of 80 m. The random plots were assigned to each zone on the basis of their position on the survey grid, and without regard to their vegetation characteristics. For each tree species, the mean density of stems in each zone was determined from the plots assigned to that zone.

Examination of the species distributions across the width of the forest suggested that the zonation might be represented more appropriately by two zones. Accordingly, all plots were assigned to north and south groups on the basis of their positions in the north and south halves of the grid. The null hypothesis of no difference in the mean densities of the stems of each species between north and south groups was tested using Student's t-test. The null hypothesis of no difference in the mean values of each soil variable between north and south groups was also tested using the t-test.

Following log(X + 1) transformation of Abundance Values and soil data to normalize the distributions (Green 1979), canonical correlation (variate) analysis was performed to determine the degree of covariation between species abundances and soil variation (Pielou 1969). Subsequently, each species was subjected to multiple regression analysis on the set of soil variables, to determine the extent to which the pattern of abundance of each species could be explained in terms of the variation in the soil data. In these analyses only the quantitatively important species, i.e., those species present in > 10% of the plots, were included. All analyses were performed using programs from the BMDP package (Dixon 1975).

Results and Discussion

Overstory Composition and Structure

Density and basal area of stems ≥ 5 cm dbh on the study area were, respectively, 1256 stems/ha and 20.26 m²/ha (Table 1). Peach-leaved Willow, Manitoba Maple, and Green Ash had, respectively, the highest Importance Values. Of the three species, Peach-leaved Willow had the greatest density and by far the greatest basal area. Manitoba Maple was the most ubiquitous species, occurring in 59% of the plots, yet had half the basal area of Peach-leaved Willow. This apparent inconsistency could be explained by the differential distribution of the stems of each species among the various diameter size classes (Figure 1). Twenty-three per cent of the stems of Peach-leaved Willow exceeded 20 cm dbh, compared to 18% for Green Ash, but only 7% for Manitoba Maple.

All species showed a maximum density in the smallest size class, and a sharp drop in density thereafter (Figure 1). The size-class frequency curves for maple, willow, and to a lesser extent, ash, approximate the classic reverse J-shaped curve (i.e., negative exponential distribution) suggested by Meyer (1952) as characteristic of any large forest which contains a reasonable diversity of sizes. Evidently, Peach-leaved Willow had

![Figure 1. Mean density of stems per ha by diameter size class for the major tree species in the dune-ridge forest, Delta Marsh, Manitoba. Stems are grouped into classes of 5 cm dbh.](image-url)
preceded the nonpioneer species, maple and ash, in colonizing the ridge forest, and had been more successful to date in establishing permanently, even though it showed a greater drop in density from size classes I to II (84% decrease compared to 60% for maple, 47% for ash), because it showed a greater density of large trees than the other two species.

Sandbar Willow is usually considered a shrub rather than a tree, and would not, therefore, be expected to show the same size distribution as the tree species. On the study area it seldom exceeded 10 cm dbh, but because its life form here resembled that of a tree rather than that of a shrub, and because of its important role as a nest site for several passerine species, it was included as a tree species in the analyses.

Topoedaphic Gradient and Vegetation Heterogeneity

For much of the length of the study area, the extreme north edge of the dune ridge, between the foreshore vegetation and the ridge forest proper, is colonized by Sandbar Willow (Figure 2). Here, this species forms a low shrubby band and, in places, a narrow discontinuous zone (< 5 m wide) of dense saplings, too small to have been included in the sampling scheme. Where this zone occurs, it has tended to stabilize the edge of the dune formation; elsewhere, serious erosion is evident. Inward from the north edge, the density of Sandbar Willow decreases quickly, being replaced by Peach-leaved Willow and the more shade-tolerant species, Manitoba Maple and Green Ash. These species reach their maximum density in the north half of the ridge forest, and decrease in density toward the south edge, being replaced eventually by a broad zone of Sandbar Willow that becomes progressively more shrub-like until it disappears in the transition to marsh or wet meadow.

A plot of the frequency distribution of the stems of these four species across the width of the ridge forest indicates a different pattern of abundance for each species (Figure 3). Manitoba Maple and Green Ash were each significantly more dense, and Sandbar Willow was significantly less dense, in the north half of the ridge forest than in the south half (Table 2). The difference in Peach-leaved Willow density between the north and south halves was not significant.

This vegetation gradient coincides with a slight topographic and edaphic gradient from north to south. The north zone, containing the dune formation, averages 2 m higher than the south zone, which is at or near lake level for most of the length of the study area. The soil in the north zone is drier, sandier, less saline, and contains less organic matter than that of the south zone (Table 3). Because of the rather abrupt change in topography at the south edge of the dune formation along much of the study area, the ridge forest may be characterized by a distinct north zone, roughly corresponding to the forested dune, and a broader, more or less distinct, but still highly variable

![Figure 2. Diagrammatic cross-section of the dune-ridge forest, Delta Marsh, Manitoba.](image-url)
south zone, rather than by a gradual change in vegetation composition and structure from north to south. The relatively greater variability of the south-zone vegetation is due, in part, to the occurrence of clumps of Peach-leaved Willow, conspicuous among the Sandbar Willow, and also to localized stands of Cottonwood, but to a lesser extent. The reason for this clumping is unclear, but may be related to subtle topographic variation. In one segment of the study area, the dune appears to have been levelled off somewhat and the sand driven southward. Here, a stand of mature Manitoba Maple and Green Ash extends the full width of the ridge forest. The occurrence of mature trees of these species in the south half of the ridge forest also contributes to the greater heterogeneity of the south zone. The increased elevation of the south zone resulting from this broad blanket of sand

Table 2. Density of stems of tree species in north and south halves of the dune-ridge forest, Delta Marsh, Manitoba

<table>
<thead>
<tr>
<th>Species</th>
<th>North half (N = 53)</th>
<th>South half (N = 47)</th>
<th>Significance level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manitoba Maple</td>
<td>4.0 ± 0.59</td>
<td>2.1 ± 0.48</td>
<td>P = 0.01</td>
</tr>
<tr>
<td>Green Ash</td>
<td>2.9 ± 0.51</td>
<td>1.3 ± 0.37</td>
<td>P = 0.01</td>
</tr>
<tr>
<td>Peach-leaved Willow</td>
<td>3.7 ± 0.79</td>
<td>2.7 ± 0.75</td>
<td>P &gt; 0.05</td>
</tr>
<tr>
<td>Sandbar Willow</td>
<td>1.2 ± 0.41</td>
<td>6.6 ± 1.43</td>
<td>P = 0.001</td>
</tr>
</tbody>
</table>

1Expressed as stems per 5 x 20 m (0.01 ha) plot  
2Mean ± standard error  
3Based on t-tests of means (with unequal variances)

Table 3. Values for soil variables from plots in the north and south halves of the dune-ridge forest, Delta Marsh, Manitoba

<table>
<thead>
<tr>
<th>Variable</th>
<th>North half (N = 26)</th>
<th>South half (N = 24)</th>
<th>Significance level</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moisture (%)</td>
<td>7.6 ± 1.40</td>
<td>27.0 ± 3.20</td>
<td>P &lt; 0.001</td>
</tr>
<tr>
<td>Organic matter (%)</td>
<td>2.0 ± 0.54</td>
<td>7.5 ± 1.60</td>
<td>P &lt; 0.001</td>
</tr>
<tr>
<td>pH</td>
<td>7.4 ± 0.08</td>
<td>7.3 ± 0.07</td>
<td>P &gt; 0.05</td>
</tr>
<tr>
<td>Salinity (mmhos/cm³)</td>
<td>0.3 ± 0.03</td>
<td>0.7 ± 0.09</td>
<td>P &lt; 0.001</td>
</tr>
</tbody>
</table>

1Mean ± standard error  
2Based on t-tests of means (with unequal variances)
may have led to increased stability of the south zone at this point, allowing maple and ash to replace the willows in the course of succession. Thus, the vegetation pattern of the ridge forest corresponds more to a mosaic of north- and south-zone vegetation types, perhaps, than to a division into equal north and south halves. Indeed, 68% of the soil samples were classified as very fine sand (Table 4), although only 52% of the plots were actually located in the north half of the ridge forest (Table 3).

Species-Soil Relationships

Canonical correlation analysis was performed to determine to what extent the overall forest community pattern could be reflected in the pattern of covariation of the set of soil variables. Only the first canonical variable showed a significant correlation between the tree species Abundance Values and the soil data (Table 5). It showed high positive correlations with Manitoba Maple and Green Ash, and high negative correlation with Sandbar Willow. Thus, the positive-negative polarity of the first canonical variable was interpreted as a north-south contrast (see Figure 3).

Table 4. Occurrence of tree species at sites with different soil types in the dune-ridge forest, Delta Marsh, Manitoba

<table>
<thead>
<tr>
<th>Soil type</th>
<th>Manitoba Maple</th>
<th>Green Ash</th>
<th>Peach-leaved Willow</th>
<th>Sandbar Willow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Peat</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Peaty, very fine sand</td>
<td>3</td>
<td>2</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Very fine sand</td>
<td>34</td>
<td>25</td>
<td>9</td>
<td>18</td>
</tr>
<tr>
<td>Loamy, very fine sand</td>
<td>9</td>
<td>3</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Loam</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Total</td>
<td>50</td>
<td>30</td>
<td>20</td>
<td>23</td>
</tr>
</tbody>
</table>

1Number of plots containing a given soil type
2Number of plots in which the species is present
3Number of plots in which the species is absent

Table 5. Correlations of tree species Abundance Values 1 and soil variables from the dune-ridge forest, Delta Marsh, Manitoba, with the first canonical variable from canonical correlation analysis 2

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Correlation</th>
<th>Soil variable</th>
<th>Correlation</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manitoba Maple</td>
<td>0.829</td>
<td>Moisture</td>
<td>-0.517</td>
</tr>
<tr>
<td>Green Ash</td>
<td>0.581</td>
<td>Organic matter</td>
<td>-0.386</td>
</tr>
<tr>
<td>Peach-leaved Willow</td>
<td>-0.032</td>
<td>pH</td>
<td>-0.511</td>
</tr>
<tr>
<td>Sandbar Willow</td>
<td>-0.665</td>
<td>Salinity</td>
<td>-0.539</td>
</tr>
<tr>
<td>Canonical correlation</td>
<td>0.725 (P &lt; 0.01)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1Defined in Methods section of text
2N = 44

The high negative correlations of the soil variables with the first canonical variable supported this interpretation because all four variables showed negative correlations with maple and ash abundances, and positive correlations with Sandbar Willow abundance (Table 6). Although the second canonical variable was not significant (P > 0.05), it was characterized by a high positive correlation with Peach-leaved Willow. This would suggest that the pattern of Peach-leaved Willow abundance was independent of those of the other species, and could not be explained easily in terms of the set of soil variables.

Multiple regression analysis gives valuable insight into the extent to which individual dependent variables (here, tree species) can be explained by a set of ‘independent’ variables (here, soil variables). Significant regression models emerged from multiple regression of Manitoba Maple, Green Ash, and Sandbar Willow Abundance Values on the set of soil variables (Table 7). No significant relationship was found, however, between Peach-leaved Willow abundance and the set of soil variables.

Stepwise regression analysis indicated that Manitoba Maple and Green Ash abundances could be explained significantly (P < 0.05) using only two variables in each case, according to the following models:

Maple:

\[ Y = 10.036 - 1.141(\text{moisture}) - 1.067(\text{pH}) \quad r^2 = 0.36 \]

Ash:

\[ Y = 9.374 - 1.169(\text{pH}) - 0.683(\text{organic}) \quad r^2 = 0.22 \]

Thus, the pattern of Manitoba Maple was negatively related to variation in moisture and pH; that of Green Ash was negatively related to variation in pH and organic matter. No single variable or subset could explain the distribution of either willow species. The pattern of abundance of Sandbar Willow could be explained significantly, however, using the complete set of variables, with pH and moisture the best predictors (Table 7).

Thus, the major pattern in the ridge forest is a north-south gradient in tree species composition associated primarily with a moisture gradient. A secon-
Table 6. Matrix of Pearson correlation coefficients for tree species and soil variables from the dune-ridge forest, Delta Marsh, Manitoba

<table>
<thead>
<tr>
<th></th>
<th>Manitoba Maple</th>
<th>Green Ash</th>
<th>Peach-leaved Willow</th>
<th>Sandbar Willow</th>
<th>Moisture</th>
<th>Organic matter</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manitoba Maple</td>
<td>1.00</td>
<td>0.14</td>
<td>-0.04</td>
<td>-0.21</td>
<td>-0.40**</td>
<td>-0.30**</td>
<td>0.21</td>
</tr>
<tr>
<td>Green Ash</td>
<td></td>
<td></td>
<td>1.00</td>
<td>-0.53***</td>
<td>-0.07</td>
<td>-0.04</td>
<td></td>
</tr>
<tr>
<td>Peach-leaved Willow</td>
<td></td>
<td></td>
<td></td>
<td>-0.25</td>
<td>0.26</td>
<td>0.24</td>
<td></td>
</tr>
<tr>
<td>Sandbar Willow</td>
<td></td>
<td></td>
<td></td>
<td>1.00</td>
<td>0.23</td>
<td>0.17</td>
<td></td>
</tr>
<tr>
<td>Moisture</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.92***</td>
<td>-0.46***</td>
<td></td>
</tr>
<tr>
<td>Organic matter</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>-0.52***</td>
<td>1.00</td>
</tr>
<tr>
<td>pH</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salinity</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

N = 44

**P < 0.01

***P < 0.001

Table 7. Multiple regressions of tree species Abundance Values on soil variables from the dune-ridge forest, Delta Marsh, Manitoba

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Regression equations</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manitoba Maple</td>
<td>Y = 8.44 - 1.39(M) + 1.13(OM) - 0.85(pH) - 0.81(S)</td>
<td>0.38***</td>
</tr>
<tr>
<td>Green Ash</td>
<td>Y = 9.99 - 0.23(M) - 0.56(OM) - 1.19(pH) + 0.12(S)</td>
<td>0.22*</td>
</tr>
<tr>
<td>Peach-leaved Willow</td>
<td>Y = -9.31 + 0.89(M) + 0.41(OM) + 1.25(pH) - 0.35(S)</td>
<td>0.25*</td>
</tr>
</tbody>
</table>

1Defined in Methods section of text

2M = moisture, OM = organic matter, S = salinity

*P < 0.05

***P < 0.001

Acknowledgments

I gratefully acknowledge the field assistance of L. W. Brownlie and G. D. Sutherland, without whom the painstaking task of surveying the ridge forest and establishing the random plots would have been impossible. J. M. Shay and B. Wallis provided the facilities of the University of Manitoba Field Station. This paper profited from many discussions with M. See and G. Tande, and from valuable criticisms offered by G. H. La Roi, G. E. Bradfield, R. I. C. Hansell, J. D. Rising, and S. G. Sealy also commented on an earlier draft. M. Levin offered useful insights into the analysis of the vegetation structure of the ridge forest.

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References


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Influence of Nordic Skiing on Distribution of Moose and Elk in Elk Island National Park, Alberta

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Effects of cross-country skiing on distribution of Moose and Elk during winter were studied on Elk Island National Park, Alberta. Aerial observations, and track and pellet-group counts provided indices to distribution that could be related to ski-trail location and/or use. Cross-country skiing influenced the general overwinter distribution of Moose but not of Elk. Both species, however, tended to move away from areas near heavily-used trails during the ski season (January–March). Day-to-day movements away from trails occurred after the onset of skiing, but such displacement did not increase with the passage of additional skiers.

Key Words: Nordic skiing, Moose, Elk, animal distribution, human disturbance, Alberta.

There have been numerous studies of effects of vehicles and other human-related disturbances on ungulate populations. Dorrance et al. (1975), Richens and Lavigne (1978) and Eckstein et al. (1979) investigated impacts of snowmobiles on White-tailed Deer (Odocoileus virginianus); and highway traffic—ungulate interactions have been examined by Carbaugh et al. (1975), Ward (1976), Singer (1978) and others. Disturbances from aircraft (Klein 1974; Miller and Gunn 1980) and pipelines (Child 1974; Cameron et al. 1979) have also been examined. However, relatively few studies of direct human-ungulate interactions have been made (Schultz and Bailey 1978; Hicks and Elder 1979; MacArthur et al. 1979), and no published reports on effects of nordic (cross-country) skiing on ungulates are known to us.

Nordic skiing rose steadily in popularity in Canada and the northern United States during the 1970's. By 1975–76, there were 1.3 million participants in Canada (Statistics Canada 1978); and by winter 1977–78, there were 2.3 million participants in the United States (U.S. Forest Service 1980). In Elk Island National Park, Alberta, the most common backcountry activity is cross-country skiing. It is limited to daylight hours and takes place mainly on weekends. In response to increasing public pressure, a cross-country ski-trail system was opened in 1973–74 (R. Jones, Elk Island National Park, personal communication). Nordic skiing rose from about 1800 user-days in 1972–73 to 18 000 in 1977–78 (Marshall 1978). During 1978–79, use declined to an estimated 10 000 user-days (Ferguson and Keith 1981), probably due to poor snow conditions and extended cold periods.

The high intensity of use has evoked two types of responses among Parks Canada personnel. Resource Conservation staff are concerned about possible reduction in winter range available to ungulates. Interpretation staff feel that increased winter visitation could provide a unique opportunity for public education in wildlife ecology.

The present study resulted largely from these concerns. Its general objective was to evaluate the influence of cross-country skiing on winter distribution of Moose (Alces alces) and Elk (Cervus elaphus) in Elk Island National Park.

Study Area

Elk Island National Park is located in central Alberta, about 40 km east of Edmonton. The park covers approximately 195 km², divided into two sections surrounded by 2.4-m-high fences. The northern section of 136 km² is accessible to the public for cross-country skiing (Figure 1). The kettle-and-knob topography, underlain by dead-ice moraine, provides an interspersion of uplands and lowlands; but elevation varies only from 710 to 755 m.

The park is situated in a southern island of Boreal Mixedwood Forest (Rowe 1972). Repeated and extensive fires prior to 1892 removed all but a remnant of the climax White Spruce (Picea glauca) forest. Upland plant communities include a deciduous forest of Trembling Aspen (Populus tremuloides) and Balsam Poplar (P. balsamifera), the dominant vegetation type in the park; open grass and shrub meadows; and scattered White Spruce stands. Lowland communities are Cattail (Typha latifolia) and sedge (Carex spp.) lake margins, sedge meadows, willow (Salix spp.) dominated shrublands, and Black Spruce (P. mariana) bogs (Polster and Watson, unpublished report, Techman Ltd. for Parks Canada). These vegetation
types, and a large number of lakes and sloughs, form a mosaic of small stands and openings on the irregular topography.

For over 50 years the park has held large populations of Elk, Moose, and Bison (*Bison bison*), and some Mule (*O. hemionus*) and White-tailed deer (Telfer 1978). Without important natural predators, these ungulates have had a major effect on vegetation composition, structure and possibly production (Holsworth 1960; Telfer 1978). Numbers of Elk and Moose have been regulated through trapping and shooting by park personnel. During an aerial survey in the northern park area in February 1979, we counted 452 Elk, 253 Moose, and 49 deer. The bulk of the Bison herd was within an enclosure over winter; only 42 were seen outside it during our aerial survey.

**Methods**

Moose and Elk distributions were determined by different methods within four time frames: (1) aerial counts from winters 1970–71 to 1977–78; (2) pellet-group counts for October–March 1978–79; (3) track counts during the ski season, January–March 1979; and (4) aerial counts over 3-hour periods during winter 1978–79. During January–March 1979, a questionnaire survey of skiers was used to estimate: (1) total numbers of skiers on each of 21 trail sections (Figure 1) during the January–March ski season; (2) mean number of skiers/trail section during days covered by track counts; and (3) total number of skiers/trail section on days of aerial counts.

The data were analyzed largely by comparing animal distribution at distances within and beyond 500 m from trails. This was done because: (1) locations of animals seen during past aerial surveys were allegedly accurate within ± 0.4 km (E. S. Telfer, Canadian Wildlife Service, Edmonton, personal communication); (2) there was high innate variability in track and pellet-group counts; and (3) a preliminary inspection of our data indicated that differences in distribution tended to appear at 400 to 550 m.

**Aerial Counts, 1971–78**

We used Parks Canada aerial counts to compare Moose and Elk distribution in winter before and after ski-trail development. These counts were from fixed-wing aircraft flying 0.4-km transects over the northern park area during 1971–78. They were conducted on weekdays, whereas about 90% of the skiing was probably on weekends (Marshall 1978).

We tabulated Moose and Elk distribution as numbers within or beyond a 500-m belt on either side of ski-trail locations. These data were further partitioned into: (1) before and after trail development (1971–73 vs 1973–78), and (2) before and during ski seasons (November–December vs January–March) (Table 1). Chi-square tests were used to compare distributions.

**Pellet-group and Track Counts, 1978–79**

Track and pellet-group counts were conducted on seven sites. These rectangular sites were 100 × 800 m or 100 × 1600 m; the shortest sides of which were based on ski trails. Sites were positioned randomly, at least 300 m apart, along segments of trails meeting the following criteria: ready access; closer to the adjacent ski trail than to park roads, parking lots and other trails; more than 400 m from park boundaries; and located within ungulate habitat. Lakes and sloughs greater than 100 m in diameter, and the Bison enclosure were considered non-habitat. Interiors of trail loops were not used.

During May–July 1979, we counted pellet groups that had been deposited during the previous winter from about October through March. Within study sites, pellet groups were sampled by lines of plots that
paralleled the trail and were spaced at successive 50-m intervals from it. Each line was 100 m long and had 11 equally-spaced plots. Each plot was composed of four circular, 0.001-ha sub-plots. Groups of 30 or more pellets centered within a sub-plot were given a value of 1. All other groups wholly or partially within a sub-plot were given a value of 0.5. Pellet shape, size, color, and internal texture indicated species. Visual classification of habitat as forested upland, open upland, and lowland was made at each plot during sampling.

A logarithmic transformation of pellet-group numbers was used to normalize distributions and stabilize variances. These transformed data, characterized by distance from trail and intensity of use by skiers, were subjected to 2-way analyses of variance. Means of untransformed values for each species were set into a 0-to-10 scale for presentation by dividing each by the largest and multiplying by 10.

Comparison of pellet groups in plots centered on ski trails vs. those 1-500 m from trails was limited to upland habitats because trails adjacent to study sites did not cross lowlands. Numbers of pellet groups 501-1600 m from trails were compared with numbers at 1-500 m, within forested uplands, open uplands, lowlands and all habitats combined.

To determine Moose and Elk distribution during the ski season, we partitioned the perimeter of each study site into 25-m line-transects, and counted tracks crossing each one. The observer skied to the study sites along existing trails and snowshoed around the sites to count tracks. Study sites were sampled 2-6 times during January-March 1979. Intersecting tracks had to diverge at least 2 m from line-transects before being recounted. Backtracking distinguished species and overlapping tracks as needed. Track counts were divided by numbers of days since last snowfall. Habitat on each 25-m transect was classified as forested upland, open upland, or lowland.

Numbers of Moose and Elk tracks/day since last snow/25-m transect were log transformed to normalize distributions and stabilize variances. Transformed values, characterized by distance from trail and trail use, were analyzed by 2-way analyses of variances. Means of untransformed values were set into a 0-to-10 scale. Track distribution in relation to ski trails was analyzed as described above for pellet groups.

**Aerial Counts, 1978-79**

From 17 December to 8 March 1978-79, we conducted seven aerial surveys on random weekdays and weekends to determine numbers and locations of Moose and Elk. The helicopter flew east-west transects 0.8 km (1 survey, 0.4 km) apart between 12:30 and 15:30, thereby combining peak numbers of skiers and good visibility. One weekday survey was made before the ski season. One weekday and one weekend survey were conducted in January, one weekday and two weekend surveys in February, and one weekday survey in March. Animal sightings were plotted on 1:50 000 maps, mostly within 0.1 km. Numbers of individuals in large groups were counted by hovering or circling.

To examine gross changes in Elk and Moose distribution, we first partitioned observations into locations within vs. beyond 500 m of any trail. Numbers of Moose and Elk were further partitioned into: (1) before vs. within the ski season, and (2) weekdays vs. weekends (Table 4). Chi-square tests were used to make comparisons between time periods.

Impacts of different intensities of trail use were examined by further subdividing animal locations into five 100-m-wide belts within 500 m of the 21 trail sections (total 105 belts). Numbers of skiers on these trail sections were known from questionnaire data for the day of each aerial survey. The total number of Moose and Elk counted varied irregularly between flights (136-253 Moose; 188-452 Elk) even though the populations were enclosed and stationary. Locations of observed animals were assumed to be representative of distances from ski trails for the total park population. We thus standardized numbers within the 100-m-wide belts between surveys by multiplying each by the maximum count for Moose (253) or Elk (452), then dividing by the total count for a given survey. For example, on 7 January we saw a total of 285 Elk, 3 of which were in one 100-m-wide belt. The count of 3 was standardized to 4.76 (3 x 452/285). In each of the 105 belts we measured area of ungulate habitat which varied with trail length, configuration, and relation to non-habitat. Division of the standardized number (above) by area of habitat then gave a standardized density for each belt. Because no animals were seen in many belts, standardized densities were not normally distributed within the categories of distance-from-trail and intensity-of-trail-use that we wished to examine by 2-way analyses of variance. To normalize distributions and stabilize variances, we randomly pooled the data, four belts at a time, within the above categories, and then log transformed the calculated densities. Following analysis, means of species densities were set into a 0-to-10 scale for tabular presentation.

**Analysis of Variance**

Two-way analysis of variance was used to determine effects of distance from trails and/or intensity of trail use by skiers on Moose and Elk distribution. This analysis tested for significant effects of distance, human use and distance-human use interaction. When interactions were not significant (P > 0.05), as for example when effects of human use on track density were independent of distance from trail, then
significant \((P \leq 0.05)\) main effects (human use and distance) were considered additive. When interactions were significant, main effects were not tested (Sokal and Rohlf 1969). In such cases, the effect of one factor upon the dependent variable was contingent on the level of the second factor. We therefore compared means within categories of distance and human-use (Table 2) through an adjusted Tukey's test (Cicchetti 1972) and a correction for unequal sample sizes (Kramer 1956).

**Results**

**Aerial counts, 1971–78**

The analyses of 1971–78 aerial counts examined overall effects of ski-trail development on distribution, not effects of human use levels on particular trail sections. These aerial counts were conducted on weekdays — when trail use was generally low.

**MOOSE.** During the three winters before ski-trail development, the proportion of Moose observed within 500 m of future trail locations decreased between November-December and January-March, but not significantly \((P > 0.21)\) (Table 1). This decrease was more pronounced \((P < 0.01)\) during 1973–78, after trail development. However, during the ski season (January-March), Moose distribution differed little \((P > 0.16)\) before vs. after trail development (i.e. 45 vs. 42% within 500 m). We, therefore, conclude that establishment of trails had slight, if any, impact on what seems to be a normal seasonal shift in Moose distribution.

**ELK.** The proportion of Elk sighted within 500 m of trail locations also decreased \((P < 0.01)\) between pre-ski and ski seasons; but this decrease was greatest before trail construction (Table 1). There was no indication of a negative impact of ski-trail development of Elk distribution, because the proportion within 500 m of ski trail locations during January-March increased \((P < 0.001)\) after trails were developed (i.e. 32 vs. 38%). As with Moose, there is evidently a long-standing seasonal change in Elk distribution from early to late winter that reduces Elk numbers in areas on which ski trails have been built.

**Pellet-group Counts, 1978–79**

Pellet-group counts reflected distribution of animals overwinter. These data were analyzed relative to skiing intensity on trail sections adjacent to study sites.

**MOOSE.** Overall, pellet group densities were higher \((P \leq 0.05)\) within 1-500 m of lightly-skied trails than 501-1600 m away (Table 2). The difference was greatest in upland forest habitat. On the other hand, pellet group densities tended to be higher 501-1600 m from heavily-skied trails than within 1-500 m; and much lower near heavily-skied than near lightly-skied trails. These findings strongly suggest than only heavy use of trails by skiers reduced Moose numbers on nearby sites overwinter.

**ELK.** The general pattern of Elk pellet-group densities in relation to ski trail proximity and use was largely opposite to that noted above for Moose (Table 2). Highest densities of Elk pellet groups on uplands occurred where trail use by skiers was heavy; and densities there tended to be higher within 500 m of trails than further away. In contrast, where trail use was light, Elk pellet group densities on uplands were highest beyond 500 m. There were no significant differences \((P > 0.05)\) in Elk pellet group densities in lowland areas. Although we cannot explain these characteristics of Elk distribution over winter, there is no indication that skiers were responsible.

**Track Counts, 1979**

Track data indicated effects of skiing intensity on distribution during the ski season.

**MOOSE.** Track densities were lower \((P < 0.01)\) near heavily-skied trails in open uplands and lowlands, but not in forested uplands \((P > 0.14)\) (Table 3). Overall,

---

**Table 1. Distribution of Moose and Elk observed in Elk Island National Park during aerial counts before and after development of ski trails. Vertical lines indicate differences at \(P < 0.01\) when tested by chi-square; for all other comparisons \(P > 0.16\).**

<table>
<thead>
<tr>
<th>Time period</th>
<th>Moose</th>
<th></th>
<th>Elk</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total number</td>
<td>Percent within 500 m of trails</td>
<td>Total number</td>
<td>Percent within 500 m of trails</td>
</tr>
<tr>
<td>Before trails (1970-73)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-ski season (Nov-Dec)</td>
<td>524</td>
<td>49</td>
<td>653</td>
<td>52</td>
</tr>
<tr>
<td>Ski season (Jan-Mar)</td>
<td>881</td>
<td>45</td>
<td>1411</td>
<td>32</td>
</tr>
<tr>
<td>After trails (1973-78)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre-ski season (Nov-Dec)</td>
<td>732</td>
<td>49</td>
<td>944</td>
<td>43</td>
</tr>
<tr>
<td>Ski season (Jan-Mar)</td>
<td>1505</td>
<td>42</td>
<td>2046</td>
<td>38</td>
</tr>
<tr>
<td>Grand total</td>
<td>3642</td>
<td>45</td>
<td>5054</td>
<td>39</td>
</tr>
</tbody>
</table>
Table 2. Relative density of pellet groups of Moose and Elk in relation to distance from trails, human use of trails, and habitat in Elk Island National Park. Pellet groups were deposited largely during October-March 1978-79 and counted during May-July 1979. Vertical and horizontal lines indicate differences at $P \leq 0.05$.

<table>
<thead>
<tr>
<th>Habitat and distance from trails (m)</th>
<th>Moose pellet group density</th>
<th>Elk pellet group density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Column 1</td>
<td>Column 2</td>
</tr>
<tr>
<td>Forested upland</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1-500</td>
<td>Light</td>
<td>Heavy</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>4</td>
</tr>
<tr>
<td>501-1600</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Total</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>Open upland</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1-500</td>
<td>Light</td>
<td>Heavy</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>4</td>
</tr>
<tr>
<td>501-1600</td>
<td>9</td>
<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>9</td>
<td>5</td>
</tr>
<tr>
<td>Lowland</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1-500</td>
<td>Light</td>
<td>Heavy</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>501-1600</td>
<td>6</td>
<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td>All habitats</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1-500</td>
<td>Light</td>
<td>Heavy</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>501-1600</td>
<td>7</td>
<td>5</td>
</tr>
<tr>
<td>Total</td>
<td>7</td>
<td>4</td>
</tr>
</tbody>
</table>

1 See text for explanation of calculation, pp. 71-72. For Moose, "10" = 1.7 pellet groups/0.004-ha plot; while for Elk, "10" = 2.3.

2 Human use determined by questionnaire surveys from January to March, 1979: "Light" = 113 to 470 persons and "heavy" = 963 to 1403 persons from January to March.

3 Determined by two-way analysis of variance (or Tukey's test, where interaction $P \leq 0.05$). Where interaction $P \leq 0.05$, main effects were ignored (*); for all other main effects $P > 0.08$ and for all other interactions $P > 0.26$.

Moose tracks were also less numerous ($P < 0.01$) at 1-500 m than at 501-1600 m from trails. These indices thus indicate a negative influence of trails on Moose distribution during the January-March ski season. Elk track densities showed the same relationship to trail distance and use by skiers as that shown by Moose tracks (Table 3), and likewise imply a displacement of animals. In both uplands and lowlands, higher track densities ($P < 0.01$) occurred near lightly-skied than near heavily-skied trails. In uplands too, track densities were higher ($P < 0.05$) 501-1600 m from trails than at 1-500 m.

**Aerial Counts, 1978-79**

As with our earlier analysis of the 1971-78 aerial counts by park staff, the following examined effects of the trail network as a whole on Moose and Elk distribution rather than local effects of skier numbers on specific trail sections.

MOOSE. The relative number of Moose observed within 500 m of trails on our 1978-79 aerial surveys was less ($P < 0.03$) during the ski season than before it (Table 4). This trend, noted earlier, was also evident in aerial counts by park staff in previous winters, both before and after trail development. There were, however, proportionately more Moose ($P < 0.02$) within 500 m of trails on weekends (high-use days) than on weekdays during the 1978-79 ski season. Thus, Moose distribution appears to shift between early and late winter, and between weekdays and weekends as well. The seasonal change in distribution is apparently unrelated to skiing; and the weekday-weekend change...
Table 3. Relative density of tracks\(^1\) of Moose and Elk in relation to distance from trails, human use of trails\(^2\), and habitat in Elk Island National Park. Track counts were made from January to March 1979. Vertical and horizontal lines indicate differences at \(P<0.05\).\(^3\)

<table>
<thead>
<tr>
<th>Habitat and distance from trails (m)</th>
<th>Relative Moose track density</th>
<th>Relative Elk track density</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Level of human use</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Light</td>
<td>Heavy</td>
</tr>
<tr>
<td>Forested upland</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1-500</td>
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</tr>
<tr>
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<td>5</td>
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<tr>
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<tr>
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<td>501-1600</td>
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<tr>
<td>Total</td>
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<td>5</td>
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</tbody>
</table>

1 See text for explanation of calculation, p. 72. For Moose, “10” = 0.35 tracks/day since last snow/25-m transect; while for Elk, “10” = 0.56.
2 Human use determined by questionnaire surveys during the track count period: “Light” = < 1 person per day and “Heavy” = 8 to 21 persons per day since last snowfall before track count.
3 Determined by two-way analysis of variance; for all other main effects \(P > 0.08\) and for all interactions \(P > 0.05\).

Table 4. Distribution of Moose and Elk observed in Elk Island National Park during aerial counts in winter 1978-79. Vertical lines indicate differences at \(P < 0.03\) when tested by chi-square.

<table>
<thead>
<tr>
<th></th>
<th>Moose</th>
<th>Elk</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total number</td>
<td>Percent within 500 m of trails</td>
</tr>
<tr>
<td>Pre-ski season (December)</td>
<td>161</td>
<td>60</td>
</tr>
<tr>
<td>Weekdays</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ski Season (January-March)</td>
<td>539</td>
<td>50</td>
</tr>
<tr>
<td>Weekdays</td>
<td>607</td>
<td>57</td>
</tr>
<tr>
<td>Grand total</td>
<td>1307</td>
<td>55</td>
</tr>
</tbody>
</table>
implies that increased numbers of skiers do not cause an exodus of Moose from areas adjacent to the trail system. The foregoing analyses compared effects of high vs. low human use within the park as a whole. We next examined Moose distribution around trail sections having different daily numbers of skiers. On days of aerial surveys, intensity of daily trail use where skiers were present fell conveniently into three categories: 1-9, 10-99, and 100-215 persons/trail section. Animal sightings were grouped into successive 100-m intervals within 500 m of trails. When tested by analysis of variance, relative density of Moose did not differ with intensity of trail use \( (P > 0.37) \), distance from trails \( (P > 0.44) \), or with their interaction \( (P > 0.13) \). However, density was higher \( (P < 0.005) \) when no (0) vs. some (1-215) skiers were present (Table 5). The above analysis suggests that an onset of skiing reduces Moose numbers within at least 500 m of trails, but thereafter intensified use causes no further displacement.

ELK. In contrast to Moose, proportionately more Elk \( (P < 0.01) \) were seen within 500 m of trails during the ski season than before it (Table 4). This distribution was opposite to that recorded on surveys during previous winters. Like Moose, proportionately more Elk \( (P < 0.01) \) were within 500 m of trails on weekends than on weekdays during the January-March ski season.

For trails used by skiers, relative density of Elk was unrelated to intensity of trail use \( (P > 0.35) \), distance from trails \( (P > 0.50) \), or to their interaction \( (P > 0.48) \). However, relative density within 500 m of trails decreased \( (P < 0.01) \) between no use and some use of trails by skiers (Table 5). Thus, there is probably an influence of skiing on Elk distribution that is not accentuated by increased numbers of skiers.

**General Synopsis**

We used several field techniques to measure possible effects of cross-country ski trails on Moose and Elk distribution in winter. The resulting data differed in time-frame and accuracy. The eight years of aerial counts by park staff provided a general comparison of early- to late-winter distributions, before and after ski-trail development. Our pellet group counts indexed overwinter distribution in 1978-79, whereas track counts were restricted to the January-March ski season. Aerial counts during December-March 1978-79 were the most time-specific data, permitting same-day comparisons of animal distribution with intensity of trail use by skiers.

The above indices consistently indicated that cross-country skiing influenced Moose distribution: (1) a traditional overwinter shift was accentuated after ski trails were built in areas from which Moose normally moved; (2) during October-March, there were far fewer Moose near heavily-used than near lightly-used trails; (3) during the January-March ski season, densities were notably lower near heavily-used trails and where trails passed through open terrain; (4) there were evidently day-to-day movements of Moose away from trails with the onset of skiing, but this initial displacement was not accentuated by the passage of additional skiers.

We found no indication that cross-country skiing effected a change in the general overwinter distribution of Elk. However, shorter-term indices of distribu-

<table>
<thead>
<tr>
<th>Distance from trails (m)</th>
<th>Relative density of Moose</th>
<th>Relative density of Elk</th>
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</thead>
<tbody>
<tr>
<td></td>
<td>Human use of Moose</td>
<td>Human use of trails</td>
</tr>
<tr>
<td></td>
<td>No use</td>
<td>Some use</td>
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</tr>
<tr>
<td>Total</td>
<td>9</td>
<td>6</td>
</tr>
</tbody>
</table>

1 See text for explanation of calculation, p. 9. For Moose, "10" = 3.3 animals/km²; while for Elk, "10" = 6.5.
tion during the ski season suggested that Elk did move away from trails, especially when these were heavily used. As with Moose, day-to-day movements in response to skiing appeared to be independent of frequency of trail use once the first skier(s) passed.

Discussion

Other disturbances were concurrent with skiing. To reduce their influence on our measurements, we selected sites for track and pellet-group counts that were closer to ski trails than to any other potential disturbances. During the ski season, trails were groomed or "set" once or twice by snowmobile. No grooming was done within at least two days of aerial counts or periods covered by track counts.

Pellet-group data indicated that during October-March Moose utilization of areas near heavily-skied trails was about 60% of utilization of areas near lightly-skied trails. The ratio of forested uplands, open uplands and lowlands (4:3:3) was similar along both sets of trails. Approximately 90% of all trail use by skiers occurred during only 4% of the October-March period (Ferguson and Keith, 1981), with no skiing before January. The degree of reduction in pellet groups near heavily-skied trails in 1978-79 suggests that Moose may have learned over previous winters to avoid such areas. Trails that were lightly skied during our study were also least used by skiers in 1977-78 (Marshall 1978). Geist (1971) theorized that animals will learn to avoid disturbances which are "common and localized."

Overall distribution of Elk during October-March, as indexed by pellet-group counts in spring, appeared unaffected by ski trail location, but track counts during the ski season indicated a movement away from heavily-used trails. The magnitude of this shift in January-March is reflected by pellet-group densities (October-March) within 500 m of heavily-skied trails being 1.3 times those within 501-1600 m of lightly-skied trails, whereas track counts (January-March) were only half as high. We could not relate this change to pellet-group and track counts indexing different activities of Elk nor to possible overwinter changes in habitat use with changing snow depths and temperatures (Beall 1976; Cairns 1976; Telfer 1978).

Other studies have indicated displacement of ungulates from areas of human activity. In the Cypress Hills, Saskatchewan, logging and road traffic allegedly caused Elk to avoid an area that historically had heavy use (Keith 1977). Batcheler (1968) reported relatively greater use of previously unpreferred habitats by introduced Red Deer (C. elaphus) in New Zealand following a population reduction program. Near Rochester, Alberta, Moose tended to avoid roads and dwellings (Rolley and Keith 1980); and Elk avoided roads in Washington, Colorado and Montana (Perry and Overly 1976; Rost and Bailey 1979; Lyon and Jensen 1980).

The duration of impacts on ungulate distribution varies with type of disturbance and past experience of ungulates. In Wyoming, Elk preferred to be 800 m or more from active logging sites, moved through these sites only at night, and returned to them within three weeks after cessation of logging (Ward 1976). In Rocky Mountain National Park, Colorado, Elk used residential areas at night (Schultz and Bailey 1978), and in Scotland Red Deer returned to hunted areas within a day (Staines 1977). During our study, Elk use of areas near heavily-skied trails declined soon after skiing commenced in January.

Dorrance et al. (1975), Richens and Lavigne (1978) and Eckstein et al. (1979) found only short-term impacts of snowmobiles on White-tailed Deer. Movement away from used snowmobile trails was greater among annually-hunted deer than unhunted deer (Dorrance et al. 1975); and deer responded more frequently to hikers and skiers than to humans on snowmobiles (Richens and Lavigne 1978; Eckstein et al. 1979).

Our finding that additional skiers on a given day did not cause further displacement of Elk or Moose from areas near trails paralleled the conclusions of Dorrance et al. (1975) and Eckstein et al. (1979) on effects of increased snowmobile traffic upon White-tailed Deer.

Richens and Lavigne (1978) found that White-tailed Deer used snowmobile trails as travel routes during winter, while McCourt et al. (unpublished report, Arctic Gas Biological Report Series 5) reported that Caribou utilized cutlines and roads. We wished to determine if Elk and/or Moose used ski trails because such use might influence off-trail distribution. Densities of Moose pellet groups on ski trails were less ($P < 0.001$) than densities within 1-500 m of both lightly- and heavily-skied trails. With Elk, pellet-group densities were also less on lightly-skied trails, but similar on and off trails where skiing was heavy. There were no differences between on- and off-trail track densities in either species, and thus again no indication that ski trails provided attractive travel routes for Moose or Elk.

It was probably awkward for Moose to walk along a ski trail because the hard-packed area capable of supporting them averaged only 31 cm wide compared to 40 cm for Moose tracks. Although Elk tracks were about as wide as packed ski trails (29 vs. 31 cm), Elk appeared no more inclined than Moose to utilize them. For example, 8 of 9 Moose and 14 of 15 Elk tracked by us went directly across ski trails; the remaining 2 individuals walked along the trail for less than 10 m.

To determine if the distribution of Moose was
affected by the presence of Elk (or vice versa), we tabulated the 251 group and individual locations observed during a February 1979 aerial survey, according to the species observed and the species of its nearest neighbor. Whether the species of the observed groups was Moose or Elk, the proportion of Elk groups (39%) that were their nearest neighbors did not change ($P > 0.14$). Therefore, it was highly improbable that Elk and Moose affected each other's distribution around ski trails or elsewhere.

Numerous studies have documented responses by wild ungulates to a variety of human disturbances. Most commonly, movements and changes in distribution have been monitored, but also increased activity and heart rate (Batcheler 1968; MacArthur et al. 1979; A. N. Moen, Cornell University, personal communication). Although there seems to be a tacit assumption that such responses are detrimental to individuals and populations, they have rarely been linked to changes in reproduction, survival or any other demographic parameters. We certainly do not know if cross-country skiing was demographically detrimental to Moose or Elk in Elk Island National Park. It may well be that, at both the individual and population level, compensations occur which negate potentially detrimental effects of disturbance. An extreme case of disturbance that did lower reproduction was reported by Batcheler (1968) in New Zealand. There, Red Deer moved into dense scrub cover during a 4-year control program and suffered food shortage.

Acknowledgments

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Literature Cited


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Fall and Winter Homesite Use by Wolves in Northeastern Minnesota

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Post-abandonment homesite use by wolves (Canis lupus) was studied by radio-tracking and simulated howling in two packs in the Superior National Forest, Minnesota. Pups, yearlings, and adults returned intermittently to former homesites up to four months after abandonment, usually after prolonged separation from the pack in early fall. Returns sometimes exceeded one week. Preferred summer homesites were revisited most frequently. Visits declined as the season progressed either because attempts to relocate the pack were not facilitated, or simply because separations became rare. While temporarily at homesites, single wolves replied significantly more to simulated howling than when anywhere else, suggesting that homesites may provide reassurance for separated wolves.

Key Words: Wolves, behavior, habitat use, movements, homesites, vocalization, howling.

Throughout summer, wolves center their activity around a series of homesites (HS) or pup-rearing areas (Murie 1944; Joslin 1967). Once pups are sufficiently developed to travel throughout the pack’s home range, HS use ceases, usually by early fall. Previous studies of wolf HS use terminated after the HS’s were abandoned (Murie 1944; Joslin 1967; Theberge and Pimlott 1969; Van Ballenberghe et al. 1975). The present study examines the details of sporadic, late-season HS use and its implications for wolf behavioral ecology.

Study Area

This study was conducted in the Superior National Forest of northeastern Minnesota between June 1972 and April 1974. The habitat is primarily mixed deciduous/conifer forest interspersed with extensive bogs and waterways (see Ohmann and Ream [1971] for details). Elevation is less than 600 m, the terrain is rugged, and visibility is limited. The forest supported a population of about one wolf per 26 km² (Mech 1973). This population has been under intensive study since 1968 (Mech and Frenzel 1971; Mech 1980).

Methods

Wolves were captured, radio-collared and, after release, were relocated twice a week or more by aircraft, and daily, as possible, from the ground by truck (Mech 1974). We focused on packs in two contiguous territories. The Harris Lake Pack (HLP) occupied a home range of 130-180 km². There were four members in 1972 (breeding pair plus two pups) and five during 1973 (the same pair, one yearling, and two pups). The breeding female was radio-collared during summer 1973. We followed HLP movements close enough to determine when HS abandonment occurred, but were unable to obtain reliable data about post-abandonment use.

The neighboring Jackpine Pack (JPP) occupied a larger 270 km² home range. There were seven members during 1972 (three adults [one collared] and four pups [all collared]). In 1973, three adults were accompanied by two yearlings (both collared) and six pups (four collared). In both years, contact with two of the pups was lost within four to six weeks of HS abandonment.

Aerial observations, ground sign, and howling responses (see below) permitted us to chart individual and pack movements. Because the packs were relatively small, and several members were collared in each, we were able to determine when individuals became separated from the pack (pack defined as the group containing the breeding pair). If several days elapsed between the last location with the pack and the first observation alone, or vice versa, we arbitrarily assumed that separation (or reunion) had occurred midway between the two observations. Individuals were assumed to remain alone (or with the pack), even though one or more days without data might occur between consecutive observations. However, animals were only recorded as being at HS’s if they were actually observed there. Thus an animal that was separated for five days and located at a HS on day 1 and day 5, but was not located at all on the intervening days, was only recorded as being at the HS on two days. Thus our data will under-estimate the amount of time wolves actually spent at HS’s.

In conjunction with a study of wolf howling (Har-
ringon and Mech, 1979) wolves were located nightly, if possible. We drove within 500 m of them, where we attempted to elicit howling replies using human simulations of wolf howling (Pimlott 1960). Subsequent vocal replies and movements were recorded. We defined a Session (S) as a continuous period spent near a particular radio-collared wolf (usually less than 1 hour). A Trial (T) was a single series of howl stimuli (about 30 seconds). Usually three to five trials comprised a session. Reply rate (RR) was measured with reference to sessions (RR/S) or trials (RR/T).

Results
Abandonment
The HLP abandoned continuous HS use after the first week of September in 1972 and in early to mid-August in 1973. During those same years, in contrast, the JPP abandoned its HS on 1 October and 24 September, respectively. The nearly one month difference between packs may be related to differences in physical maturity. Compared with a standard weight (Van Ballenberghne and Mech 1975), the HLP pups were significantly heavier (96% of standard, n = 2) than the JPP pups (64% of standard, n = 8), and presumably were more advanced physically.

HS abandonment was often abrupt. In 1972, JPP pups were rarely located away from the HS before 1 October (twice, n = 26) and then were only short distances away (1.6 and 4 km). In the two weeks following abandonment, however, they were found an average 8.3 km away (n = 5) and moved at least 4.7 km between locations. Abandonment was equally abrupt for the JPP in 1973 and HLP in 1973 (Harrington and Mech 1979), but data were not sufficiently detailed to characterize the HLP HS abandonment in 1972. Thus by early September or October, HS use terminated and the pack, or the pups as a unit, did not revisit such sites until the following summer.

Post-abandonment HS use
Although packs did not return to their HS's after abandonment, single animals often did (Figures 1 and 2). Most such visits (92%) occurred in the two months following abandonment. All of the radio-collared individuals, including the alpha female of the HLP, returned at some point to a HS, but there was considerable variation in the extent of individual HS use. Unfortunately, we did not have an alpha male radio-collared during that period.

Most post-abandonment HS use occurred at only one HS in the JPP. During 1972 and 1973, the JPP used at least eight HS's, but only one was used extensively each summer (55 and 71 days, respectively). Others were occupied for up to 16 days. The extensively used HS later became the focus of post-abandonment use (51 of 67 wolf-days). Each of the other two sites used were visited by single animals soon after their release from foot-hold traps nearby. Thus temporary limited mobility may have influenced the use of the latter sites. At the primary HS used after abandonment, limited mobility did not appear to be an influencing factor.

![Figure 1](image_url)

**Figure 1.** Percent of time that individual radio-collared pups of the Jackpine Pack were located at homesites just prior to and after pack abandonment in 1972 and 1973. Each period is 15 days, with Period 1 commencing on the day of abandonment for each year (see text). “HS” = 15-day period prior to abandonment. The insert is the combined data for all seven pups. Some of the pups could not be followed through all 11 periods due to radio failure or death. Mean sample size for each point = 9.6 (± 5.9).

![Figure 2](image_url)

**Figure 2.** Percent of time that individual radio-collared yearlings or adults of the Jackpine Pack were located at homesites just prior to and after pack abandonment in 1972 and 1973. The periods and insert are the same as in Figure 1. Circle = yearling female; triangle = yearling male; star = adult male. Mean sample size per point = 9.6 (± 6.1).
Pups were usually captured by foot-hold traps one to two weeks before abandonment occurred. If injuries or physical development had limited pup travel, HS use should have gradually tapered off following pack abandonment. Instead, one of seven pups failed to return to the HS for at least two weeks, and four remained away for at least a month (Figure 1). One of the latter was a poorly developed male (47% of standard weight — Van Ballenberghe and Mech 1975), suffering severely from malnutrition (Seal et al. 1975). He was able to keep up with the pack for five weeks before his unexplained disappearance in early November.

Adults and yearlings were more likely to abandon HS’s gradually (Figure 2). Two of the three adults were located at HS’s within two weeks of pack abandonment. A yearling female continued to visit a HS for over two months and rarely traveled with the pack. Usually she trailed the pack, lingering at abandoned kills. Much of the rest of the time she spent at HS’s, sometimes in the company of one or two pups. However, she did not regularly travel with those pups. Rather, each had become separated from the pack in turn, and were reunited at the HS.

There was additional evidence that separation from the pack prompted many post-abandonment HS visits. We observed 38 instances when pups, yearlings, or adults were separated from the pack for periods ranging from 1 to 30 days (\( \bar{x} = 6.8 \)). During 15 separations, individuals returned one or more times to a HS, where they remained for minimum periods of 1 to 8 days (\( \bar{x} = 1.8, \ n = 22 \)). Separations that included HS visits were typically long (\( \bar{x} = 13.3 \) days, range 2–20); separations not involving HS visits were significantly shorter (\( \bar{x} = 2.7 \) days, range 1–8) (Mann-Whitney U = 328.5, \( n = 15, 23; P < 0.001 \)). During separations with HS visits, individuals were just as likely to visit HS’s early in the separation (22 of 48 locations) as they were later in the separation (16 of 44 locations). Normally, many days intervened between a HS visit and reunion with the pack (\( \bar{x} = 6.5 \) days, \( n = 14 \)).

Separations became rare by early December, coinciding with a significant increase in pack cohesiveness as measured by both the proportion of radio-collared animals located together and the actual pack size as observed (Figure 3). Prior to late November or early December, however, the pack traveled as a unit, and separations were uncommon until mid-February (Harrington and Mech 1979).

On occasions when several animals were located together at a HS after abandonment, there seemed to be little cohesiveness among them. Usually we knew by previous tracking that each had returned to the HS independently. For example, pup no. 5065 returned to a HS on 11 October, where he was joined by yearling female no. 2445 on 17 October and pup no. 5069 on 24 October. However, during their overlapping tenures at the HS, they were frequently 0.5 to 1.0 km apart. On 24 October, both pups howled spontaneously (no known stimulus) for several hours. During the howling they were 50-100 m apart, and did not move closer during the howling bout, suggesting that their howling was intended for animals not at the HS. Harrington howled after the pups quieted, and they immediately moved towards each other as they replied. Several days later pup no. 5069 left the HS, but pup no. 5065 remained for at least another week. The yearling had departed previously.

**Elicited howling**

After continuous HS use terminated, single animals were not likely to be found at HS’s. This section will deal solely with them, although data from pairs or trios paralleled those from singles.

Separated pack wolves, except alpha males, rarely reply to simulated howling when alone and away from HS’s (Harrington and Mech 1979) (Figure 4). However, they are very responsive when at HS’s, even though alone (Figure 4: HS vs. non-HS, \( G = 22.298, P < 0.001 \)). For example, beta-male no. 2449 never replied to howling at non-HS locations (\( n = 14 \)), but did at HS’s (\( n = 3 \)). The only adult to reply at a non-HS location, when alone, was an alpha male.

During sessions when they replied, single pack wolves answered more trials at HS’s (59%, \( n = 56 \)) than at non-HS locations (35%, \( n = 49 \); \( G = 6.224, P < 0.05 \)). At the latter locations, over half the replies were obtained from an alpha male; because he was
never located alone at a HS, we do not know his reply rate there.

The number of howls elicited during a session was significantly greater at HS’s (Figure 5) (Mann-Whitney U = 24, P < 0.05). In addition, all of the non-HS sessions were terminated by the wolf either retreating or no longer replying. However, during nearly half of the HS sessions the wolf gave no indication of ceasing to howl until we left.

Data from the two most responsive adults is of further interest. Though alpha male no. 2499 howled 66 times at a non-HS location, these howls were obtained in 16 trials. His longest two bouts were of seven and 11 howls. In contrast, beta-male no. 2449 howled 54 times at a HS in reply to only five trials. His longest bouts were of 18 and 24 howls. Thus our data suggest that, once stimulated, a single wolf’s reply is typically much longer at a HS.

Also, we found that single pack wolves never (n = 20) abandoned HS’s during howling sessions, some of which lasted an hour or more regardless of whether they replied or not. At other locations, however, retreats occurred during 32.5% (n = 77) of howling sessions, and were more common, and often immediate, if the animal replied (50%; n = 8) than if the animal remained silent (30%; n = 69). Yearling male no. 2489, for example, replied with one howl to a trial and then retreated so quickly that radio contact indicated that within 10 min it was 3-5 km away.

A final example further illustrates this difference in wolf behavior while at HS’s and other locations. Pup no. 2445 had separated from her pack 1-2 days prior to 6 November, when she was located 2 km from a HS. During a howling session, she replied to only one of five stimuli with five howls, two of which were abnormally short (0.2 and 1.7 s). Immediately after her last howl, she started traveling, and had reached the HS within 30 min. She then replied to two of four trials with three and 13 howls respectively, and remained at the site throughout the session.

**Discussion**

Previous studies have indicated that HS usage is related to pup development, and that once pups are able to travel, HS use is terminated (Murie 1944; Joslin 1967; Clark 1971). Our results were consistent with this view, at least as far as the initial abandonment was concerned, since its timing correlated with pup development. However, our results also indicated that HS’s continued to play an important role for wolves of all ages after their use as pup nurseries ended. In this later role, limited mobility due to development or injury did not seem to be an important factor.

Our data suggest that HS’s can serve as safe refuges where wolves can retreat when threatened, disturbed, or separated. Most long separations, which undoubtedly cause distress in pack members, especially pups, were typified by visits to HS’s. The animal may remain there for days and not retreat despite alien howling nearby. Thus, at this time, HS’s can serve as true “rendezvous” areas, since the site itself no longer harbors any other important attractant (i.e. food, young, etc.).

We found that typically only one HS was used consistently after abandonment, and that this HS was one used most often during summer. This suggests that positive reinforcement plays an important role in the acquisition of this site preference. For example, yearlings and adults usually travel alone or in small groups during summer (Joslin 1967; Mech 1966; Clark 1971). They are most likely to meet at HS’s (Clark 1971), especially the most frequently used site. Such meetings are normally a positive event (Mech 1970; Peterson 1977), and should provide positive reinforcement for HS visits. For pups, HS’s are areas
of contact with adults, of feeding, and of play (Murie 1944; Theberge and Pimlott 1969). Thus the pups, too, should form a positive association with the site. When separated, and perhaps distressed, these animals seek out and remain at HS's simply because of former positive experiences there.

The decline in HS use throughout fall could result from lack of continued reinforcement provided by reunions with packmates. Most HS visits we recorded did not lead to reunion for the separated wolf. Generally, an individual eventually left the site and traveled for an additional week before it was reunited. The lack of reinforcement for HS visits should lead to their termination as individuals learn that returning to a HS is not an effective way of relocating their pack.

It seems puzzling that wolves should have difficulty relocating the pack, since howling (Harrington and Mech 1979) or scent trailing (Mech 1970; Clark 1971) provide ready means for making contact. It would be of interest to know whether these separations are voluntary or involuntary. An involuntary separation could be caused by either slow physical development or injury that limits mobility, or by social pressures that force the animal into a peripheral role (Zimen 1976). Voluntary separations could include lingering at a kill to continue feeding while the pack resumes travel, or foraging independently, as most wolves do in summer.

In our study population, there may be no compelling reason for wolves to associate closely in the pack until early winter. Groups of wolves are rarely found away from HS's during summer when hunting is easily accomplished by single animals (Joslin 1967; Mech 1977, 1970). In fact, since summer prey such as deer (Odocoileus virginianus) and moose (Alces alces) young, and beaver (Castor canadensis), are relatively dispersed, solo hunting should result in more prey items encountered per unit effort than would group hunting.

However, by early winter, these prey become scarce. Beaver are effectively locked under ice by early December; deer concentrate in winter (Nelson and Mech 1981), and moose are large enough to require group hunting. Thus the increase in pack cohesiveness, and the decline in separations and HS use, may result from these changes in prey availability. Undoubtedly yearlings and adults are affected more by this change than pups, since pups are still largely dependent on others for food at this age (Mech 1970). Thus, once solo hunting becomes ineffective, individuals begin to associate more closely with the pack (Mech 1966; Clark 1971), ending the need for HS's.

As demonstrated by their responses to simulated howling, single wolves of all ages appear to be more confident and secure at HS's than elsewhere in their pack's range. During howling sessions their replies were more frequent and prolonged, and in contrast to their behavior elsewhere, they never retreated. They often continued to reply as long as we howled; one replied for over an hour and was still going strong when we left. Away from HS's, wolves usually replied with only one or two howls.

The attachment by wolves to a HS is independent of any important resource, such as food, a den, or young. Such site-attachment can be an important phenomenon in the dynamics of a species' spacing system (Waser and Wiley 1980). We have suggested elsewhere that the spacing pattern of wolf packs is maintained by avoidance, together with site-attachment (Harrington and Mech 1978). The present study, with its demonstration of strong site-attachment independent of a resource, supports that hypothesis.

Finally, this study provides insight into the use of captive situations to draw conclusions about certain aspects of wild wolf behavior. All captive situations are basically similar to year-round HS's. Wild wolves, on the other hand, utilize HS's regularly only during summer, sporadically through fall, and rarely if ever in winter or spring. Because behavior can differ dramatically between HS's and elsewhere, one must be cautious about the conclusions drawn from captive studies. This seems particularly true regarding the responses of captive wolves to the howling or scent marks of strangers.

Acknowledgments
This study was supported by the U.S. Fish and Wildlife Service, North Central Forest Experiment Station (USDA), World Wildlife Fund, Ober Charitable Foundation (now Mardag Foundation), and an NSF grant to the Psychobiology Program, SUNY, Stony Brook. We thank the following individuals for their assistance: Robert Himes (deceased), Jeff Neenber, Glynn Riley, Dwight Streblow, Tim Wallace, and numerous student interns.

Literature Cited


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Notes

Weasel Skull in Short-eared Owl Pellet

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The first record for the utilization of a Short-tailed weasel for food by a Short-eared Owl is documented.
Key Words: Mustela erminea, Asio flammeus, skull, pellet

Numerous studies of the foods of the Short-eared Owl (Asio flammeus) have been reported (e.g. Craighead and Craighead 1956; Mikkola and Sulkava 1969 and Clark 1975). No records of weasels (Mustela spp.) as prey of Short-eared Owls are given in these or other publications consulted.

In the late evening of 15 June 1980 an adult Short-eared Owl was observed to turn quickly and dive into a patch of alfalfa (Medicago spp.) in the middle of a large field of early wheat, east of Dauphin, Manitoba. On 17 June I located one dark brown, downy-plumaged young in the alfalfa patch. An adult owl flew into view, doubtless in response to the hissing of the owl, but no nest was discovered. On 8 July I returned to the field and found 2 young Short-eared Owls, both capable of short flights, and an adult owl which maintained a vigil over the young. I collected a number of raptor pellets from the top of an old bale of hay at the edge of the alfalfa patch.

One pellet contained the skull of a weasel. Measurements of the skull were: condylobasal length 36 mm; zygomatic breadth 19 mm. The postglenoid length of 19 mm was 53 percent of the condylobasal length which identified the species as a Short-tailed Weasel Mustela erminea (Hall and Kelson 1959). The posterior half of the parietal region of the skull was fractured and indented (Figure 1) which suggested that the weasel was killed by the raptor's bill. The pellets also contained the skulls of Meadow Voles (Microtus pennsylvanicus).

On 10 July, an adult Short-eared Owl was seen standing on the hay bale. No other raptors were seen in the vicinity. Neither owls nor any other raptors were seen in the area on 11, 14 and 17 July. The pellet containing the weasel skull was almost certainly cast by a Short-eared Owl.

Literature Cited


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Accepted 11 June 1981
Range Extension of the Threespine Stickleback, *Gasterosteus aculeatus*, to Manitoulin Island, Ontario

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Eleven Threespine Sticklebacks were found in the waters of Southbay, Manitoulin Island. This extends the range in the Great Lakes from Niagara Falls to central Lake Huron. The fish were of the *trachurus* form.


During the week of 22 June 1980, I collected 11 Threespine Sticklebacks, *Gasterosteus aculeatus*. Their identification was confirmed by Dr. E. J. Crossman, Department of Ichthyology and Herpetology, Royal Ontario Museum. The fish have been deposited there under accession number 4192.

These fish were found at the Ontario Ministry of Natural Resources South Baymouth Fisheries Research Station, Manitoulin Island, Lake Huron (45° 35'N, 82° 01'W). Specimens were caught with a 10 m seine net in a bed of *Scirpus* adjacent to the workshop at the research station.

This is the first collection of Threespine Sticklebacks to be taken above Niagara Falls. This species has not been found in Lake Erie or Lake Saint Clair (E. J. Crossman, personal communication). This record extends the range of this species some 300 kilometers.

Three forms of Threespine Sticklebacks exist: *trachurus* the marine form, *leirus* the freshwater form and a hybrid form. Using the criteria established by Hagen (1967) for lateral plate counts, standard length, body depth into standard length, and number of dorsal and anal fin rays, the 11 fish caught in Southbay were of the *trachurus* form. Another case of finding the marine form in a land-locked situation has previously been reported by Münzing (1962).

There were three females and eight males. All were in the prespawning condition. The following year seven more Threespine Sticklebacks were caught by seine netting in the same area.

I thank E. J. Crossman of the Royal Ontario Museum and Dr. B. A. Henderson and J. A. Reckahn who encouraged me to write this note.

**Literature cited**


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Accepted 18 November 1981
Apparent Case of Surplus Killing of Caribou by Gray Wolves

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Seven apparently healthy adult Caribou were killed and only partially consumed by a pack of Gray Wolves in late March 1979 along the Copper River in southcentral Alaska. Deep snow apparently contributed to the vulnerability of the Caribou.

Key Words: Gray Wolf, Canis lupus, Caribou, Rangifer tarandus, surplus killing.

Several investigators have documented instances in which Gray Wolves (Canis lupus) killed more prey than they consumed. Most of the reported incidents of surplus killing (Kruuk 1972) occurred during winter months. Mech et al. (1971) reported surplus killing of White-tailed Deer (Odocoileus virginianus) in Minnesota; in Sweden, Bjarvall and Nilsson (1976) reported surplus killing of eight domestic reindeer. Miller and Broughton (1974) observed surplus killing of Caribou (Rangifer tarandus) calves during summer 1970. All of those observations, although of interest to students of predator/prey relationships, represent the exception to generally accepted principles of predation. To better interpret their significance to both predator and prey, further explanation of circumstances surrounding such observations is needed. We describe what appeared to be surplus killing of Caribou by Gray Wolves during winter 1979 in the Nelchina Basin of southcentral Alaska, and provide an interpretation of the events leading to it.

On 31 March 1979, seven Caribou carcasses were observed within a 1 km radius along the Copper River near its confluence with the Indian River. Tracks and puncture marks suggested the Caribou had been killed by a pack of two to four Gray Wolves. The amount of flesh taken from these carcasses was subjectively estimated as follows: 1–90%, 5–50%, 1–20%. Because all carcasses were scavenged by Bald Eagles (Haliaeetus leucocephalus), Ravens (Corvus corax), and Red Foxes (Vulpes fulva), we were unable to estimate the amount consumed by wolves.

Ages of Caribou were estimated on the basis of tooth wear (Skoog 1968). Percent femoral fat was used as an indicator of physical condition (Neiland 1970). Ages ranged from 2-5 years. The percentage of fat in femurs ranged from 52-88%, and averaged 74% (Table 1). We concluded, therefore, that the animals were in fair-good physical condition. Neiland (personal communication) considered Caribou with less than 25% femoral fat to be in poor physical condition.

Mech (1970) discussed the likelihood of deep snow contributing to excessive killing of ungulates by wolves. On 29 March 1979 snow depth at a snow course near the Sanford River was 92 cm (U.S. Geological Survey 1979). This was 44% above the 12-year average of 64 cm. Only during the severe winter of 1971-72 did snow depths exceed those recorded on 29 March 1979 at that station. Therefore, deep snow probably made the Caribou more vulnerable to wolves than normal. Four of the Caribou were killed on the Copper River where snowpack was hard and footing was good, but tracks indicated they were chased through deep crusty snow before reaching the river, and they likely were exhausted. The other three caribou were killed in deep crusty snow which undoubtedly reduced their speed.

During relatively mild winters, Wolves completely consume most Caribou killed (Ballard et al. 1981). However, during relatively severe winters, trappers, guides, and others report the occurrence of multiple, simultaneous killing of Caribou, and a subsequent failure of the wolves to consume all of the flesh. Human disturbance probably caused some of the kills to be permanently abandoned by the wolves. Whether all of the flesh would have been consumed at such kills is unknown. Perhaps during severe winters surplus killing by Wolves may be more common than pre-

### Table 1. Ages and physical condition of Caribou, R. tarandus, killed and not fully consumed by wolves in late winter 1979 in the Nelchina Basin of southcentral Alaska.

<table>
<thead>
<tr>
<th>Caribou No.</th>
<th>Age (Yr)</th>
<th>Sex</th>
<th>Femoral Fat</th>
</tr>
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<tbody>
<tr>
<td>55108</td>
<td>3-5</td>
<td>F</td>
<td>88.0</td>
</tr>
<tr>
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<td>3-5</td>
<td>F</td>
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</tr>
<tr>
<td>55113</td>
<td>3-5</td>
<td>F</td>
<td>83.0</td>
</tr>
<tr>
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<td>2+</td>
<td>F</td>
<td>63.0</td>
</tr>
<tr>
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</tr>
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<tr>
<td>S.D.</td>
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</table>
First Breeding Record for the Nashville Warbler, *Vermivora ruficapilla*, in Alberta

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The first documented breeding record for the Nashville Warbler (*Vermivora ruficapilla*) in the province of Alberta is described. This extralimital breeding record may be related to unusual weather during the spring migration.

Key Words: Nashville Warbler *Vermivora ruficapilla*, Alberta, migration.

The breeding range of the Nashville Warbler (*Vermivora ruficapilla*) is unique among North American parulids in that there are disjunct populations in eastern and western North America, separated by a wide gap in the region of Alberta and western Saskatchewan (A. O. U. 1957; Godfrey 1966; Mengel 1964, 1970). The species is considered accidental in Alberta, although there are a number of spring and fall reports (Salt 1973; Sadler and Myres 1976; Salt and Salt 1976). A reported breeding record in the Cypress Hills in extreme southeastern Alberta (Smith and Wershler 1968; Salt 1973) must be discounted because of the probable misidentification of the species (Smith and Wershler 1969). The present account provides the first substantive evidence of breeding by the Nashville Warbler in Alberta.

On 29 May 1980 we observed and tape-recorded a male Nashville Warbler singing loudly and frequently in a large area of willows bordered by aspen-pine woods on Link Creek, approximately 50 km southwest of Calgary. This male was seen or heard in the area on eight other occasions between 30 May and 3 July. We had been in the area daily since 1 May and should have detected the bird if it had been present (or at least singing) prior to 29 May.

At 0845 on 4 July, the male and a female were observed carrying insects in the area where the male had been seen most frequently. Over the next hour, both birds repeatedly carried food to at least three locations in the willows, where we finally found a fledgling perched. It was capable only of flights of less than 10 m and had certainly come from a nearby nest.
M. R. L. judged the fledgling to be 12–14 days old, leading to a calculated initiation for the clutch of 7 June ± 3 days.

Sadler and Myres (1976: 210) suggested that records of Nashville Warblers in Alberta represent birds from the western population, and certainly the British Columbia breeding populations are closest (ca. 250 km) to the location of our record. However, our breeding pair conceivably could have come from the east.

From 22 – 27 May a major low pressure center was situated over the northern Great Plains, bringing heavy rain and strong (40 – 60 km/h) northerly winds to the Calgary region. Between 26 – 29 May we saw a male Bay-breasted Warbler (*Dendroica castanea*) and at least four Magnolia Warblers (*D. magnolia*) on our study area. Neither species had been recorded in the vicinity during the previous six years of field-work. A similar wave of unusual “northern” migrants was noted in Calgary during the same period (A. N. Wiseley, personal communication). The counter-clockwise movement of air around this center could have carried Nashville Warblers from west-central Manitoba (ca. 900 km away) across the Canadian prairies and into western Alberta.

**Acknowledgments**

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**Literature Cited**


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**Use of Trees by Ermine, Mustela erminea**

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A review of the literature indicates that weasel arboreal activity was usually observed in the contexts of escape or prey capture. We report seeing an Ermine (*Mustela erminea*) at rest for several hours in a tree.

Key Words: Arboreal, Ermine, *Mustela erminea*, weasel.

It has been suggested that weasels are semi-arboreal. For example, Seton (1929) stated that weasels are “perfectly at home” in trees. However, his comment was, for the most part, based on observations of frightened weasels escaping into trees. In fact, most recorded observations of weasels climbing trees in the wild fit into one of two contexts: escape or prey capture. Rutter (1930) frightened a Long-tailed Weasel, *Mustela frenata*, which took refuge in a tree. De Vos (1960) used a freshly killed rabbit to entice a Long-tailed Weasel to climb a tree. Both Ermine, *M. erminea*, (Frith 1958) and Long-tailed Weasels (Jeanne 1965; Pearce 1937) have been observed pursuing Eastern Chipmunks, *Tamias striatus*, up trees. Booth (1945) saw a Long-tailed Weasal attempting to prey upon the nest of a flicker, *Colaptes* sp. In several
The following observation was made at Heart Lake on 1 November 1978, at a temperature of about – 5°C, under overcast skies, and with no snow on the ground. At 1000 h we introduced a male Ermine into a 900-m² fenced-in area of natural Jack Pine, Pinus banksiana, forest and observed it unobtrusively. In the course of exploring the pen the animal frequently climbed trees, including several near the edge of the pen, apparently trying to escape. During 4-5 h of intermittent activity it took no obvious notice of the observers. Finally it climbed to a height of about 7 m in a Jack Pine, and found a fork in a branch about 40 cm from the trunk. Within about 15 min the animal curled up; with the aid of binoculars we noted that its eyes were closed, from which we inferred that it was sleeping. Despite several gusts of wind and our attempts, after 2 h of observation, to dislodge it by shaking the tree, the animal stayed put. Between 2 and 3 h after we left it, the weasel was captured in a livetrap set at the base of the tree.

What possible explanation is there for the behavior we observed? The weasel showed no obvious notice of either of us, so it was probably not frightened. There was no food in the tree, and the animal showed no searching behavior. Snow acts as an insulator, so the lack of it, combined with the low air temperature may have created one of the lowest burrow temperatures of the year; thus trees may have been warmer than burrows. The initial exploratory behavior, and possibly attempts to escape from the pen, undoubtedly caused the weasel to climb trees, but the fact that it slept in one tree for several hours indicates that under certain circumstances Ermine may use trees for rest sites as well as for escape and prey capture.

Literature Cited

Seton, E. T. 1929. Lives of game animals: an account of those land animals in America, north of the Mexican border which are considered "game" either because they have held the attention of sportsmen, or received the protection of law. Doubleday, Doran; Garden City, N. Y.

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Reaction of Bison to Aerial Surveys in Interior Alaska

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The Delta Bison herd (Bison bison) in interior Alaska has habituated to some degree to certain human disturbances.

Key Words: Bison, Bison bison, aircraft disturbance, habituation, ungulates.

The behavioral reactions of Bison (Bison bison) to low-flying fixed-wing aircraft were recorded during aerial surveys (8 flights between 18 March–17 June 1980) of the Delta Bison herd in Interior Alaska. This introduced herd numbered about 280 adult animals in April 1980. Observations were made from a Cessna 185 or Helio Super Courier aircraft flying between 61 and 150 m agl. Forty-eight percent of the 59 Bison groups encountered were circled once as the pilot and biologists counted and recorded the reactions of the group to the aircraft; 20% of the groups were circled two or more times.

Only two of the 59 different Bison groups encountered showed any visible reaction to the aircraft. One group of 15 adult and yearling Bison standing on a frozen lake shore ran about 5 m as the plane circled once 30 m agl at a lateral distance approximately 61 m from the group. The second group of 20 adults and yearlings were lying and dusting on a dirt road as the aircraft approached. The group showed no visible reactions as the plane circled at 91 m agl; however, as the pilot increased the throttle suddenly to gain altitude, the group stood up and ran for about 1-minute. The 57 groups that showed no reaction to the aircraft included lone bulls, groups comprised of adults and yearlings, and groups containing calves; group size varied between one and 39 animals. I found no relationship between the reaction of a group to the aircraft and the size or composition of the group.

Previous studies on the reaction of Bison to fixed-wing aircraft in Wood Buffalo National Park have found that circling at altitudes of 180 to 240 m agl caused a few cows and sub-adults to run, but that the majority of animals appeared unaffected. Single flyovers at 120 m agl caused Bison groups to run, and circling at that altitude resulted in agonistic behavior among bulls and “appreciable flight behaviour and intra-specific strife” within the herd (Tempany et al. 1976). In this study, groups circled once or twice at altitudes between 100 and 150 m agl showed no visible reaction to the aircraft.

Herd differences in the reactions to aircraft disturbance suggest that the Delta Bison have habituated to some degree to certain human disturbances. The Delta Bison herd is subjected to a greater level of human activity than is the Wood Buffalo National Park herd. The summering and calving grounds of the Delta herd is within and adjacent to a military target range, where both small caliber and mortar fire is used. The Bison are harassed by farmers and the Alaska Department of Fish and Game in an attempt to keep them out of agricultural fields, and both sexes are hunted each fall. The Delta Bison are also subjected to a greater level of civilian and military air traffic than are those in Wood Buffalo National Park. The Bison I observed were in good physical condition, and therefore their general lack of response to the aircraft cannot be explained by poor condition.

Disturbances may cause physiological stress and increased energy expenditures in an animal even though no visible reaction is observed (MacArthur et al. 1979). Reactions to disturbances may also be delayed (Altmann 1958), and therefore not noted by observers in a rapidly-moving aircraft. Although most Bison groups in this limited study showed no visible reaction to the aircraft circling at altitudes as low as 90 m agl, this altitude should not be taken as a recommended minimum altitude because of the above considerations.

Acknowledgments

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Literature Cited


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On May 29, 1979, shortly after celebrating its 100th anniversary, the Ottawa Field-Naturalists' Club was saddened by the death of one of its most outstanding and beloved members, W. K. W. ("Bill") Baldwin. He was born on January 29, 1910, in York Township (now a part of Metropolitan Toronto), the youngest of seven children of Lawrence Heyden Baldwin and Ethel Mary Sylvia (Martin) Baldwin of Mashquotch, whose Irish ancestors had deep roots in southern Ontario, Canada West, and Upper Canada. The family record since 1799 included public service in politics, medicine, law, architecture, commerce, the armed forces, natural history and in museums of art and the natural sciences.

Bill received his early schooling at Bishop Strachan's School and Upper Canada College in Toronto (1917-1922) and later grades at Trinity College School, Port Hope (1922-1927). He graduated from the University of Toronto in 1931 with a B.A. degree in Biology (First Class Honours). Following graduation, he carried out research in plant morphology, under the direction of Professor R. B. Thomson in the Department of Botany, and was awarded the M.A. degree in 1932. His thesis was a study of sporulating development in a quillwort, _Isoëtes engelmannii_ A. Br.

In 1934 Bill travelled in the United States and abroad (United Kingdom, Germany, and France), visiting correspondents and research centres. He returned to Toronto to continue research in plant morphology, and to assist with the teaching of undergraduate courses in Botany at the University. In 1937 he joined K. M. Mayall in a pioneer study in conservation of the natural resources of King Township, York County, Ontario. Similar conservation studies were carried out by Baldwin in Durham and Northumberland Counties, Ontario, until the outbreak of war in 1939. Returning from a canoe trip in northern Ontario, he enlisted immediately as a private soldier in the Queen's York Rangers. In June 1940, he transferred to the Toronto Scottish Regiment (M.G.), and as a lieutenant went overseas in August where he faced the grim days of the "Battle of Britain" as a platoon commander. In September 1943, Bill married Margaret Stewart Patch of Montreal. Margaret had survived the sinking of the "Athenis" early in the war, and had been involved in Red Cross and other volunteer work.

Bill had returned in 1942 as an instructor and was posted to the infantry training centre at St. Johns, Quebec. He received the award of Member of the Order of the British Empire (M.B.E.), Military Division, in the King's Birthday Honours List of June 1944. He was demobilized in 1945 with confirmed rank of Major. Bill returned temporarily to teaching, first briefly at Dalhousie University, Halifax, and then as Senior Demonstrator for laboratory classes in the Botany Department, University of Toronto.

In May 1947 Bill Baldwin was appointed Botanist in the National Herbarium of Canada, Ottawa, under the late Dr. Alf Erling Porsild, then Chief Botanist. He began a series of botanical field surveys which soon focussed on the vegetation of the Canadian Boreal Forest Region. In 1947 he travelled up the east coast of James Bay and Hudson Bay by canoe with Ilmar Hustich, co-leader of a Finnish-Canadian expedition. In 1949 he accompanied T. H. Manning and four others in a Peterhead boat from Moosonee to Foxe Basin, where the party made the first known landing on islands later named Prince Charles and Air Force Islands, N. W. T. Subsequent field work was entirely in the Boreal Forest Region: in 1950, the Turtle Mountains to Baralzon Lake, Manitoba (with H. J. Scoggan); in 1951, to the Cochrane River and Nueltin Lake; from 1952-1955, throughout the Clay Belt in northern Ontario and Quebec; from 1956-1958, in the Hudson Bay Lowlands; in 1961, to the Upper English River area in western Ontario; in 1962, to Nichicun Lake, Quebec; and in 1966-1967, to the Mixedwood Forest Section located in parts of Manitoba, Saskatchewan and Alberta.

The IX International Botanical Congress was held in Montreal in 1959, and a number of field trips were arranged for the delegates, Bill led Field Trip No. 7 to the Boreal Forest Region, with nineteen members of the Congress participating. For this trip he produced a guide book and afterwards edited the report on the botanical excursion and its findings.

Bill Baldwin's interest in natural history was stimulated at an early age by association with the Toronto Field Naturalists Club and with the Federation of Ontario Naturalists up to the time of his enlistment. He was also a member of a small group of naturalists who secured a piece of land and built a cabin at Rattlesnake Point on the Niagara Escarpment, near Milton, Ontario. This group called itself the "RATTLESNAKE SYNDICATE" and included, among others, several notables of the Toronto region such as A. F. Coventry, J. R. Dymond, and T. F. Mellwrath.

In 1947, at a meeting of the membership committee of the Ottawa Field-Naturalists' Club, Bill suggested...
William Kirwan Willcocks ("Bill") Baldwin.
that the club launch a project to draw in young naturalists of school age. The Council of the club received this proposal enthusiastically and on February 21, 1948, appointed a Junior Membership Committee with Bill as chairman, to investigate the possible courses of action. With assistance from Herbert Groh, who had just retired from his position as Botanist at the Central Experimental Farm, the Macoun Field Club was founded under the joint sponsorship of the Ottawa Field-Naturalists' Club and the National Museum of Canada. The new group was managed by Bill for the first five years and has continued to the present day in fostering active interest in natural history among young people of school age. Membership is limited and at three levels, junior, intermediate and senior; its members meet weekly during the school year, carry out individual and group projects, and participate in hikes, field studies, and camping trips. Soon after the Macoun Field Club began, David Maddox, a retired geologist, was instrumental in starting an illustrated club journal called URSA MINOR (The Little Bear) to record the activities of the members. Members have included Victor Haines, Eric and Ruth Mills, John Smith, Francis Cook, Chris Durden, Cynthia Millman, Bill Seabrook, Pierre Taschereau, John, Elizabeth, and Hugh Scoggin, and more recently Arnet Sheppard, Gordon Hamre, and Loney Dickson. Some of these have gone on to professional careers in the natural sciences, conservation and museology. Early members can recall the relatively pristine environments of the Champlain Bridge region, the Hog’s Back, Rockcliffe Park, Dow’s Swamp, Campbell’s Quarry, and other favourite study haunts that have either changed drastically
or totally disappeared during Ottawa's more recent urban expansion.

Bill served on the Council of the Ottawa Field-Naturalists' Club for twenty years, including the immediate post-75th anniversary term of President (1955-1956). He was especially concerned with conservation issues and devoted long hours to the Mer Bleue conservation project in consultation with regional communities. Bill served also as a Director of the Federation of Ontario Naturalists. He took part in natural history radio broadcasts, both on local Ottawa stations (CFRA) and on the trans-Canada network (CBC). He lectured in the National Museum's Wednesday evening and Saturday morning series and served on the Lecture Committee for ten years. When, shortly after its formation in 1965, the Canadian Botanical Association formed special interest groups, Bill joined the Systematics & Phytogeography Section, participating actively on the Executive and later as Chairman of that Section. He was appointed chairman of a Subcommittee on Canadian Herbaria and was responsible for the production of seven parts of a "Review of Canadian Herbaria". The data gathered for this review were periodically updated and forwarded to the International Association for Plant Taxonomy in Utrecht for inclusion in INDEX HERBARIORUM, which gives information about the herbaria of the world. Bill's efforts are acknowledged in the Preface to the 6th edition of that work, published in 1974. Research on the Boreal Forest Region kindled in Bill an interest in the post-glacial history of the vegetation in northern Canada, especially in the Hudson Bay Lowland area. He was associated with INQUA (International Association for Quaternary Research) for several years and participated in the VII Congress in 1965, the first to be held in the New World. This consisted of a field conference in midland North America and sessions at Boulder, Colorado.

In 1968 Bill headed up a newly-formed museum committee to develop and implement plans for a botanical exhibition hall. The Victoria Memorial Museum building was closed from 1969 to 1974 to permit renovation of several display galleries and preparation of new exhibits to fill other halls. The Hall of Plant Life, occupying an entire wing on the fourth floor, was the last of the exhibit halls to be completed, and opened officially in May 1981. 0n a nearly full-time basis, Bill co-ordinated the preparation of approach papers and story lines by museum staff and specialists in universities, in consultation with designers, architects, and personnel from the display unit of the museum. Consequently, there was little time for his research and botanical field work, the latter reduced mainly to short trips to collect materials for the botanical dioramas and other exhibits. Bill eventually co-ordinated the planning of all the renovations and new exhibits for the Museum of Natural Sciences and also integrated these plans with similar developments for the Museum of Man, located in the west half of the museum building. This three-level assignment was conscientiously and successfully fulfilled by Baldwin until his retirement in 1972.

Bill Baldwin's research strengths were a result of his ability to organize, explore, examine and document carefully, an ability which may be traceable to his earlier military training. His field notes were made in pencil and later copied meticulously in ink. He kept accurate records of meetings and telephone enquiries; his memos were composed of numbered items and were always dated, with copies kept in personal files. To each assignment he brought a sense of responsibility, stability, and the need for thoroughness. Although, after retiring from the National Museum of Natural Sciences on May 15, 1972, Bill did not fulfill his declared intention of summarizing his botanical investigations in the Hudson Bay Lowlands, he will be remembered for his contributions to our knowledge of the flora of the Boreal Forest Region of Canada. His name is perpetuated as principal collector on the labels of thousands of specimens filed in the National Herbarium of Canada in Ottawa and on the numerous duplicates distributed to other herbaria in Canada and abroad.

Bill had a friendly, outgoing personality, "six foot plus" of energy and enthusiasm. He often referred to himself as the human step-ladder when helping others of shorter stature to reach specimens on top shelves of a herbarium case. A characteristic reply when greeted by a telephone caller by "How are you, Bill?" was "All the better for hearing your voice!" His favourite cuss-word was "Holy myrtilloides". On hearing that the
administrators in their ivory tower uptown had requested that the budget be resubmitted on their newly-devised set of forms, or that a ten-year forecast was required by 5 p.m. the next day, he was wont to remark that “somebody is playing silly buggers again.” A difficult job or a detailed report could be completed on schedule only, or preferably, by retiring behind closed doors “with a wet towel and a bottle of whisky”. Bill was widely read, a fine extemporaneous speaker, and a great conversationalist who for many years enlivened the museum’s “12:15 luncheon club” with his cogent observations and friendly homilies. His habit of cigarette chain-smoking was captured admirably by museum artist Pat Haldorson in a caricature submitted for the commemorative scrapbook presented to Bill on the occasion of his retirement party at the R.A. Centre on October 28, 1972.

Dr. Homer J. Scoggan, an intimate associate of Bill’s for twenty-five years, has noted the remarkable fact that never during that long period had he heard Bill pass a hurtful remark about anyone and that, if given the opportunity, he would certainly have chosen Bill as another quarter-century colleague. Bill was his ideal companion in the field, when friendships often undergo the supreme test.

During his early days in Toronto, Bill became interested in the wild flower paintings by Robert Holmes (1861-1930), seventy-three of which are housed in the Art Gallery of Ontario at Toronto. Bill identified the botanical subjects in these water colours by scientific and common names and was influential in pressing for their public exhibition. While at the University of Toronto, Bill was a founding member and president of the choral society which became the Hart House Glee Club and was later a member of the Ottawa Choral Society. His other hobbies and interests were remarkably diverse. He was a “home gardener” and also maintained a life-long interest in the Royal Botanical Gardens at Hamilton, where he presented a lecture entitled “Forest to the Northern Treeline” on February 10, 1972. In the sporting world he enjoyed curling, squash, and billiards, and was a long-time fan of Toronto professional hockey and football teams. He was an ardent canoist and keen outdoorsman, ready to suffer the vagaries of weather and challenges of topography during collecting expeditions in the uncharted wilderness of the Hudson Bay Lowlands.

Bill was an active member of St. Columba’s Anglican Church and served on the Ottawa East Diocesan Program Committee. He took part in the civic affairs of Manor Park, including a stint with the Volunteer Fire Brigade, and served on the Executive of the Manor Park Community Association and the Home and School Association. A life-long Conservative, in post-retirement years he campaigned for his party in the riding of Ottawa East.

Bill is survived by his wife Margaret and two daughters, Heather of Montreal, and Katherine (Mrs. Gordon Black) and grandson Douglas of Ottawa. His contributions to the natural sciences live on through his long service for the Ottawa Field-Naturalists’ Club, in his published writings, mainly on his favourite subject of the Boreal Forest Region of Canada, and through the extensive museum collections and modern botanical displays he helped to build. More subtly and far-reaching was Bill’s impact on the minds and hearts of his colleagues and on generations of young “Maconers” who came under his kindly and quietly inspirational leadership.

Acknowledgments
The writers are especially grateful to Vi Humphreys for her stimulus and encouragement and to Margaret Baldwin for her helpful contributions and permission to use the portrait and the caricature by Pat Haldorson.

List of Publications


Baldwin, W. K. W. 1938. Report on duck food, cover plants and survey work. In The Natural Resources of King
Township, Ontario. By K.M. Mayall. Published privately by Aubrey Davis, Toronto. 54 p., maps.


News and Comment

Notice of an Amended Motion Passed at the 103rd Annual Business Meeting of The Ottawa Field-Naturalists' Club

Notice of four motions to amend the Constitution of The Ottawa Field-Naturalists' Club was given in the Canadian Field-Naturalist 95(3): 369-370.

At the 103rd Annual Business Meeting, 12 January 1982, it was moved by P. Naraway (2nd C. Gruchy) that the proposal to amend Article 10 be amended further to read as follows:

Article 10. Standing Committees. Seven standing committees, each consisting of at least six members, shall be appointed by the Council, namely: an Executive Committee, a Publications Committee, an Excursions and Lectures Committee, a Finance Committee, a Conservation Committee, a Membership Committee and an Awards Committee. The Chairman of the Executive Committee shall be the President. The Chairman of each other standing committee shall be chosen from among the members of Council.

Both Vice-Presidents and the Recording Secre-
tary shall be members of the Executive Committee. The membership of each standing committee shall contain at least one of the Vice-Presidents. The Treasurer and the Business Manager of The Canadian Field-Naturalist shall be members of the Finance Committee. The Editor of The Canadian Field-Naturalist and the Business Manager of The Canadian Field-Naturalist shall be members of the Publications Committee. The Chairman of the Excursions and Lectures Committee, the Conservation Committee and the Membership Committee shall have power to add to their committees.

The Naraway amendment added the Awards Committee to the list of standing committees.

The motion as amended was carried, as were the other three motions.

E.F. Pope
Recording Secretary

Lois Fenna — Honoured

The Edmonton Natural History Club is pleased to announce that Lois Fenna was awarded the seventh annual Loran L. Goulden Memorial Award for outstanding work on the natural history of Alberta at the Club's Annual Meeting on 12 January 1982. Dr. Fenna is recognized by this award for her efforts in educating naturalists of the future through her work at the Ministik Hills Field Study Centre near Edmonton.

Martin K. McNicholl
Chairman, Loran L. Goulden Memorial Award
Selection Committee

The St. Lawrence Valley Natural History Society

On 7 December, The St. Lawrence Valley Natural History Society launched its program to build its ecomuseum TAWINE:KE*. The site chosen for the facility comprises 50 acres on the Macdonald Campus at Ste. Anne de Bellevue, Quebec.

The living natural museum is designed to broaden the visitor's perception of the St. Lawrence Valley. It is an entertaining and educational experience which will take the uninitiated through the region's geography, geology and biota to man's use of its resources in time. Hopefully, the visitors' appetites wet by their experience in the living museum, they will go on to the interpretation centre. At this point, and with the help of interpreters and docents, the visitors will spend additional time learning about one or more facets of the Valley's natural resources. Beyond the guided interpretation program, visitors will be able to walk in a 35-acre low-intensity use area, managed particularly for wildlife and its viewing.

Weather will be an important factor in the selection

* TAWINE:KE is pronounced "Dawenaiga", and is the Mohawk expression for "where the otter lives". The playful otter ecologically bridges land and water and has played an important role in the fur trade which began in the Valley. Thus it was chosen the emblem of the Society.

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of interpretive programs and the use of the wildlife area, but not in the living museum. This facility will be open 365 days a year. Visitors will enter an underground building and in the next two hours move through a series of displays which will characterize the evolution and natural history of the Valley. Some exhibits such as those dealing with geology, geography or plant communities will be inside and static, but the largest number of the displays will be living, active and outdoors — viewed from the comfort of the indoors. The museum will not concentrate on natural history alone but will go on to describe how man has developed the resources of the Valley for his own use, and how man can live within the limits of those resources.

In keeping with this theme, the building will itself be a testimony to man's ability to adapt himself to the sometimes harsh environment of the St. Lawrence Valley. The building will be an energy miser using solar energy, heat from lights, heat pumps, thermal mass and the most modern insulation techniques in order to conserve energy and demonstrate how this might be done.

When does this all happen? The Society has planned to open the museum's doors in 1984. Meanwhile, several committees have been formed to cope with the financial design, engineering, and landscape aspects of this project. The 4-million dollar program is ambitious but there are more than four million people within the Valley and these people should know more about their home so that they, too, can sit back and really appreciate the splendors of this part of North America.

**J. Roger Bider**
President
Société d'histoire naturelle de la vallée du St. Laurent/St. Lawrence Valley Natural History Society, 2111 Bord du Lac, Ste. Anne-de-Bellevue, P.Q. H9X 1C0

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**The Ontario Breeding Bird Atlas**

The Federation of Ontario Naturalists and the Long Point Bird Observatory are co-sponsoring a project to produce detailed, up-to-date maps of the breeding distribution of every species of bird which breeds in Ontario. Data collection for the Ontario Breeding Bird Atlas began in 1981 and will continue through 1985.

The concept of producing distributional maps based upon a grid system was originated with the *Atlas of the British Flora* in the 1960's. Birdwatchers soon adopted the idea and, after five years of field work, produced the *Atlas of the Breeding Birds in Britain and Ireland* in 1976. The popularity of atlassing (10-15,000 people contributed information to the British atlas) spread quickly. All European countries are either collecting data for their atlas projects or have already completed them. The European Ornithological Atlas Committee is organizing an atlas of the whole of Europe, which will be mapped using a 50 km grid from 1985-1989. Outside of Europe, breeding bird atlases are also underway or recently completed in several African countries, Australia, New Zealand and numerous U.S. states. The Ontario Atlas is the first project of its kind in Canada*, although it is only one of many similar projects underway world-wide.

The 10 x 10 km squares of the Universal Transverse Mercator grid, which is found on 1:250 000, 1:50 000 and 1:25 000 scale topographic maps, have been used to produce maps for the Ontario Atlas project. Volunteer participants (atlassers) visit a square during the breeding season (most data will be collected from February to August) and record breeding evidence for each species they encounter. The 16 types of "breeding behaviour" which are likely to be encountered are assigned to three levels of breeding evidence: a singing male in breeding habitat would be a "possible" breeder; a territorial bird would be a "probable" breeder, and a nest and eggs would "confirm" breeding for that species in that Atlas square. Probable migrants and other non-breeders are listed separately. For each species observed in a square, the atlasser records breeding evidence and an estimate of abundance on an Atlas data card. At the end of the breeding season, the cards are sent to one of 41 regional coordinators.

When data collection has been completed, distribution of every species will be represented by a computer-produced map showing the squares in which breeding evidence was found. The level of breeding evidence and the abundance of the species in each square also will be shown.

At least 16 hours of atlassing by an experienced observer are necessary to cover a square "adequately".

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*A similar project, including the three Maritime Provinces, is in the planning phase, and data collection is hoped to begin in 1983. For more information, contact David Christie, RR #1, Albert, New Brunswick E2A 1A0, phone 506-882-2100.
Adequate coverage has been defined as the recording of breeding evidence for at least 75% of the species expected to occur in a square in that region. Most squares in southern Ontario are home to approximately 100 breeding species — a total far higher than was predicted before atlassing began, which illustrates our ignorance of breeding bird distribution in the province. The required coverage can be spread over several years if necessary, but coverage in one year is encouraged so that atlassers can begin work on another square the following year.

Although the bulk of Atlas data will be collected by atlassers who take responsibility for the coverage of a square, other more casual information will also be used. For example, researchers, banders, park naturalists and other field workers also can record breeding evidence. This information will then be added to that already available for that square. Evidence for common as well as unusual species will be useful to the project because, no matter how much effort an atlasser puts into coverage of a square, some species will always be overlooked.

The Atlas project is aiming for comprehensive coverage of the province by the end of the 1985 breeding season — that is, at least the minimum coverage of every square in the province. However, owing to the large area to be covered and the uneven distribution of the atlassers, priorities of coverage have been established. The province has been divided into 3 sectors. Sector 1 consists of the portion of the province roughly north to Sudbury. Sector 2 is a strip about 70 km wide along the top of Lakes Huron and Superior, and Sector 3 is the area north of Sectors 1 and 2 up to Hudson Bay. The highest priority of the project is to cover each of the 2000 squares in Sector 1 before the end of the 1985 breeding season. Sector 1 is the most populous and environmentally disturbed portion of the province; it is the area where avian populations are most likely to undergo changes in the future. The effort expended in atlassing Sector 2 will depend to some extent upon progress in Sector 1. Coverage of Sector 3 will depend somewhat on the progress in Sectors 1 and 2, but will probably include only (say) one 10 x 10 km square in each 50 x 50 km square.

In 1981 approximately 500 atlassers took part in the project, but there may be 1000 people in the province with the skills necessary to collect information for the Atlas. Solicitation of assistance is continuing. This project, by utilizing the enormous potential of the many bird-watchers in the province, is an important step towards increasing cooperative naturalist projects in Canada. Detailed work on this scale would be impossible by any other means.

Atlas maps will give a far more detailed representation of breeding bird distribution than has previously been possible. It will not be necessary to assume that a species occurs throughout the area between known breeding locations, as has been the case to date in the preparation of maps of breeding distribution, because coverage of the province will be comprehensive.

The Atlas, which will represent a large bank of information available for easy perusal or future research, will serve as a useful reference for Ontario's birders, ornithologists and environmental planners. The Atlas will establish a base against which future changes in distribution and abundance of avian species can be compared. Information contained in the Atlas will also be useful for determining the distribution and status of the province's unusual or endangered species. For example, the *Atlas of the British Flora* was used to assemble a "Red Data Book" of English plants. Any species which occurred in less than 15 of England's 2000 Atlas squares was classified as endangered. Management procedures aimed at protecting these species and their habitats are already underway. A similar procedure involving the birds of Ontario would certainly be of great value.

Book Reviews

ZOLOGY

The Age of Birds


In the 1967 undergraduate ornithology course at Cornell University I was assured that, however inconsequential the morphological divergence within avian orders might be, these were the largest groups of birds which could be considered related. The progress of avian paleontology since then has been little short of marvelous. Even with thorough reviews of old theories(5,2),(994,995) of the origin of flight, feathers, and Archaeopteryx, more than half of the paleontological and systematic references in The Age of Birds have been published since 1967. On the basis of this burst of new information Feduccia is able to allocate almost all birds to more or less well defined superordinal groups.

This is a well-written general account of the paleontology and relationships of birds, centered on three areas of research by Feduccia: 1) a persuasive defense of arboreal and flying habits in Archaeopteryx; 2) the light thrown on the affinities of water birds by the Eocene stilt-becoming-a-duck-rather-than-a-flamingo, Presbyornis; and 3) the classification of land birds by derived conditions of their bony stapes. These are interspersed with accounts of the evolution of diving and flightless birds, and classic unresolved questions: the reptilian ancestor of the birds is not located, the ‘Falconiform’ and ‘Ciconiiform’ families are poorly understood, and the ratites are considered unrelated (in apparent contradiction to DNA hybridization data).

The illustrations are numerous but of variable quality. There are pictures of bones and skeletons (though perhaps fewer lineups of the ends of long bones than one would have expected), reproductions of many classic reconstructions of extinct birds, and a multitude of drawings and photographs of extant birds. Many of the drawings of modern birds are stiff and ill-proportioned, and Heilmann’s sensitive vignettes of hypothetical proavians are replaced by crude, heavy-lined drawings.

By the end of this decade we can expect a synthesis of paleontology, comparative anatomy, and biochemical similarity which will reveal much more of the history of birds, but if (as the cladists assure us) phylogeny is the most important thing to know about a group of organisms, then this is the best introduction to ornithology now available.

FREDERICK W. SCHUELER

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Pheasants in Asia, 1979


This slim, attractively produced book contains papers which were read to an international symposium, held in the homeland of India’s famous Gurkha regiments, and it has far more to interest Canadians than its title may suggest. It not only deals with conservation, which today interests everybody, but, at point after point, those who addressed the conference in Kathmandu were dealing with problems that we also face — for example, with the Whooping Crane.

Today at least 19 of the world’s 49 species of pheasants are, like the Whooping Crane, endangered, and for the same reasons. They, too, are large edible birds, as popular on the table as the Whooping Crane was in bad old days in the West. Likewise, because today more and more new farmland is needed to feed ever-growing human populations, their natural habitats are being destroyed, as has happened to so many of our prairie marshlands where Whooping Cranes once bred. Again, their survival also depends to a sad degree on captive breeding; indeed, the plight of some of them is even worse than that of the Whooping Crane. A wild breeding population of Whooping Cranes does still survive in our Wood Buffalo Park, but of some species of pheasants no population is known to exist except in captivity; and a point worth mentioning here is the fact that Canadian breeders are helping maintain captive stocks of some seven or eight endangered pheasant species — i.e., just about the limit practicable in our climate. Yet again we know how much conservation depends on the public being aware that it is necessary — in short, on education — and hence what wide publicity has been given to
our Whooping Cranes. The same is needed for endangered Pheasants, and it is being provided, partly by Canadians. In lands where many are still illiterate, pictures can often do more than the printed word; and a loan from Canadian pheasant breeders enabled the World Pheasant Association to provide and distribute in India and Pakistan illustrated posters portraying local pheasants that need protection. The final task facing conservationists is that of restocking the wild by releasing captive-bred animals; and this is not easy, as we are so painfully finding with the Whooping Crane. Here readers may recall that, in the first five years of the “cross-fostering” program of giving Whooping Cranes’ eggs to Sandhill Cranes in Idaho to hatch and raise, seventy-five percent of these eggs, or the young from them, were lost through “predation . . . unfavourable weather and habitat conditions and accidents”, as Dr. Ray Erickson has lately written (in the International Zoo Yearbook, Vol. 20, P. Olney, ed., pp. 43-44). Similar difficulties have bedevilled release programs in Asia. In short, however different Asia and North America may seem, the same problems confront us on both continents.

The 32 papers in this book very usefully examine a broad sweep of these problems. They cover the general fields of, first, the status of different species in the various countries involved — a vital starting point for conservation programs; second, field study techniques, including censusing wild stocks; third, captive breeding, including artificial insemination and reintroduction programs; and, fourth, conservation management, including education. It closes by printing the World Pheasant Association’s policies for reintroducing captive-bred birds to the wild and the code to which it expects private breeders to conform — and both would seem relevant to more creatures than pheasants. The speakers came from no fewer than ten countries, and among them it was pleasant to see the name of a member of the Canadian Wildlife Service — Dr. A. J. Gaston — who spoke twice, first, on the status of the Pheasants found in the Western Himalayas and, second, on methods of censusing them in the field — another welcome Canadian contribution to conservation on an international front.

R. GLOVER

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Manual of Nearctic Diptera, Volume 1


This new tome on North American Diptera is the latest in a long line of publications on insects emanating from Agriculture Canada. While the two volumes, treating 108 families were intended to appear simultaneously, only volume one has appeared, to be followed at some later date by volume two. Volume one provides a systematic treatment to the generic level for 43 families comprising the Nematocera and orthorrhaphous Brachyptera, leaving volume two to deal with the 65 families of the Cyclorrhapha.

Preceding the systematic sections are chapters dealing with the terminology employed in the text and the basic morphology of both larvae and adults (pupae have not been included). Thus while some basic experience is necessary for users of the book, a detailed knowledge of entomology is not vital since the book is virtually a complete course in dipterology. The editors are to be commended for ensuring that the terminology introduced in these chapters is faithfully employed throughout the systematic sections despite the multitude of authors.

The systematic sections have been compiled by the various specialists in each field, often with more than one author contributing to a section. As such each chapter represents an up-to-date account of Diptera systematics at least to 1979. Keys to the generic level for adults of the family have been provided and, where these have been deemed feasible, to the larvae and pupae as well. Information on numbers of species and general distributions are included under each genus in the keys to adults. This arrangement, though handy for those keying adults, is awkward for those using the keys to the immatures. Even in the adult key however some sort of general definition of boundaries for such terms as “southeastern” and “western” would have been helpful.

The provision of keys to larval and pupal stages is rather erratic. In some cases keys to these stages have been excluded even where experience has shown that such keys could have been quite complete and workable. This is regrettable since it detracts from an otherwise excellent systematic account and sends users back to older and less reliable sources. Presumably this exclusion has been done primarily to conserve space since no other explanation seems evident.

Within each systematic section a detailed morphological description of adults as well as egg, larval, and pupal stages, where available, precedes the keys.
Included are short accounts on general biology and behaviour of the family, as well as classification and world-wide distribution. Chapters on general biology and ecology of the Diptera are slated to appear in volume two. Each chapter is concluded by a list of references, many of which are very recent. Again, where keys to immatures have been excluded few references dealing with these stages are included, though undeniably a large body of such literature does exist.

This book is an intermediate point in the shifting emphasis of entomologists away from the traditional approach which places little importance on the immatures. Though considerable advances have been made in this publication these old biases are still very much in evidence. This is basically a book on the adults of nearctic Diptera with only sporadic treatments of larval and pupal stages. As such it is unlikely to render obsolete any of the older works treating these stages.

Within these constraints however the book succeeds admirably. Two features lend much to its excellence: the consistent format and treatment of each family ensured by the editors and the first-class drawings by Ralph Idema which illustrate each chapter. For dipterists, whether amateur or professional, this volume in terms of quality and price represents a true bargain.

REIN JAAGUMAGI

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Birds of the Qu'Appelle, 1857-1979

By E. Manley Callin. 1981. Saskatchewan Natural History Society Special Publication No. 13, Box 1121, Regina, Saskatchewan. 168 pp. $7.00 plus 50c postage.

When the Saskatchewan Natural History Society began its series of special publications in 1958, an announcement was made that Manley Callin would publish a book on the birds of the Qu'Appelle. Callin has personal records from the area dating back to 1929. When David Hatch introduced me to Callin during the SNHS field meet at Rocanville in June 1966, Callin spoke enthusiastically about completing the project, and naturalists across the prairies waited with anticipation for it. Little did we realize that Hatch's own work in 1975 and 1976 would figure prominently in the book, which was not to appear until 1980. The final result is well worth the two decade wait!

Manley Callin's Birds of the Qu'Appelle is one of the most comprehensive local avifaunal works of which I am aware. It consists essentially of two parts: several introductory sections (p. 1-40) and species accounts (pp. 41-159); followed by a list of literature cited and a species index. The title may mislead some, as the area covered is not the entire Qu'Appelle Valley, but basically the eastern portion of it in Saskatchewan, from the Manitoba border to the eastern edge of the area covered by Margaret Belcher's Birds of Regina (originally published as no. 3 in the series in 1961, and revised as no. 12 in 1980).

The book begins with a description of the area covered, including maps of the entire area and of the eastern and western halves, and 10 photographs of habitat by Robert R. Taylor. A useful map of Saskatchewan by W. Harvey Beck shows the areas in the province covered by major avifaunal lists, numbered chronologically according to order published. Unfortunately, no key accompanies the map and readers not familiar with the Saskatchewan bird literature may be confused by such features as two widely separated areas labelled as number 2 (Earl Godfrey's 1950 report on the Cypress Hills and Flotten Lakes), or not realize that number 14, the Saskatoon area, has not yet been published.

The introductory section continues with a summary of birds in general, including a useful table of birds known or thought to breed in the area, with evidence for this status. Other features include a discussion of winter birds, characteristic birds of the valley per se, and a detailed discussion of terms used.

All historians of prairie naturalists will enjoy the next ten pages outlining the contributions of past and present resident and visiting naturalists, and including brief biographies of each.

The species accounts are primarily reports of local and seasonal status as one would expect, but are, in most cases, very thorough. Callin has not developed the unfortunate practice of many authors of ignoring distinct races and morphs, and includes in his species accounts information on many of these.

The information on the towhees, however, is incomplete. Callin remarks on the differences in songs usually heard at two different localities and speculates that these may indicate the presence of two races, but does not comment on whether or not birds at either locality are spotted, the best field mark distinguishing the races. The song of the eastern race I heard occasionally in Winnipeg was markedly distinct from those I heard from the spotted race in Alberta and
Vancouver Island, but in the latter area, they have two very distinct songs, sung at different times by the same individuals. Thus, this question should be explored further in Callin’s area. Callin is a cautious observer and is not afraid to leave a bird not specifically identified, as exemplified by his treatment of the two dowitchers separately, then together with many records not differentiating them. Less common species are sometimes reviewed according to status in Saskatchewan as a whole or even the entire prairie provinces, although some major reviews (e.g. Smith’s paper on Gray Jays in Saskatchewan) are not included.

Although the species accounts are of primarily distributional and phenological interest, a number of interesting life history notes are scattered throughout the text. The changing status of many species, some increasing, others decreasing, is documented well, as might be expected in a book based on more than a century of observations.

Callin writes well and brings life to a subject which many readers would normally find dry. The proofreaders did a thorough job, missing only four typos that I noticed. I found only one slight error of fact: Robbins et al. stated that House Finches are expanding their range in the east, referring to the introduced eastern population, not to the east. Callin’s bird most likely came from the native western population. One other fact is misleading. The six-egg clutch of Black-necked Stilts photographed by Rudi Butot at Beaverhill Lake in 1977 was the second of two nests found. One had four eggs, the other had seven, but one egg from the latter had disappeared by the time Butot visited the nest (see Bogaert, *Alberta Naturalist* 9: 86-89, 1979; Dekker et al. *Canadian Field-Naturalist* 95: 68-69, 1979; McNicholl, *North American Bird Bander* 3: 102, 1978).

The few minor errors in this book do not detract from its general high quality. No ornithological library in the prairie provinces should be without it, and I recommend it highly as a working model to anybody contemplating the writing of a regional avifaunal work anywhere.

**Martin K. McNicholl**

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The Behavior and Ecology of Wolves


The *Behavior and ecology of wolves* is an assortment of papers presented at an international symposium of the Animal Behavior Society in Wilmington, N.C. May 23-24, 1975. The text contains 25 papers presented at this symposium. The objective of the symposium as stated by the editor was to “update what has happened in wolf research and public attitudes since the last meeting of the society” (1967). An underlying theme of the text is that of reintroduction of wolves into the wild. This recent aim of wolf research is timely considering the precarious status of the species throughout the world.

The text is organized into five sections corresponding to sessions of the symposium. There are: Wolves in the wild; Analysis of behavior; Translocation and reintroduction; Wolves in captivity; and a special section on the Red Wolf.

Papers presented in the first section relate to study of the status of wolves in the United States and Europe. Peterson’s paper on wolves from Isle Royal, Michigan summarizes recent information on this well known long-term wolf-moose study. A more complete analysis of this work is given in Peterson’s monograph on the subject. Singer, in a paper on wolves of Glacier National Park, Montana, provides a history of wolves in the park from 1910 to present. It appears that wolves in this area have been decimated from a population of about 20 in 1910 to the present estimate of a single pair. The future of wolves in the park does not look promising for the available wolf habitat cannot be protected by officials.

The following two papers present data on the status of wolves in Europe. It appears that wolves in this area have been decimated from a population of about 20 in 1910 to the present estimate of a single pair. The future of wolves in the park does not look promising for the available wolf habitat cannot be protected by officials.

The analysis of behavior section presents results of studies on wolf vocalizations, pack dynamics and hunting behavior. A most interesting article in this section is presented by J.O. Sullivan on hunting variability within a wolf pack. Using controlled experimentation the author was able to show that individual wolves show specific hunting behaviors and characteristics, a point that has been suspected, but is not readily observable in field studies.

A diverse assemblage of papers are grouped under the section of translocation and reintroduction of
wolves. A paper I found most interesting and relevant to the topic was that given by Mech on considerations for reestablishing wolves. The author presents a number of points to consider when reintroducing an "exotic" species to a new ecosystem. Introduced wolves must be considered "exotic" and it is essential to attend to these procedures. First, all wolves must be removed from the transplant area. A wide variety of preliminary studies concerning ecological, social, political, economic and the legal status of the target area should be done well before transplant efforts proceed. Transplant wolves must also be chosen with care. Captive wolves are not suitable for reintroduction. Further, only wolves known to be feeding on wild prey should be used as transplants. Mech does not indicate how one determines livestock-killing wolves. The final point Mech provides is the importance of a detailed monitoring program to assess the success and impact of the transplant operation. It becomes very clear from this article that wolf reintroduction to the wild is not a simple task to be taken lightly. Much scientific background study as well as extensive follow up work is required to provide an ecologically sound reintroduction program.

The editor has, by and large, maintained his objective throughout the text. It is unlikely that all areas of wolf research are covered and the objective would be better stated: "An update on the direction of wolf research since the last meetings." I also found the editorial, and organizational inconsistencies often present in the text, to be distracting and at times confusing. Wildlife biologists with a strong background in wolf research will have much interest in this work for it presents a state of the art treatise on wolf research.

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Les oiseaux familiers du Québec

Par Julien Boisclair. 1980. Editions internationales Alain Stanké, Montréal. 183 pp., illus. $24.95.

Ce volume, de par son titre, annonce que l'auteur traitera des oiseaux les mieux connus du Québec, mais que font dans ce texte des espèces comme le Canard roux, l'Epervier de Cooper, l'Effraie, le Pic à tête rouge, l'Hirondelle à ailes hérissées, le Moqueur polyglotte et le Bec-croisé rouge, entre autres?

Le bon de commande et le dépliant indiquent que ce livre "enseigne tout ce qu'il faut savoir sur" une multitude de sujets aussi variés que "les oiseaux et l'homme, la migration, les méthodes d'observations, les chants et les cris, le mode de classification, et le baguage". L'auteur a réussi un tour de force inégalable en traitant de tous ces sujets en moins de cinq pages. Nul n'est besoin d'ajouter que le traitement accordé à chacun de ces sujets est inadéquat. Malgré tout, l'auteur a réussi à s'enliser dans un anthropomorphisme qui marque et affecte tout le reste du texte et à créer de nombreuses imprécisions qui agacent rapidement le lecteur. Dans le paragraphe traitant du baguage, l'auteur fait mention de la contribution du danois Mortenson, mais ne parle nullement du travail de pionnier des ornithologues nord-américains tels F. C. Lincoln et P. A. Tawney, grâce auxquels le baguage des oiseaux est si bien établi en Amérique.

L'auteur prétend que les 124 espèces dont il traite dans son "volume composent 50 p. cent de l'avifaune québécoise", alors que près de 375 espèces d'oiseaux ont été homologuées au Québec!

L'information fournie plus loin dans le texte sous les divers vocables est parfois erronée, souvent imprécise, généralement trop vague pour être utile et trop fréquemment teintée d'anthropomorphismes. La distribution, lorsqu'on l'aborde, est trop souvent imprécise ou erronée: j'aimerais connaître une mention acceptable de l'Effraie à La Malbaie! Les sources auxquelles l'auteur a puisé ne sont pas fiables dans plusieurs cas et il est difficile d'expliquer pourquoi l'auteur ne s'est pas servi de sources d'information récentes et précises.

La reproduction des illustrations, aussi bien en couleur qu'en noir et blanc, est d'assez mauvaise qualité. Les dessins ne sont pas l'œuvre d'un peintre animalier! Quelques photographies en couleur proviennent des expositions permanentes du Musée national des sciences naturelles et ont été faites à partir d'oiseaux naturalisés!

Le lexique contient de nombreuses imprécisions, ainsi l'auteur n'a pu distinguer entre «Bio-» et «Biotope», etc.

Que dire de plus sur un "ouvrage de luxe" ou qui se veut ainsi, sinon que le prix est exorbitant et que le seul mérite de l'auteur est d'être parvenu à rédiger son texte dans un français de bonne qualité.

HENRI OUELLET

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Advances in Ephemeroptera Biology


The papers presented at the Third International Conference on Ephemeroptera, held in Winnipeg during July 1979 make up the text of this new offering on Ephemeroptera. A total of 43 papers were presented at the conference on a variety of areas of mayfly research. Of these, 40 are reproduced in this volume. While touted by the editors as a "state-of-the-art" synthesis of Ephemeroptera biology it would be more appropriate to regard this collection as simply an overview of current areas of research by those presenting the papers.

As one would expect in any work of such a diverse nature and by such a wide variety of authors, two shortcomings are apparent. First, except in rare instances, little continuity is evident in the subject matter covered. Secondly, considerable fluctuation is apparent in quality among the papers.

The papers have been grouped by the editors into seven broad categories: Phylogeny and Systematics; Faunistics; Biology, and Ecology; Behaviour; Methods; Environmental Impact and Toxicology; and Reviews and Historical Aspects. From four to seven papers are usually included under each heading.

Noteworthy in the phylogenetic section is a series of three papers dealing with southern hemisphere Leptophlebiidae. Not only are they interesting from a zoogeographic standpoint but, due to one of the authors being common to all three, this is the only section where any demonstrable continuity is evident. Noteable too is a paper on reclassification of the Ephemerellidae in which this family is considered on a worldwide basis.

As few other studies have such wide scope, an international flavour is reflected among those papers presented. European and Australo-Asian studies complement the North American works in each section. The faunistics section as an example presents papers dealing with British, European, and North American distributions and habitats. Similarly, studies considering environmental perturbations are grouped together from such diverse geographical regions as Poland, Norway, and northern Canada.

Despite the earlier mentioned shortcomings the prime advantage of the book is that a number of new papers on a wide variety of subject areas are presented in one handy volume. As such it permits those interested in keeping up to date with new developments to do so without the high cost involved in attendance at such conferences; presumably this is one of the reasons publication of such conference proceedings has become so popular in recent years. While the book is intended to be of interest mainly to those specializing in Ephemeroptera, workers in many other specialties will find occasion to refer to sections of the book. It is anticipated, however, that few will feel the need or desire to purchase the book for themselves.

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The Peregrine Falcon


Yet another excellent book on birds of prey has come to us from a British author. Several books have already been written on the saga of the Peregrine Falcon, and though all have their place, none before ties the subject together as neatly as Derek Ratcliffe's book.

The sixteen chapters are basically a storehouse of knowledge on the Peregrine, delving into its relationship with man through the centuries, and summarizing its population trends, distribution and regulation, feeding habits, breeding density, migration, and finally, the pesticide story. The latter is considered by many to be a great piece of detective science and none other than the detective himself could tell it so well!

The book ends on a positive note, being devoted to the conservation and future of the Peregrine.

The book is adorned by some 60 black-and-white sketches, including three reproductions of beautiful paintings, all by artist Donald Watson who is obviously familiar with the Peregrine. A similar number of well-chosen black-and-white photographs depict the falcon and its ecology.

Man's historical persecution of the Peregrine is well-documented, but I honestly feel that we as scientists have too little to say about the effects of our own "research" on raptor populations. To my knowledge, a really thorough study has never been conducted on this topic, i.e. number of nest visits, manner of visit, etc., for this species as has been done for Bald Eagles (Haliaeetus leucocephalus) in the United States. Per-
haps the ongoing study by Mearns and Newton in Scotland will shed light on this subject. I welcomed the section on the practical problems of counting Peregrines, as too many populations have become "endangered" due to misinterpretation of survey data.

As Ratcliffe points out on p. 158, much controversy surrounds the hunting efficiency of the Peregrine. It is unfortunate that the author was unable to include Dick Dekker's (1980) recent published accounts of Peregrine hunting success (see Canadian Field-Naturalist. 94(4): 371-382). Along with his own extensive observations, Dekker provides an excellent review of hunting strategies and success of both migrating and breeding Peregrines. Dekker and I (Bird and Aubry, MS in prep.) have calculated values of 40% and 35%, respectively for hunting efficiency of breeding adults. I agree with Dekker that hunts by breeding Peregrines are more motivated than those of non-breeding birds and that the former have likely acquired more specialized skills.

A few specific points follow. To the author's description of the characteristic green stain on Peregrine eyries on p. 178, I would add the characteristic orange stain resulting from lichen growth found in eyries of northern-nesting birds.

On p. 196, copulatory activity in captive falcons with an ad libitum food supply was most frequent in the early hours of light (Wreg and Cade 1977), whereas Hagar (1938) recorded mid-day for high copulatory behavior in wild Peregrines. My own observations of this phenomenon suggest that the captive birds copulate most when disturbance is lowest and the wild birds use early light mainly for foraging.

Finally, for the record, I must add that the majority of Peregrine banding is conducted along the U.S. coast, particularly on Assateague Island, Maryland, and not at Hawk Mountain, Pennsylvania, as the author purports.

Overall, the book is written in a concise, succinct manner constituting an intricate balance of prose and scientific writing. Furthermore, it was not written for the purpose of entertainment, but as a source of scientific reference. Perhaps some argument could be put forth for retitling the book "The Peregrine Falcon in Britain" due to the heavy reliance on British data. However, I am inclined to give the author the benefit of the doubt, as this work undoubtedly reflects strongly the biology and the predicament of the Peregrine in virtually any country. I must congratulate Ratcliffe on his avoidance of flooding the book with facts and figures comparing the Peregrine with other raptor species.

The Peregrine today still has its adversaries and Ratcliffe makes a strong case backed by scientific fact to permit its survival. With increased leisure time and more people, I believe that rock-climbing will become the biggest threat to cliff-nesting Peregrines in many accessible areas in the near future. Is constant wardenning of eyries really the answer? The solution must lie in the instillment of an even greater public awareness of wildlife and its requirements for survival. This book, a truly inspiring one, takes a giant step toward this long-term goal.

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Birds of the Great Plains: breeding species and their distribution


Paul Johnsgard is gaining a reputation as a prolific author. Other impressive books authored by Johnsgard and printed by the University of Nebraska Press are North American Game Birds of Upland and Shoreline; Grouse and Quails of North America; Waterfowl: Their Biology and Natural History; and Ducks, Geese, and Swans of the World. This most recent contribution is another impressive success in compressing and compiling a wealth of information into one manageable volume.

Included among its 539 numbered and 45 introductory pages are 30 color bird photographs, 5 black-and-white habitat photographs, several figures and tables, 330 easy-to-read range maps, and numerous line drawings. Most of the color photographs are excellent although it is doubtful they are worth the price they added to the book. Most of Johnsgard's line drawings are appealing although a few actually are distracting.

The introduction contains a variety of informative material, including discussions of topography, landforms, climate, natural vegetation, avian zology, and ecology. Probably the major criticism that the book will receive is the geographical region selected for coverage. The area encompassed includes all of 5 states (North and South Dakota, Nebraska, Kansas, and Oklahoma) and parts of 6 others (Minnesota and Iowa, west of 95°; a corner of northwest Missouri; the Texas Panhandle; and the parts of northeast New Mexico and eastern Colorado east of 104°). It might have been better if the central prairie
region, characterized by a more biotically uniform semi-arid grassland, extending from central Saskatchewan southward to central Texas, had been covered. Leaving out the parts in Minnesota, Iowa, Missouri, New Mexico, and Colorado, and adding more of Texas and Saskatchewan might have resulted in a book with greater ecological meaning. Using Johnsgard's boundaries introduces a variety of additional habitats (i.e., boreal forest) and species, which detracts from the sizable number of birds more or less restricted to the prairie grasslands.

The informative species accounts include sections on breeding status and habitat, nest location, clutch size and incubation period, time of breeding, breeding biology, and suggested reading. Johnsgard fails to follow American Ornithologists' Union names for all species. Instead of a 14-page appendix table showing abundance and breeding status at 30 selected parks and refuges located within the region, I wish that a sentence or two had been devoted to species abundance within the species accounts. The other appendix is devoted to short descriptions of 44 bird-watching localities in the region.

Although I am certainly not intimately familiar with the exact breeding ranges throughout the entire region, some ranges that I checked in Minnesota are inaccurate. Although a few errors are tolerable, significant range map problems are more than irritating. More time is probably spent by readers scrutinizing range maps for correct coverage of familiar areas than most authors realize. It would behoove all authors intending to construct breeding range maps to review drafts of maps with local, knowledgeable birders and also to use the immensely valuable data being generated by the U.S. Fish & Wildlife Service Breeding Bird Survey.

The book is an overall success in that it should serve a broad, nontechnical audience as Johnsgard intended. It should serve the local birder in the "Great Plains" region and stimulate those interested in trying to fill in our many gaps of knowledge about breeding birds throughout the United States. Most will find the book a valuable addition to the library shelf.

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Birds of Regina : revised edition

By Margaret Belcher. 1980. Saskatchewan Natural History Society Special Publication Number 12. Regina. 151 pp., illus. $5.00 plus 50c postage.

Margaret Belcher's Birds of Regina (1961), published as the third in a series on natural history in Saskatchewan, has been out of print for some time. Furthermore, its success in stimulating resident and visiting observers in the Regina area to report their observations of birds has combined with recent avifaunal changes to outdate the original book. Thus, this revision, almost two decades later, is a very welcome addition to Saskatchewan's bird literature. In spite of the "lumping" of several species in the years intervening between the editions, the species total has risen to 295 from 268, with 13 additional hypothetical species. The length of the book has essentially doubled (151 cf. 76 pp.).

The book consists of a series of short introductory sections which define terms and describe the 48 km (30 mile) diameter circle covered, individual species accounts, literature cited and a species index. The area description includes habitat changes both since Mitchell's 1924 description of the Regina plains and since the 1961 edition of Belcher's book, and is divided into four main habitat types: farmland, wetlands, grasslands, and parklands. Species accounts are based on published literature, personal notes of several observers, TV tower kill data, records in the Prairie Nest Records Scheme, and similar sources. The inclusion of French common names for each species may surprise some readers, but is a reflection of Ms. Belcher's occupation as a professor of French at the University of Saskatchewan in Regina. A series of black and white photographs by D. Gilroy, F. W. Lahrman, L. Scott and G. W. Sieb illustrate habitats and a few of the birds. Drawings of birds by Lahrman are also scattered throughout the text.

Species are listed according to the latest (1957) check-list of the American Ornithologists' Union and the two more recent supplements (1973 and 1976). The 1976 supplement is not cited as such, but the names I checked (e.g. Carduelis including both former Acanthis and Spinus) are up to date. A welcome feature is the inclusion in the species accounts of specific information on such well-marked races as Bewick's Swan, Harlan's and Krider's hawks, Audubon's Warbler, Red-shafted Flicker, Bullock's Oriole and Oregon Junco and color morphs as Blue Goose and red and gray Screech Owls under species with more common races or phases. I would have liked to have seen this done for Palm Warbler, Rufous-sided Towhee and White-crowned Saprow also, all of which have more
than one race represented in the prairie provinces. As the eastern unspotted race of the Rufous-sided Towhee is the common race in Winnipeg, and the spotted western race at least as far east as Medicine Hat, I was particularly curious as to which race(s) have occurred in Regina. Systematists will be interested in the hybrids and/or interspecific matings of Trumpeter × Mute Swan, Cinnamon × Blue-winged Teal, Indigo × Lazuli Bunting, and Chestnut-collared × McCown’s Longspurs.

Most species accounts are restricted to status, seasonal and nesting information, but occasional tid-bits of other natural history are included, such as the record of a Western Meadowlark singing a Cardinal-like song. Status of rarities is usually compared with other parts of Saskatchewan only, but a broader perspective is considered for some.

One can find little to criticize in this well-researched book. Ouellet’s advice that Willow and Alder flycatchers cannot be distinguished safely except by song (p. 86) is appropriate to field observations, but the TV-tower killed specimens discussed should have been identifiable with the help of the keys of Phillips et al. (Bird-Banding 37: 153-171, 1966; 41: 190-197, 1970). I found only one proof-reading error — “then” for “than” under Golden Eagle. Readers looking up a given species may miss the photographs at the end of the book, since only the owl photographs are mentioned in the corresponding text.

Margaret Belcher and the Saskatchewan Natural History Society earned considerable well-deserved praise for the first edition of Birds of Regina. The revised edition surpasses the first and as the first revision in the series marks its “coming of age.”

Martin K. McNicholl

A Field Guide to the Birds East of the Rockies


Roger Tory Peterson and his field guides need no introduction to anyone interested in the out-of-doors. This latest offering is a completely revised edition of the very first guide in the Peterson field guide series. Peterson last revised this guide in 1947 and the ensuing 33 years have hopelessly outdated it. Not only have many birds’ ranges changed (e.g. the widespread Cattle Egret is not even in the 1947 edition) but ornithologists have changed the classifications and names of many birds as well (e.g. Blue Goose has been ‘lumped’ with the Snow Goose and Traill’s Flycatcher has been ‘split’ into Alder Flycatcher and Willow Flycatcher).

Peterson was not content to merely update outdated material in this new edition — it is in fact very different from the earlier editions. The most striking change is the format. Peterson has adopted the layout of the ‘other’ field guide and has put each bird’s picture facing the text. Now no longer do users need flip and fumble pages to match picture with species account.

This change in format has meant whole scale changes, the most notable being fewer birds per plate. In fact the number of plates has been more than doubled (from the previous 60 to 136). Peterson has used this opportunity to show his artistic skill. Although arrows still point out field marks, gone are the schematic birds. They are replaced by larger, more lifelike versions. These portraits range from superb (the ‘brown thrushes’ on page 223) to mediocre (the chickadees on page 211). The Black-capped Vireoes on page 229 lost their realism as a result of the touch-up job needed to correct the colour of their eyes.

A most welcome addition are range maps. These large (six to a page) coloured maps have been done by Peterson’s wife, Virginia Marie. While they are useful they are not as accurate nor as up-to-date as one would like. These maps are at the back of the book, so users must again flip pages.

Peterson has rearranged the order in which the birds appear in the book. Formerly he followed phylogenetic order but in this edition he has made his own arbitrary categories and sequence, namely; swimmers, aerialists, long-legged waders, smaller waders, fowl-like birds. While this may help novices with identification it could hinder their learning of taxonomy (even if only to locate species on a check list). The experienced birder, familiar with the standard taxonomic arrangement of species, will have to get used to finding species such as gallinules grouped with waterfowl rather than with the rail family.

This reviewer was disappointed with the number of errors. Although none of these faults is terribly serious they are not the type of mistakes one would expect Peterson to make. The third winter Herring Gull on page 91 is actually a second winter type and on the same page the first winter Ring-billed Gull is more typical of a younger bird. The Lesser Golden Plovers (page 118) should have three toes, not four. The eye rings on the Ringed Plover and Semipalmated Plover

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Entomology


Among the variety of general text books on entomology that are currently available, most tend to be much more restrictive than the titles would imply. As such the recent contribution by Gillott will come as a pleasant surprise to those anticipating a reworking of this subject in what has now come to be regarded as almost the standard format for entomology texts. Gillott has attempted, and to his credit has succeeded in producing, a textbook that is truly general in scope. Quite gratefully one discovers that his view of entomology extends beyond insect morphology and systematics.

The subject is approached through four main divisions: Evolution and Diversity; Anatomy and Physiology; Reproduction and Development; and Ecology. The importance of systematics however has not been neglected and to this end by far the largest section of the book is devoted to the evolution and classification of insects. Of particular note in this section is the wealth of new information that has been included, such as the recent theories of, among others, Kukalova-Peck on the evolution of insect wings. The unbiased presentation of the various theories on insect evolution, both classical and recent, is commendable. In using this approach the author has evidently attempted to provide his readers with an opportunity to assess the relative merits of the theories.

The taxonomic sections have been reduced from that typical of the other well-known entomology texts. Keys to the ordinal level only have been provided, though references have been included to those works affording the broadest introduction to the vast libraries of more detailed taxonomic works currently available. For each insect order a short description notes the major families and provides a brief account of the more common or larger families. Additional information dealing with generalized morphological features of the order and life history traits completes each description.

Although the author has adopted a specific classification system (obviously a necessity to avoid a chaotic treatment) he does not fail to mention that other schemes do exist. To this end a short synopsis of conflicting views is presented.

The section dealing with anatomy and physiology presents a detailed account of the various anatomical parts but goes on the explore how the parts function together. Thus the wings, musculature, and various organs are not only considered as separate entities but as a functional unit designed to permit flight.

The sections dealing with reproduction and development, and ecology complete the book. In the final section on ecology considerable space has also been devoted to the problems of insects as pests and the various mechanisms of control, both chemical and biological.

As the author indicates in the preface a scientific background at the university level is assumed on the readers part, though this is not a limiting factor for users of the book. Most sections should be readily understood (at least by the projected users) with only the rare explanation being excessively difficult. Gillott is to be commended on producing a text that, despite the complexity of the subject matter, neither oversimplifies the content nor presumes a high degree of expertise by the reader. Perhaps more important, he has created an eminently readable textbook.
Book Reviews

Migrant Shorebird Ecology — with special reference to shorebird migration along the north-eastern shore of Lake Ontario

By Peter W. Strahlendorf. 1980. Ontario Ministry of Natural Resources, Napanee Administrative District, Napanee, Ontario. 96 pp., illus. $5.

This extremely well-researched book gives over 1100 references on the biology of shorebirds (sub-order Charadrii). The purpose of this report, contracted by the Ontario Ministry of Natural Resources, is to 'delineate what research should be done in the area of inland migration ecology', with emphasis on the importance of areas in the Napanee District as shorebird habitat.

The author has detailed the contents of most of the references into about 70 pages of text. There are accounts of the 38 species which have occurred in the study area. These accounts include arrival and departure dates, suspected migration routes, and additional notes on breeding status, unusually large flocks that have been sighted, banding recoveries, etc. The information for the study area is good because the author has used the expertise of local birders extensively. The information on arrival and departure dates of species through other locations (i.e. Lake Erie, Montreal, United States) is less than satisfactory, probably because the author was not able to contact local birders or use some of the smaller journals and reports (e.g. Long Point Bird Observatory reports, Ontario Bird Banding) as sources.

The chapter on shorebird migration is the author's best attempt at a synthesis of a wide range of papers. He begins by discussing the adaptive value of migration to individual birds. The author states that birds have adapted to long, risky migrations because 'those birds which migrated contributed more genetic material to subsequent generations than those birds which spent their summers in the south'. A discussion of 15 different topics on migration, including orientation and navigation, effects of weather on migrants, migration routes, speed and altitude of migrating shorebirds, and flocking during migration cover the subject quite completely. Of particular interest to the subject of shorebirds which migrate using the inland routes are sections on detection of staging sites, length of stay at inland sites and daily patterns of migrating birds.

For any reader who has seen the phenomenon of a newly formed habitat for shorebirds (e.g. drawn down sewage ponds) fill overnight with large flocks, this discussion will be of interest. Unfortunately, as the author points out, there is too little information in the literature on the importance of these temporary sites for migrant shorebirds.

A large section on feeding ecology contributes little to our knowledge of the feeding habits of birds in the study areas. However for those interested in feeding ecology of shorebirds in general, the author has summarized an extensive literature. There are lists of diets for many species, and tables reprinted from various sources. It is unfortunate that the author did not summarize all the known information into one or two tables or figures for the sake of clarity. The section on feeding methods is long, and could also have been condensed into a single table.

There are several tables extracted from the literature on habitat preferences of shorebirds. The author attempts to relate the published habitat preferences of different species to the presence of these same habitats in the study area. Most habitats are present in eastern Ontario but the author notes that Prince Edward County has been insufficiently censused. Presumably large numbers of shorebirds could stage there, based on the habitat requirements alone.

There is much more information in this report than I could possibly review here. Most of the report is well presented, although the nature of a literature review which attempts to cover everything results in the reading being a bit rough. Another consequence of an extensive literature is an increased incidence of errors. I found 15 references in the text which were not listed in the bibliography, and over 70 typographical errors.

Despite these minor problems, the report contains very readable figures, tables and print. The bibliography itself is worth the $5.00 cost.

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The Vegetation and Phytogeography of Coastal Southwestern James Bay


This is a very valuable contribution to our knowledge of the fields of vegetation and phytogeography because it deals with a portion of the Hudson Bay Lowland. This lowland region is a terra incognita relative to the Arctic Archipelago to the north of it, and the Precambrian Shield to the south of it. Apparently, the psychological factor of the “lure of the North” has been sufficient to draw scientists to the Arctic Islands and to attract financial support for their work. Reasonably good access has permitted botanical explorations of the Precambrian Shield region at a very modest scale of funding. The Hudson Bay Lowland, however, has lain more or less fallow ground till recently when helicopters have provided an affordable means of access for small multidisciplinary teams of scientists.

Intrepid naturalists who visit this southern portion of the lowlands and whose interests are wholly or partly botanical will be intrigued by the classification presented in this paper of coastal vegetation. Once the physiographic and vegetation features of these association series (dominance types) become fixed in one’s mind, the types will be observed again and again at points throughout the entire coastal zone of Hudson Bay Lowland and the orientation of these locations with regard to their ecological niche or niches, will be readily apparent. The vascular plant check list for three interesting coastal localities, 1) Shipsand Island and nearby Arnold Point, 2) North Point, and 3) Puskwuche Point and nearby Longridge Point, will also be useful to naturalists since it specifies plant species present at each locality and indicates the ecological niche or niches which these species occupy. For comparison of the coastal vegetation with the wetland vegetation of the hinterland, a checklist is provided for the vascular plants found in the Kinoje Lake area, which is located about 90 km east-northeast of Moosonee, Ontario. Because the vegetation of this hinterland area has not been subdivided into association series, its inclusion will also serve to whet our appetites for what can, I trust, be confidently predicted as forthcoming papers of these authors dealing with the wetland ecosystems of the interior portion of the Hudson Bay Lowland.

Fifty-two species’ distribution maps are included in this paper; this is an impressive contribution to the field of phytogeography. Each map extends southward to the neighborhood of 42° N so that all southerly occurrences of disjunct species can be delineated except for those alpine species that range considerably southward on the Appalachian mountain system. In accordance with recent practice, the species distribution maps are arranged in alphabetical order of their generic name. The time saved those who use these maps most assuredly will indicate the practicality of this break with tradition.

Disjunct species are considered by the authors as those species having populations which are separated by at least 400 km (in fact only one species has populations separated by less than 500 km and the others range up to 1200 km separation). There are 27 disjunct coastal species out of a total of 273 species, a rather surprisingly high 10% of the total. The authors’ discussion of the reason for these disjunctions demonstrate that such postulations are premature at this time. This fascinating question must remain open until we know considerably more; there is no point in filling the vacuum with very tenuous speculations. For example, although a post-Pleistocene marine connection between Hudson Bay and the Atlantic seaboard may be attractive from the point of view of explaining the distribution of disjunct maritime and halophytic plants, it is decidedly unattractive from the point of view of the absence of marine deposits in northern Ontario and northern Quebec. In addition to the general challenges, which the authors offer to naturalists, to find occurrences of disjunct species within the blank spaces of the species distribution maps, the authors throw down four gauntlets: the discoveries of the orchids Platanthera lacera and Malaxis monophylla between the Great Lakes and the James Bay region, the rush Juncus ensifolius between the east coast of James Bay and the Cypress Hills of southwest Saskatchewan, and the parsley Conioselinum chinense between the mouth of the Moose River and the solid line delineated on their Figure 27.

I have highlighted here some of the features that will be of interest to naturalists with a botanical bent. The only thing I anticipate they will find wanting in this paper is a consideration of vegetation-wildlife relationship within the study area. One suspects that the authors must have some interesting data pertaining to this subject.

Arthur Boissonneau

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Vascular Plants of Restricted Range in the Continental Northwest Territories, Canada


This publication consists of a brief introduction and an annotated list (taxonomic sequence) of the 530 species which, during preparation of the Flora of the Continental Northwest Territories, were found to have restricted ranges in the Northwest Territories. The list is based on the state of knowledge at the time and is the first attempt to bring this provisional information together. Species are categorized into five distribution types, including a category for plants which are endemic to parts of boreal and arctic North America.

The value of this list from a conservation viewpoint will be in encouraging northern botanists and naturalists to fill in the many gaps in knowledge. If properly documented additions and corrections are sent to the author at the Biosystematic Research Institute, Agriculture Canada, K1A 0C6 or to The Rare and Endangered Plants Project, Botany Division, National Museum of Natural Sciences, Ottawa, K1A 0M8, this information could be used to develop a more complete list following the standardized format developed for The Rare and Endangered Plants Project. This would include an evaluation of which species, if any, should be assigned to rare or endangered categories and the removal from the list of those plants not restricted to small populations within NWT. Appropriate conservation measures should follow.

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Plants of Quetico and the Ontario Shield

By Shan Walsh. 1980. University of Toronto Press, Toronto. xvi + 152 pp., illus. cloth $25; paper $7.95.

Quetico Provincial Park is one of the great wilderness areas of North America and is considered by many to support the finest canoe country in Canada. For years now, Shan Walsh has travelled its many routes by paddle and portage and has developed an intimate knowledge of the park and its flora. His book attempts to share some of that knowledge and, in the words of the Preface by Walter Tovell, "...to assist travellers in identifying some of the many floral species that may awaken their curiosity." Sad to say, it barely achieves the former and clearly fails to achieve the latter.

Throughout its pages this work can't seem to decide if it's intended for the general (canoeing) public or the knowledgeable botanist. It attempts to satisfy the former with a copiously illustrated section discussing the major habitats of the park, including photographs of the typical and/or 'interesting' species known from each. The botanist is offered an annotated checklist of the 638 species of vascular plants. Neither is satisfactory.

The layout and design of the book is awful. The use of 'negative space' is indeed negative. There seems to be no rhyme or reason to it, forcing the reader's eyes to scramble from page to page of scattered, tiny illustrations. The maps on pages xxii and xxiii, for example, are much too small...yet utilize less than 50% of the available space. Headings in the checklist, such as Latin family names (and in the case of Carex, Section names), are printed with the same (light) type as the species' discussions and thus do not stand out.

The photographic reproduction is very poor. Of approximately 120 photographs of plants and their habitats, half (60) are substandard. By that I mean they are fuzzy, too dark, frequently much too small and often show much too little detail for identification by anyone other than those already familiar with the species. For a book that would serve as a pictorial guide for travellers (at least in part), this is inexcusable. The photographs of such common species as Goldthread (page 33), Meadowsweet (page 16). Fireweed (page 34) and Running Clubmoss (page 40) are examples of these. The photographs in such a book should be a celebration of the flora; here, I'm afraid, they have more the character of a wake.

The annotated checklist does not fare much better. The nomenclature used appears to be straight from Britton & Brown's Illustrated Flora and thus is dated. Subspecific taxa are not routinely discussed, nor are we told where (if at all) supporting vouchers may be found or when they were collected. The author cites species on the authority of other workers, without providing any supporting documentation regarding their specimens. Status is discussed in (undefined) terms such as Rare, Scarc, Occasional, etc. This is further complicated when species of apparently equal status are described differently (e.g. Potamogeton zostetiformis and Asplenium trichomanes are both known from two stations, but one is described as Rare and the other Scarc).
Much of the species' discussions are taken up by anecdotal descriptions of medicinal, aboriginal and spiritual uses of the plants. This is out of place in an examination of the flora of a wilderness area, where we especially don't want travellers to be boiling up roots, stripping bark, etc. We also end up with yet another book discussing aboriginal uses of native plants, without any indication of the accuracy of such reports. The moralistic tone expressed when describing the probable origin of Cannabis sativa ("... probably from seed accidentally dropped by a user of this dangerous drug") is irritating in light of the apparent face-value acceptance of aboriginal plant uses (presumably by "noble savages").

The author has manufactured common names in many cases "... to give a meaningful identifying label when no standard common name exists". The concept is a reasonable one (though I expect few readers who need common names will be using the checklist), but the results are often cumbersome and (frankly) downright ridiculous. Names such as "Fruit of the mud Rush" (Juncus pelocarpus), "Sir George Back's Sedge" (Carex backii) [sic] and "Narrow-branched ground-cedar clubmoss" (Lycopodium complanatum) are examples.

And what, I wonder, is the "Ontario Shield"? I presume that the author is referring to the Ontario area of the precambrian Canadian Shield, but this is not clear. One suspects that it is a publisher's ploy for widening the potential sales market of the book. Indeed, in the Preface Tovell states that it would be "... of equal value throughout the Muskoka-Haliburton area ...". With only 650-odd species discussed (as compared with the over 1000 presently known from Algonquin Park — which is less diverse than neighbouring Muskoka-Haliburton), that claim is hard to swallow.

The Plants of Quetico fails on all counts, I'm afraid. Considering the author's expert knowledge of and feeling for the floral resources of the park, this is truly unfortunate. I suspect that this was a good concept and a serious effort that became twisted out of recognition by over-zealous designers and publishers. Let us hope that Walshe still has the interest and energy to go on from this and produce a true "plants of Quetico".

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ENVIRONMENT

From Arsenic to DDT — A History of Entomology in Western Canada


Dr. Riegert, of the Department of Biology, University of Regina, offers an excellent history of the growth of entomology in western Canada, from its beginnings in the hands of interested amateurs to its establishment as a recognized science.

This scholarly work shows the result of Dr. Riegert's intensive research, but his very readable style of writing makes it as interesting to the layman as to the scientist. All aspects of western Canadian entomology are included. Details of history have been carefully gleaned from numerous sources and archives — letters, bulletins and publications that had luckily not been destroyed by periodic "housecleanings" of files and offices. The wealth of detail indicates the amount of research and reading that was necessary to provide such a complete chronicle. Extracts from the diaries of early explorers add a great deal of colour. The description of Indians eating live lice and warbles may temporarily spoil the reader's appetite but it certainly offers a clear picture.

The relation of insect life to that of the new settlers to the western provinces, and the trouble caused by pests as the immigrants tried to wrest a living from the land is clearly documented. Equally well described are the efforts of entomologists to combat the foes, study their life cycles and history, learn how to control their numbers and destructiveness, and improve the circumstances of agriculturists.

From its introduction to the detailed index, From Arsenic to DDT offers a comprehensive and complete history of entomology, a splendid record of the efforts that have gone into the establishment of entomology as a science. "From what has been, learn what will be." Dr. Riegert has compiled between these covers the legacy of learning that benefits future generations of entomologists and agriculturists, and preserves this part of Canada's history for all.

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Environmental Planning Resource Book


This book attempts to provide a comprehensive Canadian information base to assist land planners in responding to environmental problems. The authors have found that no such Canadian source currently exists. The term environmental planning refers to land use planning that incorporates protection and enhancement of environmental capacity and quality. With quotes from the Bible, the Torah, and Aristotle, the first chapter elegantly outlines humanity's historic approach to use of the earth's resources. The view that the earth's resources exist for humanity's sole benefit is presently changing, partly in response to increased popular concern for environmental quality. This has dictated a new approach — to a land use planning concept of people in nature rather than separate from it, including dynamic interaction of human activity systems and natural systems in ecosystems and ultimately in the biosphere.

The authors draw together from Canadian sources the nature of the problems facing planners taking an ecosystem approach and examples of Canadian environmental planning solutions. Canadian environmental problems, because of the vast expanse of Canada, are characterised mainly by their variety. Procedurally, environmental problem solutions are as distinctive as our political-cultural system; their differences across Canada reflect differing jurisdictional and cultural settings. Solutions to local environmental problems must therefore be context specific.

The authors examine the nature of our environment's resources (both individually and as they interact in ecosystems) and the human activities prominent in generating adverse environmental effects. They spell out how and where to find information on our resources to aid in planning, and point out some of the limitations of the information presently available to planners. Throughout the book they illustrate both environmental planning problems and their practical solutions with case histories and annotated bibliographies of both Canadian and world-wide experience. In the book are reprints from numerous reports of Canadian planning solutions that incorporate an environmental perspective.

I would highly recommend the book as a readable and valuable source of practical Canadian resource planning information. It should be of use to both private citizens concerned with land use alternatives in their local areas as well as to planning professionals.

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The Fallacy of Wildlife Conservation


The Fallacy of Wildlife Conservation appears at first to be an incongruous title for a book by John Livingston. After all the author is one of North America's leading conservationists. He is a bird lover who among other nature related projects has written award winning books on this subject. Why then would Livingston write a book whose thesis is that wildlife conservation is backed up by arguments which, though seemingly sound, are deceptive?

In this book Livingston looks critically at the conservation movement's traditional reasons for environmental concern and the generally accepted assumptions and motives behind them. Justification for wildlife preservation has taken many variations of human self interest: the wise use of natural resources will bring dividends later; our quality of life will be enhanced: it will stave off an ecocatastrophe. Living-ston believes that for the genuine conservationist this route is unacceptable.

For Livingston conservation is based on personal experience. He feels that this revelation need not occur in some exotic untamed place, but can as easily come in an urban ravine. He sees non-consumptive use of wilderness as being as damaging as hunting, simply by the sheer numbers of people involved. How can concerned naturalists reconcile untouched nature with the needs of many people to flock to wilderness parks? The conservation movement can only gain public sympathy when the general population has gained an appreciation of nature. It will be far harder for people to acquire such a sensitivity when they are denied access to wilderness areas. Livingston has had intimate encounters with rugged nature and as he himself points out, it therefore makes it difficult to ask others to forego them so that wildlife can exist solely for its own sake.
Has the conservation movement failed to convince the public of the worthiness of its cause? Livingston thinks it has. In this book he explains the arguments used to support conservation and why they have not succeeded. Conservation, he contends, is an emotional personal experience forced to define itself within rational unemotional parameters.

The Fallacy of Wildlife Conservation is written with a conservation-oriented audience in mind. Who else but an ardent enthusiast of the cause would pay $14.95 for such a thin book? How would a non-environmentally-conscious reader respond to such a critical review of the conservation doctrine? Fault finding analysis of the movement's logic may be misinterpreted by the unsympathetic as being a weakness in its basic belief.

Overshoot


Catton confronts his readers, in starkest terms, with the failures of the currently held non-ecological paradigm. Those concerned with the environment, instead of attempting to alter the present world view, have merely pleaded single causes within the accepted framework. After reading Overshoot this approach becomes untenable.

Overshoot is well laid out. The forward has a good description of the book's plan as well as a useful index and glossary. Becoming sensitive to a new concept involves the learning of an appropriate vocabulary. The author eases the uninitiated into the language required. The key themes recur frequently. Ideas appear reformulated even within the same paragraph. The author warns that there is no happy ending yet finishes on the most upbeat note of the book.

William R. Catton, Jr., is a sociology professor at Washington State University. Overshoot was written with the intention of stirring its readers by a compelling new perspective. Catton claims it differs from previous ecological analysis by its statement that die-off is unavoidable and that commonly proposed solutions will only aggravate the problem. Is it consolation enough to understand why and how our present predicament evolved without being able to remedy it?

The basic tenet that human control over nature is a great achievement in resource exploitation clashes with the reality that people benefit most from ecosystems they themselves do not dominate. We have exaggerated technology's achievement at the expense of underestimating the contribution of nature. The human community is like any other biotic community, subject to conditions which are not fixed. Yet our existence is dependent on converting a climax community into a less mature seral stage. Adaptive patterns must change in response to habitat change. Not doing so fundamentally alters the very mechanism of adaptation. Ecological principles as well as our denial of them have and will determine the human condition.

Global population now exceeds the earth's carrying capacity. America can no longer sustain its people on its own resources. Most of today's underdeveloped nations will never become developed. Since people have run out of competitors to displace, wealth has depended on stealing future supplies. Overshoot is a proclamation that the world is finite; our ability to live beyond our means temporary.

Are the truths in this book sufficiently unpalatable that Catton's insight will be ignored? The author emphasizes that only deep pessimism about our common plight is true realism. There is no single target for blame. What has happened has been the snowball effect of many people making individual choices. The Age of Exuberance of the past four centuries was based on two non-repeatable events, the discovery of the second hemisphere and the development of means to exploit the planet's deposits of energy storage. Future survival is based on an acceptance of austerity, a gracious return to a simpler life, the phasing out of fossil fuel as a combustible source of energy, a widespread understanding of the non-detritovorous relationship between people and their habitat, and an acknowledgement of the end of affluence. Do we have the collective courage to meet Catton's future?

Sarah Michaels

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A Nature Guide to Alberta


This Alberta study represents the first Canadian attempt to provide naturalists with a province-wide review of nature since the publication of the classic A Naturalist's Guide to Ontario by the Federation of Ontario Naturalists in 1964. During its five years of development the project involved people from the Provincial Museum, the Federation of Alberta Naturalists, and individual naturalists from throughout Alberta. It is truly a co-operative effort.

The end product is very attractive. The book is copiously illustrated, well laid-out and firmly bound. Although paper quality seems to be satisfactory for the most part, type from the reverse side of pages in the index and appendices does show through only too clearly in my copy. A bolder copy type could have been selected, given the fact-crammed sentences that demand particular attention from the reader. Still, these are minor considerations.

The structure and concept for the book are excellent. The Introduction includes such novel and worthwhile sections as Safety in the Field and Outdoor Ethics, in addition to the regular introductory material. A fairly comprehensive Overview follows including Alberta-wide discussions of the natural environment. The 'meat' of the text follows this ... 260 pages of detailed site descriptions for areas of natural interest throughout Alberta. Appendices complete the text and include directions for those wishing further information, an interesting "eco-tour" of the main Edmonton to Calgary highway and a detailed history of the development of the Alberta Nature Guide project. A very fine index (which includes the scientific names for all plant species, most of which are referred to only by common name in the text), rounds out the book.

Illustrations are largely photographic and are excellent on the whole. The side-ways Sapsucker (p. 251) and fuzzy Swainson's Hawk (p. 336) are unfortunate exceptions. Terry Thormin (who possibly has contributed more to this book than any other author) also provides a number of very pleasant pen and ink sketches of various plants and animals.

The Overview section is a real disappointment. One could reasonably expect this to provide a broadly-based introduction to the natural environment of Alberta. What one receives is a "pot pourri" of topics that are generally superficially treated and uninformative. They jump about from Natural Communities (biotic zones) to The Foothills (landscape units) to Alberta Peatlands (habitats) ... as well as discussing the broad floral and faunal groups which are found in the province. There is no standard format within the various discussions. Only Birds and Amphibians and Reptiles seem to satisfy the purpose of this section.

Site descriptions do follow a standard format — and a good one. The sites are identified within a provincial grid based on 1:250,000 mapsheets. A general description of the natural values within each mapsheet is provided and then each study site (which is shown on an illustration of the mapsheet) is discussed by one or more authors. Where appropriate, a Further Reading section completes the site description.

The use of mapsheets as the basis for organization of the sites is a curious and unfortunate one. Biotic zones (e.g. alpine tundra, aspen parkland, etc.) constitute a more natural structure and would hold more meaning for the reader. An artificial grid may be necessary in more complex areas (British Columbia, for example), but is not in Alberta.

The site descriptions vary tremendously in quality — as is to be expected when so many authors are involved. The editors have done well to standardize style as much as they have. Inconsistencies do sneak in, however. No reference to White-faced Ibis is made in the Pakowki Lake description (p. 77) or elsewhere in the text (beyond that of . . . rare ibises . . . " on p. 60), despite the prominent featuring of this sought-after species on the dust-jacket. Both Boreal Toad and Western Toad are used for Bufo boreas* (pp. 95 and 251, respectively) . . . even by the same author (pp. 95 and 173)! Such minor errors are inevitable, I expect.

Banff and Jasper National Parks are treated separately at the end of the site descriptions — presumably because each park straddles several mapsheets. For continuity sake, they should have been placed in the main body of text in the most appropriate mapsheet (with suitable references elsewhere). At the very least, a map of these very important areas should have been included to identify sites within each.

This is neither a guide to Alberta nature (for which it is too superficial) nor is it an Alberta naturalist's guide (for which it is too incomplete). It is rather, a guide to Alberta's accessible natural areas. It does that job well. All those who put so much time and effort into this complex and demanding project have contributed significantly to the enjoyment and appreciation of Alberta's natural environment.

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*Editor's Note: Western Toad is the common name for the species Bufo boreas while Boreal Toad applies to the subspecies, Bufo boreas boreas, that occurs in Alberta.
Ornithological and Ecological Studies in S.W. Greenland (59° 46'-62° 27' N. Lat.)


Southwest Greenland is a subarctic country of scrub forest and sheep farms. Finn Salomonsen of the Zoological Museum in Copenhagen has produced a description of this little-known land based on one season of special investigation and fifty years of experience on the huge northern island. The result is a well-illustrated monograph in the classic style of the old colonial naturalists: sprinkled with anecdotes, rich in data, and delivered at a leisurely pace. The discussion ranges widely and covers such diverse topics as the etymology of local bird names, the impact of humans on wildlife, the special vegetation of bird cliffs, and the history of animal husbandry on the island back to the time of the ancient Norse population. Special attention is given to exhaustive inventories of sea bird colonies in the subarctic zone, and to the status of six subarctic birds (boreal subspecies of the Fulmar, Black-Headed Gull, Redwing, Fieldfare, White-Tailed Eagle, Slavonian Grebe). Of the latter, all but the eagle are recent invaders from Europe. The author paints a fascinating picture of spectacular range extensions to a truly isolated patch of high-boreal habitat. The monograph concludes with notes on bird visitors to a DEW-line station on the central ice-cap, one of the most inhospitable places in the world.

The text is delivered in clear and elegant English, but with a distinct Danish accent. There are numerous curiosities of spelling and grammar, but the meaning is rarely obscure. A more serious problem is the lack of a labelled map. There are constant references to place names, most of which I could find neither in the monograph nor in the Canadian Oxford Atlas. This makes the text difficult to follow at times.

Salomonsen chastises a Canadian author at one point for ignoring the literature on Greenland and so coming to an erroneous conclusion. This monograph should help prevent the same mistake being made in the future. It is number 204(6) in the ongoing series Meddelelser Om Grønland produced by the Danish Commission for Scientific Research in Greenland (ISSN 0025-6676).

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Ecology of a Subarctic Mire


This volume consists of 15 complete research articles dealing with various aspects of a subarctic mire near Abisko, northern Sweden, chosen as the site for the investigations carried out as part of the International Biological Programme (1964-1974). This paper deals with some aspects of the functioning and environment of this mire complex, developed over permafrost, actually chosen as the tundra site for the Swedish IBP/PT Tundra Biome Project. Unfortunately, and perhaps unavoidably, this set of journal-type papers does not comprise an integrated, complete account of this northern ecosystem, and no attempt is made to tie the information together in a summary paper. Interested students of mire ecology will have to find elsewhere the many other papers that have appeared from work on this project, scattered in the literature or in IBP reports. This book provides an appendix listing these other publications. What we have are accounts of soil water relations, mineral nutrient supply, two papers on community description and classification, three on primary production, two on Sphagnum photosynthesis and growth, and single accounts of nitrogen cycling, CO₂, and methane fluxes, freeze-thaw soil phenomena, and energy flow.

Researchers interested in boreal-subarctic bogs will welcome this excellent compilation, primarily as a compendium of useful data gathered by standard international methods. It contains a wealth of interesting information, highly pertinent for Canadian ecologists who are just at the beginning of serious ecological studies of mires — the Canadian effort was largely dissipated during the 1950's and 1960's on an ill-conceived 'unique' approach, heavily funded by the Defence Research Board and the National Research Council, culminating in the widely criticised volume Muskeg and the Northern Environment in Canada (edited by Radforth and Brawner, University of Toronto Press 1977).

The present volume provides ample material on research design and methodology for sound investigations of mire ecology.

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Bioengineering for Land Reclamation and Conservation


Conservationists and environmentalists rejoice. This is a comprehensive, informative, and highly useful book that will enable man to use nature as his partner when repairing and reclaiming damaged areas. The author's philosophy is clear: "Man must learn how nature maintains her balance and work with her rather than fight against her".

The book was originally written in German by Hugo Schiechtl, a plant sociologist in Austria. The English translation and its application to North America was co-ordinated by N.K. Horstmann, Western Canada Erosion Control Ltd., Edmonton.

Engineers and landscape architects will find the book especially useful as it shows how natural materials can be incorporated into construction plans, thereby creating a more natural and aesthetically pleasing environment. Rather than using dead materials "which are not only less effective but ugly", Schiechtl demonstrates how the use of vegetation can replace hard construction with equal or greater effectiveness, greater appeal, and less cost.

The author's purpose in writing this book is two-fold; 1. To show how scientific and technical knowledge can be integrated with natural materials to develop methods of protecting, restoring, and improving the environment. 2. To aid co-operation between civil engineers and bio-engineers, so that they may appreciate each other's discipline more fully. In my opinion, he reaches his first objective completely. The success of the second will be known with time.

The book is well organized, beginning with three chapters of methodology for the preparation of bioengineering works, earthwork construction and hydro construction. These chapters involve slow, sometimes tedious reading, but the methods described are well sub-titled and are exemplified by many illustrations and photographs. Nevertheless, a knowledge of construction techniques would be helpful to the reader.

The remainder of the book is more easily read. Schiechtl mentions ecological concepts about plant establishment and growth throughout the book, which serve to focus the reader's attention on some point which otherwise would probably be overlooked unless the reader has a background in plant ecology.

The chapter on using bioengineering to its best advantage is very informative. It functions as a troubleshooter, suggesting remedies to the most common mistakes made during construction. Schiechtl's evaluation of how to choose the right construction method is brief but concise.

The chapter on the cost of bioengineering is explicit and frank. Schiechtl pulls no punches in demonstrating that conventional engineering methods are more costly than when bioengineering methods are applied.

The book contains an extensive appendix on the seed types commercially available for different climatic zones. This section will be very useful to the reclamation manager, landscape architect, and civil engineer although it will obviously become outdated as technological advances in seed production continue.

The large bibliography contains references in many languages.

My overall feeling about the book is that it is excellent. It brings together in one comprehensive volume the knowledge and methodology so badly needed in reclamation literature. Obviously, our understanding of nature will change with time, so be assured, there is more to come.

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MISCELLANEOUS

Allan Brooks: Artist Naturalist


There are so many good things to say about this book that it is difficult to do it justice. It struck a particularly responsive note with me, having been raised in Brooks' west and later frequenting many of his haunts (without knowing it until I read the book). With forward by Yorke Edwards, this is an impres- sive publication by an impressive author. Hamilton
Mack Laing, author-naturalist, was a sprightly 96 years of age as the book went to print.

Laing knew Brooks well over the last 25 years of Brooks’ life (the latter died in 1946 at age 77) and both spent much time at Comox B.C. in their later years. Laing’s excellent command of English, knowledge of western Canada, of natural history, and of Brooks, make this much more than just a biography. Here is an historical account of British Columbia natural history (with emphasis on birds of course), a subject I found myself to be woefully ignorant of.

My first encounter with Brookesiana was when given “Taverner” for Christmas in 1949, thus introducing Brooks the artist. Actually, Laing points out that Brooks didn’t care for the epithet of artist, considering himself an illustrator. This probably stemmed less from modesty on Brooks part than from his lack of interest in the larger world of art. For Brooks, painting was but one aspect of scientific description. Years later I began to come across Brooks papers and citations in the scientific literature and to realize the contribution he had made to systematic and distributional zoology, particularly ornithology. One obituary referred to Brooks as “zoologist-artist”, and while he probably wouldn’t have appreciated zoologist any more than artist, it is perhaps a contribution not given enough emphasis in this book or its title.

Brooks’ scientific achievements were not just a result of his penchant (obsession?) for collecting things to be described by eminent scientists in far away museums. He was also a critical thinker, and further, took the time to put pen to paper. He was observant and methodical — the scientist without academic qualifications (he had only 7 years of schooling, all in England), but didn’t let such trivialities get in the way. A recent bibliography of B.C. bird literature cites 71 Brooks papers in such journals as Auk, Condor and Ibis.

Fortunately for both biographer and reader, Brooks was a recorder. Evidence of his having passed this way is profligate — thousands of bird and mammal specimens in museums (mostly in the U.S. unfortunately); countless illustrations in bird and other books; 25 volumes of field diaries; and lengthy correspondence to his father (at two-week intervals for five or more years) and to contemporaries such as Taverner and Fuertes. Mack Laing, as “Boswell to Brooks” makes good use of this material. Personal letters and diaries can expose undesirable traits, and while we don’t know how selective Laing has been, the Brooks reputation seems only to be further enhanced by such close scrutiny. Not that all the gossip is excluded.

There are interesting religious arguments between Brooks (an agnostic) and his father; irreverant comments by Brooks about Francis Kermode’s curatorship of the B.C. Provincial Museum (“a little trumpery museum”); and numerous anecdotes such as when Brooks’ honeymoon (to Alert Bay of all places) got “badly scrambled with ornithology”; when Taverner tricked Brooks with specimens not normally found in the Okanagan Valley; and when Brooks poisoned himself by making biscuits with arsenic which fellow collector James Munro kept in a container labeled baking soda.

Laing quotes extensively from Brooks’ letters and diaries, including lists of specimens taken which, while of interest to me, may seem tedious to others. Bracketed notes of explanation, often nomenclatural, are included in some long quotations but it should be remembered that avian taxonomy was far from complete in Brooks’ earlier years.

The book begins with a chapter about Laing’s first meeting with Brooks near Osoyoos in 1922, then follows his life in chronological sequence from birth (1869) to death (1946). It details the early influences on him (his engineer-naturalist father W.E. Brooks; Thomas McIlwraith); his youthful collecting and big game hunting years; later expeditions to the U.S., New Zealand and Australia; his distinguished military career (attained rank of Major and awarded D.S.O.); his late marriage (age 57) and family life; and emergence of recognition of him as an artist.

Some readers may have difficulty reconciling the naturalist title with Brooks’ penchant for collecting (among others, he shot Trumpeter Swans, Gyrfalcons and Sandhill Cranes with a rifle), but as aptly pointed out by Yorke Edwards in the foreword, Brooks not only lived in a frontier environment where the gun was used to procure food, but in an era when the shotgun was ornithology’s “most important and heavily used scientific instrument”. Brooks’ correspondence with contemporaries such as Fuertes shows his displeasure with anti-collaborating sentiments which grew in his later years. It also reveals his thoughts about predators, which coincided with those of Jack Miner, and lost him some friends.

The book contains over 120 illustrations (about 95 by Brooks; the remainder of him or related subjects), including seven full-page colour plates, worth the $12.95 price alone. There is no index, which limits the reference value of the book. It is remarkably free of typographical errors. The B.C. Provincial Museum is to be commended for maintaining the high quality of its Special Publication Series, and encouraged to produce more of the same.

DONALD A. BLOOD

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Observations of Wildlife


The number of people who have had the good fortune to make a living as a conservationist and artist can probably be counted on the fingers of one hand. Sir Peter Scott is one of those people. His new book Observations of Wildlife supplies insights into the personality that undoubtedly made him an internationally famous artist and wildlife conservationist. The lucid style reveals a man of optimism, confidence, and humility with an obsession for observing wildlife.

Observations of Wildlife is a collection of 96 paintings and sketches that span more than 40 years of Scott's life and travels throughout the world. Only 36 paintings are in colour but those are well reproduced. Peter Scott is concerned that critics don't like his paintings and I suppose someone in his position may wonder if his artwork sells because of who he is and the company he keeps rather than for its own artistic merits. Nevertheless, I don't think Scott is painting for art's sake. Instead, painting serves as a release for his emotions. It's the mood that counts, and that is where he excels. "Shelducks in morning mist" is one such painting. In this painting a flock of 12 shelducks are depicted in flight over open water. The white morning sunlight is reflected off blue water and the haze progressively obliterates the distant shelducks whereas those in the foreground are boldly represented. It is a mood I have observed many times but never dared attempt to recreate with paint.

In another painting Scott has created an interesting juxtaposition between a large flock of Red-breasted Geese and a pattern of broken, white parallel lines of spring snow in a furrowed field.

Perhaps the most evocative painting is of a flock of snow geese flapping their wings hard in take off. The viewer's eye is lead upwards and to the left by the directionality of the birds' flight. The viewing position is slightly below horizontal. One blue-phase snow goose adds just the correct balance to prevent monotony. Unfortunately the illustration is small and in black and white.

Of the 96 paintings and illustrations over 70 are of waterfowl, which might be expected, considering Peter Scott's interest in this order. Nevertheless, it is refreshing to see waterfowl painted from numerous perspectives and not in all-too-often perspective as hunter's quarry.

Another powerful illustration is a two-page colour painting of three humpback whales swimming below two skin divers. The deep tropical blue water is bisected by shafts of paler blue surface light. Green dappled colours reflect waves from above on the whales' backs and marine blue plays off the whales' bodies. The skin divers on the water surface give perspective and a feeling of gracefulness to the whales. From the painting one is certain that Peter Scott has dived among whales.

The text is not as strong as the illustrations. As with so many art books, the text is added supposedly to make the book more meaningful. Although the text is lucid and generally well composed, it does not seem to tie in with the accompanying illustrations. In Chapter 1, for example, Scott begins by telling how he began his painter-naturalist career, but the accompanying painting is dated 1975. I would have preferred a series of illustrations depicting his development in a time sequence.

The overleaf says the book will appeal to those "who wish to learn more about the habits and environment of wildfowl". The book provides some of that information but it is primarily an artbook. I recommend it to wildlife artists, those who enjoy wildlife art, and those with an interest in the monumental conservation efforts of this amazing man.

ROBERT W. BUTLER

Canadian Wildlife Service, Box 340, Delta, British Columbia V4K 3Y3
NEW TITLES

Zoology


†Bird banding in Alberta. 1981. Edited by Martin K. McNicholl. Special Publication No. 2. Federation of Alberta Naturalists, Edmonton, Alberta. 73 pp., illus. $3 plus $.50 postage.


Botany


†Die Kustenvegetation Ostkanada. 1981. By Dietbert Thannheiser. Munstersche Geographische Arbeiten, Schonging, Paderborn, West Germany. 201 pp., illus. DM 41.50.


Environment


The art of Canadian nature photography. 1980. Edited by J. A. Kraulis. Hurtig, Edmonton. 128 pp., illus. $27.50.


Miscellaneous


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The objectives of this Club shall be to promote the appreciation, preservation and conservation of Canada's natural heritage; to encourage investigation and publish the results of research in all fields of natural history and to diffuse information on these fields as widely as possible; to support and cooperate with organizations engaged in preserving, maintaining or restoring environments of high quality for living things.

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Growth of Painted Turtles, *Chrysemys picta*, in Manitoba and Louisiana

DONALD R. HART

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Juvenile growth rates of Western Painted Turtles, *Chrysemys picta bellii*, in Manitoba are very similar to those of Southern Painted Turtles, *Chrysemys picta dorsalis*, in Louisiana. Growth patterns differ between these populations primarily as a function of differences in size at maturity. Male growth rates are sharply reduced at maturity in both populations. Manitoba males show a protracted period of slow growth after maturity, and approach the females in maximum size. Louisiana males stop growing shortly after maturity, and never approach the size of mature females. Non-growing adults in both populations consume increased quantities of plant material.

Key Words: Painted Turtle, *Chrysemys picta*, Manitoba, Louisiana, growth.

Most of the information available on the growth of painted turtles pertains to the Midland Painted Turtle *Chrysemys picta marginata* (Sexton 1965; Gibbons 1967; Wilbur 1975) or intergrade populations involving this subspecies (Ernst 1971; Moll 1977). Other subspecies have not been adequately studied, although size differences between them imply major differences in the pattern of growth. The Western Painted Turtle, *Chrysemys picta bellii*, may attain a carapace length of 25.1 cm, while the record length for the Southern Painted Turtle, *Chrysemys picta dorsalis*, is only 15.6 cm (Conant 1975; Pearse 1923; Wisconsin) and Quinn and Christiansen (1972; Iowa) did not distinguish male and female growth patterns in the *C. p. bellii* populations which they studied, although females attain greater sizes than males in this and all other subspecies. Cagle (1954) reported growth rates for juvenile *C. p. dorsalis* in Louisiana, but not for adults. The paucity of complete growth data for Painted Turtle subspecies other than *C. p. marginata* prompted the present comparative study of growth in Manitoba and Louisiana populations.

Study Areas

Western Painted Turtles were collected from a population in Crater Lake, near Pinawa, Manitoba (50°10′N, 95°51′W) during the spring and summer of 1980. Crater Lake is a slightly widened (maximum diameter 1 km) part of the Winnipeg River, situated in mixed boreal forest. Its maximum depth in the river channel is 7 m and most of the lake is much shallower (1–4 m). Water levels fluctuate periodically, due to the presence of a hydroelectric dam 18 km upstream. During high water periods, turtles spend most of their time in the narrow inlet of a small creek on the north shore of the lake, but they wander over the entire lake when low water levels prevent access to the inlet. Granite rock outcrops along the shoreline and in the middle of the lake are usually used for basking. The lake bottom is uniformly muddy. The dominant plants are submerged pondweeds (*Potamogeton*) and the most common aquatic insects are mayfly nymphs (*Hexagenia limbata*). Snapping Turtles, *Chelydra serpentina*, are present in the lake, but not common.

Southern Painted Turtles were collected from a population in Bayou Boeuf, near Kraemer, Louisiana (29°50′N, 90°37′W). Collection was continuous from the fall of 1976 through 1978. Bayou Boeuf flows for 10 km through a cypress-tupelo swamp, connecting two marshy lakes. Turtles are seldom seen or caught in the lakes, due to an abundance of alligators and a scarcity of basking perches, but are locally common on the bayou and its tributaries. The maximum depth of the bayou is 5 m and the bottom is very muddy. Branches of fallen and overhanging trees provide basking sites. Slightly raised natural levees on either side of the bayou are normally lined in summer by thick floating mats of aquatic vegetation dominated by water hyacinths (*Eichornia crass*, duckweeds...
The Vol. linear females) = Walford formula formation to the approaches provide volumetrically. Residuals divided abruptly appropriate regression between Walford females p > 0.09). Proportions contents were included abdominal (mm). Methods

Turtles were captured by hand or dip net, and in baited funnel traps. Sex was determined by dissection, or by the presence of elongated foreclaws and pre-anal tail regions in mature males (Cagle 1954; Gibbons 1968; Moll 1973). Enlarged ovarian follicles (>10 mm) were used as the criterion for sexual maturity in females (Cagle 1954; Gibbons 1968; Moll 1973). Plastral measurements, made with vernier calipers, included total plastron length (L), abdominal scute length (C), and lengths of discernible annuli on the abdominal scute (C). These measurements were used to calculate plastron lengths at the time of annulus formation (Cagle 1954; Ernst 1971), according to the formula L1/L = C1/C.

Calculated plastron lengths were used to construct Walford plots of growth (Walford 1946). These plots provide a graphical description of the relationship between length in one season and that in the previous season. The relationship is linear when length approaches an asymptotic value smoothly, following the Bertalanffy growth model (Poole 1974). This model approximated female growth closely and linear regression lines were fitted by least squares to the female data. The linear model was considered inappropriate for males, since their growth slowed more abruptly near maturity, causing non-linear trends in residuals (Durbin-Watson test, p < 0.01 in Manitoba, p = 0.053 in Louisiana).

Gut contents of dissected turtles were examined and divided into plant and animal categories. The proportion of plant material, after drying, was determined volumetrically. Stomach, small intestine, and colon contents were pooled (Clark and Gibbons 1969) since proportions did not differ significantly between stomach and colon (paired t test, angular transformation, p > 0.09).

Results

In Manitoba, 39 seasonal growth increments were calculated from 22 captured turtles (12 males, 10 females), and food was recovered from 12. In Louisiana, 20 turtles were captured (9 males, 11 females) and food was recovered from 18; 26 seasonal growth increments were calculated from 18 individuals that had completed at least one full season of growth. Walford plots of growth are shown in Figures 1 and 2.

![Figure 1](image1.png)

**Figure 1.** Walford plot of growth in Western Painted Turtles from Crater Lake, Manitoba. Plastron length at end of growing season (L_{(t+1)}) is plotted against length at end of previous season (L_t). Measurements are from 12 males and 10 females. Regression line is fitted to data for females only (L_{(t+1)} = 28.5 - 0.84 L_t; r^2 = 0.995). Size of first maturity in females based on Moll (1973).

![Figure 2](image2.png)

**Figure 2.** Walford plot of growth in Southern Painted Turtles from Bayou Boeuf, Louisiana. Measurements are from 8 males and 10 females. Format as in Figure 1 (L_{(t+1)} = 31.6 - 0.75 L_t; r^2 = 0.984).
for Western Painted Turtles and Southern Painted Turtles, respectively. Juvenile growth, prior to maturity, was rapid and differed little between the populations. Turtles entering their first full season of growth at a plastron length of approximately 4 cm had increased in size by 50–60% (100 (L_{t1} - L_{t0})/L_{t0}) at the end of that season. Subsequent growth rates declined steadily. Males and females grew at similar rates until the onset of male maturity, when male growth was sharply reduced.

Growth patterns differed between populations primarily as a function of differences in size at maturity. The smallest mature male in the Manitoba population was 10.0 cm in plastron length, while the smallest mature male in the Louisiana population was 6.5 cm (Tables 1 and 2). The largest male captured in Louisiana was 8.6 cm, well below the size of the smallest mature male in Manitoba. Consequently, the adult males in Louisiana grew more slowly than the immature Manitoba males of comparable size (Figures 1 and 2). Similarly, the largest Louisiana female captured was below the size of first maturity in Manitoba females.

Manitoba males showed a protracted period of slow growth after maturity (Figure 1). This period was either abbreviated or lacking entirely in Louisiana males (Figure 2). Thus, the largest male *C. p. dorsalis* captured was only 65% of the maximum female size. The corresponding value for *C. p. bellii* was 82% of the maximum female size.

Cessation of growth near the maximum size was often associated with an increased consumption of plant material. Tables 1 and 2 show that all juveniles and many mature adults were highly carnivorous, with plants accounting for less than 5% of the diet. Animal food consisted mainly of insects in Manitoba *C. p. bellii*, and of insects and freshwater sponges in Louisiana *C. p. dorsalis*. Only non-growing individuals deviated from this carnivorous pattern. Plants contributed more than 20% of the diet in certain non-growing males of both subspecies, and more than 60% in some females.

**Discussion**

The Painted Turtles in these populations show the same general pattern of growth as those in Michigan (Gibbons 1967; Wilbur 1975), Pennsylvania (Ernst 1971) and Illinois (Moll 1977). Female growth

<p>| Table 1. Size, maturity and plant consumption in Western Painted Turtles from Crater Lake, Manitoba. |</p>
<table>
<thead>
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<th>Plastron Length (cm)</th>
<th>Maturity</th>
<th>Plant Consumption (%)</th>
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<tbody>
<tr>
<td>Males</td>
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<td>9.5</td>
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<td>10.0</td>
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<td>10.3</td>
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<td>10.6</td>
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<td>10.9</td>
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<td>12.4</td>
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<td>13.5</td>
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<tr>
<td>14.8*</td>
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<td>15.1*</td>
<td>+</td>
<td>–</td>
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<td>15.3*</td>
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<tr>
<td>15.5*</td>
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<td>16.0*</td>
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<td>21</td>
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<td>Females</td>
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<td>9.1</td>
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<td>17.8*</td>
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<tr>
<td>19.5*</td>
<td>+</td>
<td>61</td>
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*non-growing individuals lacking plastral annuli

<p>| Table 2. Size, maturity and plant consumption in Southern Painted Turtles from Bayou Boeuf, Louisiana. |</p>
<table>
<thead>
<tr>
<th>Plastron Length (cm)</th>
<th>Maturity</th>
<th>Plant Consumption (%)</th>
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<tbody>
<tr>
<td>Males</td>
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<td>4.1*</td>
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<td>6.5</td>
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<td>7.0**</td>
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<td>7.3</td>
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<td>13.3**</td>
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**hatchlings captured before first annulus formation**

**non-growing individuals lacking plastral annuli**
approximates the Bertalanffy model, slowing gradually as maturity approaches. Male growth is usually curtailed more sharply at maturity, since males mature at a smaller size, and hence a greater growth rate than females. Sexual dimorphism in emydid growth varies from extreme in the Map Turtle, *Graptemys pseudogeographica* (Moll 1976) to virtually absent in the Spotted Turtle, *Clemmys guttata* (Ernst 1975). Growth dimorphism in the Painted Turtle is intermediate between these two extremes.

Size at maturity varies considerably among Painted Turtle populations. Male and female *C. p. marginata* mature at approximately 8.0 cm and 11.5 cm respectively in Michigan populations (Gibbons 1967; Wilbur 1975). Male and female *C. p. bellii* in Wisconsin mature at 9.6–10.1 cm and 13.6 cm respectively; the corresponding values for *C. p. dorsalis* in Louisiana and Arkansas are 6.0–6.7 cm and 10.0 cm (Moll 1973). These values are consistent with my limited data on maturation of *C. p. bellii* and *C. p. dorsalis*, and suggest that the sharp reduction of male growth in Manitoba and Louisiana populations is associated with sexual maturity.

Growth before and after maturity depends strongly on food supply. In Sheriff's Marsh, Michigan, where animal food is scarce, juvenile *C. p. marginata* grow slowly and adult growth after maturity is curtailed at a smaller size than in the Kalamazoo River where more animal food is consumed (Gibbons 1967; Gibbons and Tinkle 1969). Male *C. p. marginata X bellii* in Chautauqua Lake, Illinois, where juvenile growth is poor, stop growing very shortly after maturity (Moll 1977). These studies suggest that a protracted period of slow growth after maturity is associated with good juvenile growth prior to maturity.

Male growth in Manitoba *C. p. bellii* is protracted up to 6.0 cm beyond the size at first maturity, while that in Louisiana *C. p. dorsalis* stops within 2.1 cm of the mature size. Since this difference is not associated with an obvious difference in juvenile growth prior to maturity, it is probably not due to differences in food supply; turtles in both populations are highly carnivorous throughout their growing period. Rather, the data suggest that there are inherent differences between these populations in the potential for growth after maturity, which parallel inherent differences in size at maturity. It is uncertain whether the differences typify the subspecies involved or arise from local evolutionary constraints on the particular populations studied. Possible evolutionary constraints include competition with other emydid turtles in southern populations and short growing seasons in the north (Cagle and Chaney 1950; Ernst 1971; Moll 1973).

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**Literature Cited**


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The Wood-inhabiting Fungus, *Aleurodiscus dendroideus*, sp. nov., and the Distinctions Between *A. grantii* and *A. amorphus*

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The wood-inhabiting fungus, *Aleurodiscus dendroideus*, sp. nov., from Alberta is characterized by its small, pezizoid basidiomes, smooth, amyloid spores, botryose acanthophyses, apically moniliform pseudocystidia and clamp connections. *Aleurodiscus grantii*, formerly considered to be a synonym of *A. amorphus*, is recognized as a distinct species based on microscopic features and restricted geographic distribution.

Key Words: Wood-inhabiting fungi, taxonomy, *Aleurodiscus* species, distribution, habitats.

During the study of wood-inhabiting fungi of the western cordillera of North America, three distinct species were recognized among specimens closely resembling *Aleurodiscus amorphus* (Purton) Schroet. A collection from Alberta is proposed as a new species (*A. dendroideus*). Also, *A. grantii* is recognized as a distinct species rather than as a synonym of *A. amorphus*. The three species are described and the distinguishing features of the three are discussed.

Methods

Macroscopic features were taken from dried specimens unless otherwise specified. Color codes are from Munsell (1942). Most details of the microanatomy were obtained from thin (ca 10 μm), vertical sections of basidiomes (=fruiting bodies). Sections were mounted in several standard mycological reagents (2% W/V aqueous KOH, Melzer’s reagent, sulfobenzaldehyde and cotton blue). The reagents were prepared according to the directions in Singer (1975, p. 92-100). Terms describing hyphal wall thicknesses follow the definitions in Ginns (1976, p. 107). The listings of Specimens Examined includes at the end of each entry the code letters of the herbarium where that specimen is housed. Details of the location of these herbaria are included in the Acknowledgments.

Descriptions

*Aleurodiscus dendroideus* Ginns, sp. nov.

Basidiocarpaceae usque ad 1.5 mm diam. Hyphae hyalinae, fibulatae, Acanthophysae botryosae. Basidiosporae ovoidae, leaves, amyloideae, (14.5)-16-18.5 X 9.5-11 μm.

Holotypus: Canada: Alberta: SW of High Level, 3 September 1964, on *Picea glauca*, Gautreau (CFB 6329).

Etymology: from the tree-like branching habit of the acanthophyses.

Badidiomes (Figure 1 A-B) pezizaeciform, up to 1.5 mm diam, sessile, attached by a central, white radicating base up to 0.5 mm diam; exterior white, granulose to a rather matted cottony; margin white, determinate, of fine granulose-appearing hairs (= acanthophyses) that extend slightly over the edges of the hymenial surface; hymenial surface pale yellow to yellow, finely granulose, smooth, slightly convex; context pure white.

Hyphal system monomitic; context hyphae closely packed, parallel, essentially vertically arranged, distinct, rather frequently branched, hyaline, thin-walled, with clamp connections and infrequent simple septa, 4-5 μm diam, nonamyloid, acyanophilous; acanthophyses (Figure 1 E-F) numerous, on the exterior of the basidiome and in the hymenium, they are responsible for the granulose texture of the basidiome, composed of a cylindrical, thin-walled pedicel 4-5 μm diam with a weakly amyloid, dendroid head 20-30 μm wide and up to 60 μm tall, occasionally the apex of the pedicel becomes inflated up to 12 μm diam; pseudocystidia (Figure 1 C) uncommon to rare, narrowly clavate, occasionally cylindrical, nonamyloid, the color and texture of the contents similar (i.e., not granulose or oily) to the basidia but staining blackish grey in sulfobenzaldehyde, up to 8.5 μm diam, with or without one to four successively smaller, acropetal, apical swellings; hyphidia rather frequent, cylindrical to narrowly clavate, typically slightly wavy, thin-walled, nonamyloid, 4-5 μm diam, with an obtusely rounded apex: basidia (Figure 2) narrowly clavate, 140-150 X 12-13 μm, tapering to an essentially cylindrical base 4 μm diam, with four sterigmata, each up to 8-11 μm long: spores (Figure 1D) ovoid in face view, ovoid to broadly ellipsoid in profile, adaxially sometimes slightly flattened, (14.5)-16-18.5 X 9.5-11 μm, with a broad, blunt apiculus; the wall smooth, thin, hyaline, amyloid.
Figure 1. Aleurodiscus dendroides. A–B. Basidiomes. C. Pseudocystidium. D. Spores. E–F. Acanthophyses. All from holotype. Scale equals in A 2 mm, B 1 mm, C, D & F 20 μm, and E 50 μm.
Figure 1. Aleurodiscus dendroides. Five basidiospores, the terminal segment of a sparsely branched acanthophyllum and a basidium. From holotype.

Habitat

The basidiomes were emerging either between or from somewhat under bark scales on the sides and lower surface of a 7 mm diameter branch of Picea glauca. It is not known whether the branch was on the ground, on a dead tree or a dead branch on a live tree. The latter is a preferred habitat for some species (e.g., Aleurodiscus amorphus).

Aleurodiscus grantii Lloyd (1920, p. 927).

Basidiomes disciform or pezizaform, 1-4 mm diam (resembling Figure 5), scattered to gregarious, sometimes confluent, in vertical section 0.5-1 mm thick, attached by a short, central base; margin determinate, ringed with white, shiny fascicles of hyphal hairs, up to 0.2 mm long; hymenial surface plane to slightly convex, finely granulose, typically pale orange pink to pink (Munsell 2.5YR7/6)), sometimes faded when aged or after storage; abhymenial surface white, grey or pale brown, finely hirsute or matted.

Hyphal system monomitic; generative hyphae in the context hyaline, thin- to sometimes rather thin-walled, the wall often with a 1.5 µm thick gelatinized exterior as viewed in 2% KOH, branched, some septa with clamp connections (Figure 3 B), 3-5(6.5) µm diam; abhymenial surface sometimes with hyphae parallel, compact, rather thin- to thick-walled, brownish yellow, to 7 µm diam; hyphal "hairs" on the abhymenial surface of the basidiomes and the margin around the hymenial surface straight, rarely branched, branches arising dicotomously, simple septate, thin- to rather thin-walled, 3-5(6) µm diam; hymenium, sybhymenium and adjacent context with few to numerous, square to angular crystals up to 10 µm wide; pseudocystidia lacking; hyphidia (Figure 3 C) hyaline, thin- to rather thin-walled, infrequently thick-walled, straight to wavy, unbranched or with up to four short branches, cylindrical or with the apex irregularly swollen or strangulated, swellings sometimes moniliform, 4-6 µm diam; basidia clavate, tapering to a 4 µm diam base, with a clamp connection around the basal septum, ± 230 X 25-28 µm with four sterigmata, each up to 21 µm long; spores (Figure 3 A) broadly ellipsoid to subglobose, 22-32(-39) X 18-24 (-28) µm, the wall to 1 µm thick, hyaline, acyanophilous, with amyloid spines up to 4 µm long, with a broad (-3 µm), blunt apiculus.

Habitat

Typically occurring on the lower surface of small (1-6 cm diam), dead branches in the lower crown of live coniferous trees, sometimes on the trunks of dead saplings or on fallen stems. It is most frequently collected on species of Abies, especially A. grandis and A. lasiocarpa, and less frequently on other tree species (cited in Specimens Examined section).
Figure 3. *Aleurodiscus grantii*. A. Basidiospores with amylloid spines. B. Clamp connection across a septum of a hypha. C. Narrow hyphidia. From isotype of *A. grantii* (TRTC).

Distribution

In western North America from 113°W longitude extending west to the Pacific Ocean and from 38° to 64° N latitude (Figure 4). More specially in the cordillera from Yukon, British Columbia, western Alberta, western Montana, Idaho, Washington, Oregon and northern California.

Specimens examined (selected)

Canada. Yukon: Barlow Dome, on *Abies lasiocarpa*, Ginns & Cody (DAOM 177674), South Canol Road km 8, Ginns & Cody (DAOM 177430), Howard Pass, Rosie 19 (DAOM 175699). Alberta: Waterton

*Aleurodiscus amorphus* (Burton) Schroet. in Cohn, Krypto.

Fl. Schles. 3(1): 429. 1889.


Basidiomes (Figure 5) disciform or pezizaefiform, 1-5 mm diam, typically circular in outline, scattered to gregarious, sometimes confluent and then of irregular outline, attached by a short, central base, up to 0.5 X 0.5 mm which expanded to 1 mm diam beneath the outer cortex layer of the host; margin determinate, ringed with white hairs, cottony to fimbriate, sometimes fasciculate and then appearing hirsute, up to 1 mm long; hymenial surface plane to slightly convex, finely granulose, when fresh and actively sporulating salmon pink (Munsell 10R6/8 or 2.5YR7/8), in aging or after herbarium storage pallid (2.5Y8/4), pinkish orange (5YR7/6) or olive ochreous (2.5Y7/4, 10YR6/4); abhymenial surface white, grey, balckish grey or pale brown, matted tomentose to finely hirsute.

Hyphal system monomitic; generative hyphae in the context hyaline, simple-septate, thin- to rather thin-walled, the exterior surface of the walls swelling in 2% KOH, with few to numerous segments crystalline incrusted, branched, nonamyloid, acyanophilous, 3-5 m diam; external hyphae, including those form-
ing the “hairs” around the hymenial surface and those of the abhymenial surface, hyaline, pale yellow or some on the abhymenial surface yellow-brown, thin-to rather thin-walled, septate, rarely branched, the branches arising as an apical dichotomy, incrusted with few to numerous small (-5 μm), roughed or angular crystals, (3-)4-6.5 μm diam; hymenium and context with few to numerous, small to large (-10 μm diam) crystals scattered throughout; hyphidia (Figures 6A & D) scattered, cylindrical or some irregularly swollen, straight to wavy, some with one or two branches, (2-)3-5 μm diam; pseudocystidia (Figure 6B) usually numerous, typically with 1 to several, successively smaller, acropetal, apical swellings up to 10-11 μm diam, acyanophilous, nonamyloid, not darkening in sulfobenzaldehyde; basidia (Figure 6C) clavate, tapering to a narrow (4-5 μm diam) base, basal septum simple, about 200 X 22-28 μm with four sterigmata, each 30-40 μm long and up to 7.5 μm broad at the base; spores broadly ellipsoid to subglobose, (22-)24-28(-32) X (18-)20-23(-26) μm, the wall either hyaline and thin or thickened and pale yellow, acyanophilous, with amyloid spines up to 4 μm long and a broad, blunt apiculus.

**Habitat**

Occurring on the lower surface of dead branches in the lower crown of live conifers, especially species of *Abies*, also on fallen branches and stems. Persisting for several months, perhaps as long as one year. Erumpent through the bark but not distorting the substrate (i.e., not causing or associated with a canker).

**Distribution**

Across North America where species of *Abies* occur but not confined to *Abies*. Rare to uncommon within the range of *Aleurodiscus graniti* (Figure 4). Found in Europe, Siberia, Japan (Lemke 1964) and China (Lemke 1964).

**Specimens examined**

Europe. France: Aude, near LeClat, 1333 m, on *Abies alba*. Fenwick-Owen and Darker 3970 (DAOM 127127). Sweden: Ostrog, in monte Omberg, on *A. alba*, Schotte (DAOM 72058), Switzerland: St. Cergue, on *A. alba*, Darker 4029 (DAOM 72424).

Canada (host is *A. balsamea* unless specified). Nova Scotia: Kentville, Harrison 96 (DAOM 95381). New Brunswick: Fundy National Park, Cain (TRTC 41581). Quebec: Parc Chibougamau; Lac Nicabau, on dead branches on live tree, Ginns (DAOM 175406); Upper Lachute, on *Pinus strobus*, Gordon 1285 (DAOM, Dearness species no. 475); Gatineau Co.: Cantley, Ginns (DAOM 177755). Ontario: Matachewan: SW of Burt Lake, on log, Ginns (DAOM 175409); Nipigon: Black Sturgeon Lake, Ginns (DAOM 175408); Algoma District: Township 4F: Aubinadong River, Cain (TRTC 34038, DAOM); Kenora, Buller (DAOM F6699). Manitoba: Victoria Beach, Bisby (DAOM 33925); Island Lake, Tidsbury, WINF 7715 (CFB); Snow Lake, Tidsbury, WINF 9973A (CFB); Portage: Cranberry, Lawrence, WINF 10875 (CFB). Saskatchewan: La Ronge, Beveridge, WINF 8273b (CFB); White Swan Lake, Lawrence, WINF 7641 (CFB); Doré Lake, Riley 48-35 (DAOM 30459). Alberta: Seebe, on *A. lasiocarpa*, Whitney & Riley 50-15 (DAOM 30903) and on *Picea glauca*, Riley 794 (CFB); Kananaskis, on slash of *P. glauca*, Riley & Patterson 49-567 (DAOM 30904); Robb (42 km SE of Hinton), Baranay (CFB 4283); Nordegg, on *A. lasiocarpa*, Etheridge (CFB 1164 and 1300); Waskahigan River, on *P. glauca*, Laut (CFB 3651). Yukon: South Canol Road km 15, on dead *A. lasiocarpa*, Ginns (DAOM 178788) and km 84, Quiet.

**Figure 6. Aleurodiscus amorphus.** A. Broad, cylindrical to irregularly swollen hyphidia. B. Broad, moniliform pseudocystidia. C. Immature basidium. D. Narrow hyphidium. From lectotype of *Nodularia balsamicola* (NYS), a synonym of *A. amorphus.*

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Mexico. Mt. Popcatepetl (72 km SE of Mexico City), on *A. religiosa*, Lemke (TRTC 37150 and 37102).

USSR. Siberia: District Jara, on *A. sibirica*, Murashkinsky (TRTC).

Discussion

Macroscopically the basidiomes (Figure 1 A-B) of *Aleurodiscus dendroides* closely resembled apothecia of species of Helotiaceae. The combination of features that distinguishes *A. dendroides* from the other species of *Aleurodiscus* are the peziziform basidiomes, clamp connections, botryose acanthophys, pseudocystidia, and smooth, slowoid spores (Figure 1).

Several microscopic features of *A. dendroides* warrant particular mention. In the hysenium the individual cells (i.e., basidia, acanthophys, etc.) had arisen at the same level and were approximately the same length, thus the hymenium seems to be of the euhyphal type. Some pseudocystidia lack apical swellings and are thus indistinguishable from immature basidia when observed in Melzer’s, KOH or cotton blue reagents, but in sulfobenzaldehyde they stain blackish grey unlike the basidia. The botryose acanthophys are unusual in *Aleurodiscus*. The only other species with extensively branched acanthophys are *A. botryosus* Burt and *A. petelotii* Pat. *Aleurodiscus botryosus* has narrower and more densely packed branches on the acanthophys, corticioid basidiomes, apically attenuated pseudocystidia, simple septa, echinulate spores and short (-68 μm) basidia (Lemke 1964). *Aleurodiscus petelotii* has a pale reddish hysenium, asperulate spores 23-25 × 14-15 μm and is known only from Viet Nam (Patouillard 1924).

*Aleurodiscus grantii* was placed in synonymy with *A. amorphus* by Rogers and Jackson (1943, p. 269) following their examination of the three specimens upon which Lloyd (1920) based his new species. This synonymy was reaffirmed by Lemke (1964, p. 227). He too examined Lloyd’s specimens. As a result all collections with discoid- or pezizoid-like basidiomes with large, spiny, amyloid spores have been labelled *A. amorphus*. However, there are sufficient distinguishing characters of taxonomic importance to recognize *A. grantii* as a species distinct from *A. amorphus*.

The principal character distinguishing *A. grantii* from *A. amorphus* is the presence of clamp connections in *A. grantii* (Figure 3 B). Clamps were found at about 10% of the septa on the context hyphae. In specimen DAOM F8966 clamps were unusually frequent, i.e., at 30-40% of the septa. A clamp was present at the base of nearly all mature basidia. *Aleurodiscus amorphus* lacks clamps (Lemke 1964; Eriksson and Ryvarden 1973, p. 63). In addition *A. amorphus* has slightly smaller spores, broad (8-12 μm diam), apically moniliform pseudocystidia (Figure 6B), and apparently is of wider geographical distribution. The differences in spore sizes may not be obvious when the size ranges in the descriptions are compared but by measuring the largest spores in each collection it became evident that *A. grantii* typically has spores 30 μm or longer whereas in *A. amorphus* it was unusual to find spores over 28 μm long.

The two species produce cylindrical hyphidia (Figure 3 C & 6 D). In *A. grantii* some hyphidia in some specimens have the apical portion strangulated to form irregular to moniliform swellings. These strangulated hyphidia resemble the pseudocystidia of *A. amorphus*, but never produce swellings which are as uniformly globose or as broad (-11 μm diam) as those in *A. amorphus*. In both species the size and number of crystals in the hysenium and context varied between specimens, and both species had hyphal walls swelling in 2% KOH.

Lloyd (1920) in distinguishing *A. grantii* from *A. amorphus* emphasized macroscopic features which, to me, are not important in separating the two species, i.e., the “free but not raised margin” and basidiomes “entirely different in shape” in *A. grantii*. He continued, “microscopic characters as in *A. amorphus*.” As noted above the microscopic features are of primary importance in separating the species.

*Aleurodiscus amorphus* is redescribed, and host and geographic records are given. All are based on specimens examined by me, unless otherwise specified. The description of *A. amorphus* gives my circumscription of the species and allows comparison with the features of *A. grantii*. There are few and only minor differences between the description herein and the one presented by Lemke (1964), where *A. grantii* was accepted as a synonym of *A. amorphus*. The above description extends the abhymenial color from white to include grey, blackish grey and pale brown, notes the swelling of hyphal walls in 2% KOH and the size of the sterigmata to be twice that given by Lemke.

The segregation of *A. grantii* from *A. amorphus* necessitates a critique of the hosts and geographic
distribution that have been reported for A. amorphus in western North America where both species occur. Despite the examination of nearly 130 specimens labelled A. amorphus from western North America only 13 proved to be A. amorphus, the remainder were redetermined as A. grantii. Therefore the records of A. amorphus from British Columbia (Connors 1967) and on Picea from Idaho, California and Colorado (Martin and Gilbertson 1977) probably were based on specimens of A. grantii. The record (Connors 1967, p. 5) of A. amorphus in British Columbia on Abies pinsapo was based on a specimen (cited above) of Aleurodiscus grantii. Although A. amorphus occurs in the cordilleran on Abies concolor, A. lasiocarpa, A. religiosa, Picea glauca and P. sitchensis no specimens of Aleurodiscus amorphus were seen from British Columbia. The numerous specimens in DAOM from Canada east of Alberta were with few exceptions on Abies balsamea, whereas Aleurodiscus grantii is not known from Abies balsamea.

The northern and southern limits of Aleurodiscus grantii and the degree to which its range overlaps the range of A. amorphus remain to be defined. The ranges of the two species are known to overlap at two points: in central Yukon and the Alberta foothills. A lone collection of A. amorphus was seen from coastal Oregon, the heart of the range of A. grantii. Confirmation that the Oregon specimen was from the coast as indicated by the specimen label was supplied by Dr. I. Brodo of Ottawa who examined the lichens growing on the branch adjacent to the basidiomes of A. amorphus. Two of the lichens are known only from the Pacific coastal region of North America. Although Cooke (1955, p. 13) reported A. amorphus from Alaska, the specimen (Sprague 165 at WSP) which was the basis of his report is, to me, Aleurocystidium subuentatum (B. et C.) Lemke. No other records or specimens of either Aleurodiscus amorphus or A. grantii have been seen from Alaska. To the west of Alaska only one specimen was seen from Siberia and it was A. amorphus. Parmasto (1963) recorded A. amorphus on Abies gracilis from Zhuipanovo, Kamchatka.

The close relationship of Aleurodiscus grantii and A. amorphus is emphasized by the presence of the mycoparasite Tremella mycophaga Martin, on A. grantii (e.g., DAOM 139346). Previously T. mycophaga was known only from A. amorphus.

Acknowledgments
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Literature Cited

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Characteristics of Red-shouldered Hawk, *Buteo lineatus*, Nest Sites in Southwestern Québec

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Characteristics of 54 Red-shouldered Hawk (*Buteo lineatus*) nest trees in southwestern Québec were measured to determine what role these features play in the selection of a nest site. Large Beeches (*Fagus grandifolia*) and Sugar Maples (*Acer saccharum*) were most often used, with nests in Sugar Maples occurring relatively higher (p < 0.05) than those in Beeches. Nest height was positively correlated with the height of the nest tree. There were no significant differences between nests located in the two major tree species, nor between nine successful and five unsuccessful nests in 1980.

Key Words: Red-shouldered Hawk, *Buteo lineatus*, nest sites, Québec.

There is often considerable intra-specific variability in the nest site characteristics of a given bird species. The choice of typical nest sites may be reflected in the individuals' nesting success through such mechanisms as increased predation (Evans 1978), ultimately influencing the evolution of nest placement within a species (Rich 1980). We examined Red-shouldered Hawk (*Buteo lineatus*) nest sites in southwestern Québec to determine what role, if any, features of the nest tree play in their selection. Throughout its range, this hawk nests in many species of trees, which implies that it may prefer nest trees with a particular physical structure (Bednarz 1979; Titus and Mosher 1981). Nickell (1958) suggested that differences in branching patterns and other characteristics between tree species may be very important in a bird's final choice of a nest site. Despite several recent studies in other areas (Bednarz 1979; Portnoy and Dodge 1979; Titus and Mosher 1981), relatively little is known about the Red-shouldered Hawk in eastern Canada (cf. Campbell 1975), and there has been some concern (Fyfe 1976) that declines in numbers similar to those in parts of the United States (e.g. Brown 1971; Hackman and Henny 1971) may also be occurring in Canada.

Study Area and Methods

Nests of the Red-shouldered Hawk were studied at two localities in southwestern Québec, near the northern limit of the species' breeding range (Godfrey 1966). The main study area (ca 200 km²) was in Vaudreuil County (45° 26' N, 74° 14' W), about 45 km west of Montréal. The dominant forest type is composed of Sugar Maple (*Acer saccharum*) and Beech (*Fagus grandifolia*), with Red Maple (*Acer rubrum*), Yellow Birch (*Betula alleghaniensis*), Basswood (*Tilia americana*), Largetooth Aspen (*Populus grandidentata*) and oaks (*Quercus spp.*) (Newstrom 1978). The terrain is flat to gently undulating except for Mont Rigaud (210 m), which despite recent residential growth nearby remains almost completely wooded. About 60% of this study area is forested, with agricultural, residential and recreational areas occupying the remaining area.

A second study area (ca. 15 km²) was at Mont St-Bruno (217 m) (45° 33' N, 73° 19' W), about 16 km east of Montréal. This area's geological history and resultant pedographic characteristics have produced forest associations somewhat less varied than those in the main study area (Walther 1963, Newstrom 1978). This area is centred on a provincial park, resulting in some recreational disturbance but reduced residential and industrial activity.

Fifty-four nests used by Red-shouldered Hawks in the two study areas from 1977 to 1980 were found by searching traditional nesting areas or by periodically observing soaring territorial hawks from early March to mid-April. The 15 nests in the Mont St-Bruno area were all found by local residents. Active nests received regular brief visits during the breeding seasons. Data on the nest trees were usually gathered after the young had left the nests. All heights were measured with an altimeter or a measured rope. The number of young leaving 16 nests in the main study area for which the outcome was known in 1980 was recorded. The mean diameter and depth of 16 nests examined more closely in 1979 and 1980 were used to describe the structural relationship between the tree fork and the nest. The 'nest access distance' (Bednarz 1979) is the mean distance (measured in cm at the top of the nest) between the branches supporting the bulk of the nest. The 'nest openness' is a measure of the percentage of the nest circumference not obstructed by the supporting
branches. A high value of 'nest openness' indicates that relatively little of the nest is obstructed or, conversely, that there may be relatively poor support of the nest. Student's t-tests and Mann-Whitney U tests (two-tailed) at the 0.05 level of significance were used in the data analysis.

Results and Discussion
The species of trees most frequently used by nesting Red-shouldered Hawks in southwestern Quebec were Beech and Sugar Maple (Table 1). These two species often dominate mature deciduous stands in both study areas (Walther 1963, Newstrom 1978). The height (mean 28.9 m) and diameter at breast height (mean 45.0 cm) of the nest trees were comparable to those from other study areas (e.g. Bednarz 1979, Titus and Mosher 1981) and indicated that the trees were about 150-200 years of age (based upon the growth rates cited in Graber and Graber 1976). Nest height was correlated \( r = 0.81, p < 0.001 \) with the height of the nest tree. Other studies (e.g. Gerrard et al. 1975, Loman 1979) have emphasized the importance of the structure (size, branching pattern) of potential nest trees to species such as raptors that build large nests which are often re-used and enlarged with additional nest material in subsequent years.

Sugar Maples used as nest trees (Table 1) were somewhat taller \( p < 0.1 \) than the Beeches used, perhaps because several nest were in commercial "sugar bush" (managed stands of mature maple trees). Nests in Sugar Maples were also relatively higher \( p < 0.05 \) than those in Beeches, which probably reflects differences in branching geometry of the two species. Large Sugar Maples usually branch to form suitable nest locations ("platforms") at 13-20 m and Beeches at 10-15 m, depending upon the age of the tree. Coniferous trees do not appear to provide such suitable locations for nests. The low relative nest height of Red-shouldered Hawk nests (mean 48.4\%, Table 1) places them well within the forest canopy, providing additional protection after the appearance of the foliage. Other possible selective advantages of building a nest at the lowest possible height may involve reduction of the energy required for nest construction and maintenance (Portnoy and Dodge 1979) or moderation of the nest's thermal environment (Ricklefs and Hainsworth 1969; Calder 1973). This characteristic nest position of the Red-shouldered Hawk is generally lower than those of the Red-tailed Hawk \( (B. jamaicensis) \) and Broad-winged Hawk \( (B. platypterus) \) (Bohm 1978; Bednarz 1979; Titus and Mosher 1981).

Bednarz (1979) suggested that potential nest competitors of the Red-shouldered Hawk are somewhat less agile flyers (Johnson and Peeters 1963), which apparently prefer less-obstructed (more open) sites higher in the nest trees and closer to the edge of the forest. Nest size differences among species may also be an important factor influencing their vertical placement (Rich 1980).

The Red-shouldered Hawk nests were generally large, broad-based structures of sticks and twigs, often lined with sprigs of Hemlock \( (Tsuga canadensis) \) or deciduous leaves. They were variable in size (Table 2) with a mean volume (excluding the bowl) of about 43 500 cm\(^3\) (range 20 900–95 500), generally comparable to other data (Bent 1937, Bednarz 1979). There were no significant differences in any of the characteristics between nests located in Beeches and Sugar Maples. These data may be confounded somewhat by variable ages of the nests, on which we have little information. Avian nest size may also vary during the nesting season (e.g. Calder 1973) and within a species' range (Schaefer 1976). The nests in this study were supported by a mean of 4.2 tree 'elements' (trunk and branches), similar to those studied by Bednarz (1979). Although the mean 'nest access distance' was only about 33 cm (range 11.2–54.3), also similar to that reported by Bednarz (1979), these branching configurations were often quite irregular, usually permitting less-obstructed access by the adults from at least one direction. The 'nest openness' (mean 67.9\%) also characterizes the forks in which the nests were located.

**Table 1**—Characteristics of nest sites (mean ± SD) selected by Red-shouldered Hawks in southwestern Quebec, 1977–1980

<table>
<thead>
<tr>
<th>Tree species</th>
<th>Nests Number (%)</th>
<th>Nest tree dbh (cm)</th>
<th>Nest tree height (m)</th>
<th>Nest height (m)</th>
<th>Relative nest height (%)(^1)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fagus grandifolia</strong></td>
<td>23 (43)</td>
<td>43.4 ± 8.8</td>
<td>27.6 ± 3.7</td>
<td>12.7 ± 2.3</td>
<td>44.9 ± 5.5</td>
</tr>
<tr>
<td><strong>Acer saccharum</strong></td>
<td>16 (30)</td>
<td>48.4 ± 11.3</td>
<td>30.0 ± 3.8</td>
<td>16.0 ± 3.0</td>
<td>52.5 ± 7.7</td>
</tr>
<tr>
<td><strong>Betula alleghaniensis</strong></td>
<td>5 (9)</td>
<td>39.2 ± 3.9</td>
<td>24.9 ± 3.7</td>
<td>10.8 ± 3.5</td>
<td>48.7 ± 4.5</td>
</tr>
<tr>
<td><strong>Quercus rubra</strong></td>
<td>4 (7)</td>
<td>43.5 ± 7.3</td>
<td>29.8 ± 4.5</td>
<td>15.5 ± 3.0</td>
<td>51.9 ± 5.7</td>
</tr>
<tr>
<td>Other species(^2)</td>
<td>6 (11)</td>
<td>47.8 ± 20.5</td>
<td>33.2 ± 10.2</td>
<td>15.6 ± 5.8</td>
<td>47.9 ± 5.0</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td>54 (100)</td>
<td>45.0 ± 11.0</td>
<td>28.9 ± 5.1</td>
<td>14.0 ± 3.6</td>
<td>48.4 ± 6.8</td>
</tr>
</tbody>
</table>

\(^1\)Relative nest height = (nest height/nest tree height) × 100.

\(^2\)Two nests in *Betula papyrifera*, and one in each of *Ulmus americana*, *Tilia americana*, *Acer rubrum* and *Populus grandidentata*. 

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Typical support for such bulky nests in mature trees results in nearly one-third of the nest circumference, at the top of the nest, being obstructed. Such reduced access apparently poses no problems for the approaching adults, despite their large wingspan. As well as providing this support and protection for the nests, suitable forks may also facilitate efficient surveillance for potential predators. Nickell (1958) and Ficken (1964) suggested that some species may use tactile and visual stimuli from tree forks to ascertain their suitability as nest locations.

Reproductive success of some species of birds may be related to features of the nest tree (e.g. Evans 1978; Best and Stauffer 1980) or the structural stability of the nest itself (Coon et al. 1981). However, there were no significant differences between any of the nine successful (at least one young leaving the nest, mean 1.9) and five unsuccessful nests in the main study area in 1980. Other characteristics of the general habitat, as well as accompanying behavioural factors, are probably also of significant importance in determining reproductive success (Newton 1976). Howell et al. (1978) found several differences in forest features and human land use patterns between two 'low' and two 'highly' productive Red-tailed Hawk nests, whereas McEwan and Hirth (1979) were generally unsuccessful in relating the productivity of Bald Eagles (Haliaeetus leucocephalus) in Florida to characteristics of human disturbance near the nests. Multivariate approaches have been used to relate the success of passerine nests to features of the habitat around the nests (Wray and Whitmore 1979; Blacquiere and Lemon unpublished).

Natural selection has resulted in the use by Red-shouldered Hawks of suitable nest trees which provide concealment from predators and protection from environmental conditions for both the adults and the nestlings. However, we have no evidence that any features of the nest trees have any direct effects on the success of the nests. We also have no data to suggest that there may be a current shortage of suitable nest sites in southwestern Québec. However, as mature deciduous forest continues to be cleared for residential and industrial development, such a shortage may occur in the future.

**Acknowledgments**

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**Literature Cited**


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Records of Parasitic Fungi in Manitoba Based on Collections from Riding Mountain National Park, 1979

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One hundred and thirteen species of parasitic fungi were collected in Riding Mountain National Park in 1979. Fifty-three taxa are new to the region. Some floral elements, including fungi, from the surrounding prairie gain this restricted forest upland which harbors many hosts and fungi known in wooded areas elsewhere in Canada. New records for the Park are indicated with pertinent comments on hosts, distribution, morphology and life history.

Key Words: parasitic fungi, rusts, smuts, mildews, leaf spots, Manitoba.

In 1979, the Biosystematics Research Institute, Agriculture Canada, Ottawa, conducted a floral and faunal survey of Riding Mountain National Park in southwestern Manitoba. This was the third in a series of biological surveys of our National Parks designed to offer a floral and faunal inventory of the Parks and to supplement our National Collections of insects and fungi and of Agriculture Canada's vascular plant collection. Results of surveys of the St. Lawrence Islands National Park (1975–76) and of Kouchibouguac National Park (1977–78) were tabulated and reported directly to the Park concerned. This satisfied our first objective but limited the communication of information gained. In remedy, collecting results for the parasitic fungi from Riding Mountain National Park are presented in published format.

Riding Mountain National Park was established in 1930, having been withdrawn from settlement late in the 19th century. It occupies 2978 square kilometers located about 65 kilometers west of Lake Manitoba roughly between 50°30' and 51°0'N latitude and between 99°32' and 101°05'W longitude (Figure 1). The Park is essentially a wooded plateau with a number of valleys, creeks, and small lakes; the largest of the latter is Clear Lake on the southern boundary. The plateau slopes gradually upward from just north of the Minnedosa–Reston till plain in the south at about 460 m to some 670 m in the north and east where it drops sharply to 335 m toward the Manitoba lowlands. The natural vegetation is mixed forest, predominantly spruce and poplar, maintained by a growing season of 170 days (i.e. days with an average temperature of 5.6°C or more) between late April and early October. In June, July and August average minimum and maximum daily temperatures are respectively 7 and 15°C, 13 and 25°C, and 10 and 22°C. The Park lies in an interior prairie region having an annual precipitation between 25.4 cm minimum and 61 cm maximum. During the growing season, the average monthly precipitation is between 5–10 cm (National Atlas of Canada, 1974).

The writer spent three weeks during July collecting rusts, smuts, powdery mildews and leaf spotting fungi; student assistant D. R. H. Hammersley augmented collections throughout the summer. On return to Ottawa, some months were allotted to a scrutiny of the vascular plants collected in the Park by W. J. Cody and W. Wojtas during the entire growing season of 1979. This material substantially increased the numbers of parasitic fungi included here. All fungus material is deposited in the National Mycological Herbarium (DAOM) Ottawa.

Rusts (Uredinales), smuts (Ustilaginaceae) and mildews (Erysiphales) were collected mainly. Species treated here number 113 of which 53 are new to the Park when compared with the treatment of Bisby et al. (1938). The Bisby work (1938) includes a vast prairie region. Some prairie plants and their parasitic fungi (e.g. Puccinia crepida-montana on Crepis spp., P. troximontis on Agoseris) occur in the Park but extensive parts of the Park are wooded. In these areas, woodland plants and fungi common to other parts of Canada are found. For instance, Jack pine and aster species were commonly associated in the Park and were heavily rusted with Coleosporium asterum; the same host association and heavy leaf-rust infection occurred in 1979 along the north shore of Lake Superior. Other forest tree rusts like Chrysomyxa, Cronartium and Eudocronartium are wide-spread in Canada. White leaf spot (Glomopsis corni) on bunchberry (Cornus canadensis) was present in the Park in 1979 and in previous years in St. Lawrence Islands and Kouchibouguac National Parks. All of the mildews found in the Park are known in Ontario (Parmelee...
1979). White rust (Albugo blitii) was sporadically heavy on povertyweed (Monolepis) a western herb; it is known also in Manitoba and throughout Canada on the widely-distributed pigweed (Amaranthus retroflexus). It is clear that many parasitic fungi of prairie distribution occur in the Park but fungi of forest cover and understory with a wider distribution in Canada also occur.

These fungus records supplement the treatment by Bisby et al. (1938) of the fungi of Manitoba and Saskatchewan. Where fungus names chosen differ, the Bisby nomenclature follows immediately in parentheses. Individual fungus species are variously annotated to include mention of extant material in DAOM within or close to Park boundaries. An asterisk denotes fungus or host not specifically reported for the Park in the above citation. The format of the latter is closely followed for ease of comparison. Rusts, however, are treated alphabetically by genera and species without reference to families. Throughout the present work, the Roman Numerals I, II, III denote the rust states pycnia, aecia, uredinia and telia respectively. Square brackets [0, I] denote states not collected, round brackets (II) denote a rare occurrence. Macroscopic and microscopic characters of these states are excellently illustrated in Ziller's (1974) treatment of the tree rusts of Western Canada. Additional illustrations, especially of species of Puccinia, are available in Fungi Canadenses published, as an ongoing loose-leaf series since November 1973, by the Biosystematics Research Institute. Many rusts complete their full life cycle on one host (autoecious, e.g. Phragmidium speciosum, Puccinia hieraci) or on two unrelated hosts (heteroecious, e.g. Puccinia magnusiana, Melampsora paradoxa). Rusts mostly cause localized infections on leaves and stems (e.g. P. hieraci, P. magnusiana) but some are systemic and grow with the developing plant to erupt from all, or major, parts (e.g. Chrysomyxa arciostaphyli, C. pirolata). The reproductive structures of fungi appear on various parts of the host. On leaves they may appear on the upper, lower or both surfaces (epiphyllous, hypophyllous and amphigenous respectively) on stems (caulicolous) and on the flowering parts (fruticulose).

Just prior to their listing of the fungi for Manitoba and Saskatchewan, Bisby et al., (1938) wrote: “Vale!... A sound superstructure of phytopathology requires a firm foundation of mycology and much study of specific areas is needed in many parts of the world.”

PHYCOMYCETES

PERONOSPORALES

*Albugo blitii (Biv.-Bern) Kuntze, on Monolepis nuttaliana (R.&S.) Green, Strathclair Trail. 3 km north of bison enclosure. Recorded also by Bisby et al. (1938) on Amaranthus retroflexus L. in Manitoba. Appears on leaves as white, blister-like eruptions.

*A. cruciferarum S. F. Gray (A. candida (Pers. ex Lév.) Kuntze) on Lepidium densiflorum Schrad. with the white-rusted Monolepis (above) on Strathclair Trail; 3 km north of Deep Lake Warden Station.

ASCOMYCETES

TAPHRINALES (EXOASCALES)

*Taphrina communis (Sadeb.) Gies., on Prunus nigra. Ait. in garden of Deep Lake warden station. The bladdery plum pockets were conspicuous with complete fruit loss.

PYRENOMYCETES

(DOTHIDIALES, HYPOCREALES)

*Apiospora morbosa (Schw.) v Arx, (Dibotryon morbosum (Schw.) Theiss. & Syd.) on Prunus sp. 3 km east of Audy Lake. Distribution and illustration of both species of Apiospora in Canada are given in Fungi Canadenses nos. 76 and 84 respectively.

*Claviceps purpurea (Fr.) Tul., on Calamagrostis inexpansa Gray, Wasagaming; on Calamagrostis sp., Indian cemetery north side of Clear Lake; on Koeleria macrantha (Ledeb.) Spreng., 1.6 km east of Rolling River road on Muskat Lake road; on Phalaris sp., warden station south end of Rolling River road.

Phyllachora graminis (Pers. ex Fr.) Nke., in Fuckel on Agropyron sp., Ma-ee-gun Trail; on Elymus sp., Long Lake road just south of Central Trail.

P. oryzae Theiss. & Syd., on Orzopsis sp. along Hwy. 19. 1 km east of Whirlpool Lake road. This species was treated under P. graminis by Bisby et al., but the species of Theissen and Sydow was recognized by Parbery (1967).

*Pyrenophora bromi (Diedr.) Drehsl., on Bromus inermis Leyss. Hwy. 10 near Maintenance Compound. The conidial state causes conspicuous leaf spots and the perfect state matures over winter on the dead leaves.

*Rhizogene impressa (Ell. & Ev.) Barr, (Rhizogene symphoricarp Syd.) on Symphoricarpus albus (L.) Blake, East gate to bison enclosure; Burls and Bittersweet Trail. ‘Black leaf spot’ amply describes the appearance of this fungus.

DISCOMYCETES

*Leptotrichila verrucosa (Wallr.) Schuepp, (Pseudopeziza repanda sensu Bisby) stat. conid. Placosphaeria punctiformis (Fckl.) Sacc. on Galium boreale L., Hwy. 10 across from Maintenance Compound; on Galium sp. Brulé Trail near west end Hwy. 19.
Figure 1. Map of southwestern Manitoba with location of place names mentioned in text. Riding Mountain National Park boundaries are outlined by cross hatching.

ERYSPHALES (PERISPORIALES)

*Erysiphe cichoracearum* DC. ex Mérat, on *Mertenzia paniculata* (Ait.) G. Don. Central Trail at Gunn Creek; Moon Lake; Bisby et al. (1938) list other hosts in Manitoba. Description and illustration of this and other species of *Erysiphe*, and other mildews in Ontario, are provided by Parmelee (1977).

E. galeopsidis DC. ex Mérat on *Stachys* sp. Warden Station at S end of Rolling River road.

E. graminis DC. ex Mérat, s. conid., on *Poa palustris* L. Strathclair Trail 14 km north of bison enclosure; Burls & Bittersweet Trail. See Fungi Canadenses no. 71.

E. polygoni DC. ex St. Amans, on *Lathyrus venosus* Muhl., Brulé Nature Trail; Hwy. 10 nr. Maintenance Compound; on *Polygonum achoereum* Blake, Grasshopper Trail nr. Audy Lake; see above references for other known hosts.


*Phyllactinia guttata* (Wallr. ex Fr.) Lév., *P. corylea* (Pers.) Karst. on *Cornus* sp., Wasagaming; on *Craegaus* sp., Lake Audy campground.

*Podospora clandestina* (Wallr. ex Fr.) Lév., *P. oxyacanthae* (DC. ex Bary) on *Amelanchier alnifolia* (Nutt.) Nutt., Grasshopper Trail; Audy Lake; on *Prunus pennisylvanica* L., Lake Catherine; on *P. virginiana* L., Arrowhead Trail; 1 km east of Audy L.

*Sphaerotheca fuliginea* (Schlecht. ex Fr.) Poll., *S. humuli* (DC.) Burr. var. *fuliginea* (Schlecht.) Salmon st. conid. on *Astragalus alpinus* L., Baldy Lake road south of Central Trail.

S. macularis (Wallr. ex Fr.) P. Magn., *S. humulis* (DC.) Burr. *Agrimonia striata* Michx., Strathclair Trail 6 km north of bison enclosure; on *Collybia linearis* Nutt., Mt. Agassiz; on *Viola rugulosa* Green, Moon L.

Ucinula adunca (Wallr. ex Fr.) Lév., *U. salicis* (DC.) Wint.) on *Populus balsamifera* L., Burls and Bittersweet Trail, Swanson Creek; Bead Lakes Trail; on *Salix discolor* Muhl., Central Trail at Long Lake, and, at Gunn Lake; Ominik Marsh Beaver Pond; on *Salix* sp. Central Trail at Green Lake.

BASIDIOMYCETES

USTILAGINALES

*Anthracosea heterospora* (Lindeb.) Kukk., *Cintractia heterospora* Lindeb. on *Carex aquatilis* Wahlenb., Lake Katherine; and on *C. pennisylvanica* Lam., a specimen (DAOM) labelled simply, "Riding Mt. Nat. Park."

*A. subinclusa* (Korn.) Bref. *Cintractia subinclusa* (Koen.) Magn. on *Carex atherodes* Spreng., Whitewater Lake.

*Ustilago striiformis* (Westend.) Niessl on *Poa* sp., Central Trail 15 km west of jet. with Strathclair Trail in scrub prairie.

UREDINALES

*Chrysomyxa arctostaphyli* Diet., 0 I systemic on needles of *Picea glauca* (Moench) Voss causing birds' nest or witches' broom formation. Sighted occasionally in spruce stands throughout the Park. Reported by Bisby et al. under *Melampsora cerastii* (Pers.) Schroet. which occurs only on *Abies*. Telia, not found, are known elsewhere on *Arctostaphylos uva-ursi* (L.) Spreng.

*C. ledei* (Alb. & Schw.) deBary, 0 I on needles of *Picea glauca* (Moench) Voss, L. Katherine; on *Picea mariana* (Mill.) BSP., 2 km east of Lake Catherine and along Rolling River road. II III hypophyllous on *Ledum groenlandicum* Oeder, Swanson Creek; Moon L.; Cowan L. Varietal segregation of this species is given by Savile (1955).

*C. ledicola* (Peck) Lagerh. 0 I on *Picea glauca* (Moench) Voss, II III epiphyllous on *Ledum groenlandicum* Oeder, not collected in the Park. Specimens on *Ledum* (DAOM) are from Duck Mtn. to the north.

*C. pirolata* Wint. (C. pyrolae* (DC.) Rostr.), II III systemic on *Pyrola asarifolia* Michx., near Maintenance Compound; Brulé Trail and Kinosao Trail. Pycnia and acia are known mainly on white spruce but there are no records from the Park. One specimen (DAOM) is from Hole River, near Manigotagan in eastern Man.

*C. weirii* Jacks., III only on needles of the previous year of *Picea glauca* (Moench) Voss, Peden Valley. This is the only North American species of *Chrysomyxa* producing telia on the gymnospermous host. In all other species, *Picea* spp. bear pycnia and acia.

*Coleosporium asterum* (Diet.) Syd. (C. solidaginis* Schw.) Thuem.), 0 I on needles of *Pinus banksiana* Lamb., Hwy. 19 west of Swanson Creek bridge; Deep Lake Trail rd. II III on *Aster borealis* (T.&G.) Prov.,
Jackfish Creek; on *Aster ciliolatus* Lindl., Mt. Agassiz road; Maintenance Compound; Hwy. 19 west of Swanson Creek; road to fire tower south of Hwy. 19; Brulé Nature Trail; on *A. cordifolius* L., Burls and Bittersweet Trail; on *A. simplex* Willd., Grasshopper Trail; Wasagaming; McFadden Valley; warden station, Rolling River road; Lake Katherine; jct. Strathclair and Central Trails; Sugarloaf road north of Central Trail; on *Solidago canadensis* L., Ma-ee-gun Trail; fire tower road south of Hwy. 19; on *Solidago sp.* south of Hwy. 19. On road to fire tower. Good alternate host associations were noted at many sites. A wide-ranging rust in Canada.

**Cronartium comandae** Peck, II III hypophyllous on leaves of *Comandra umbellata* (L.) Nutt., jct. Hwy. 10 and North Shore Development road; Grasshopper Trail. 0 I no collections from the Park but known on *Pinus banksiana* from Spear Hill, Man., and it is widespread in eastern Canada. Also known on *P. contorta* Doug. from other western provinces (Ziller 1974).

**Endocronartium harknessii** (J. P. Moore) Y. Hiratsuka, 0 I II on galls on twigs and small branches of *Pinus banksiana* Lamb. along Brulé and Kinosoa Trails. The spores look like the typical coarsely warted aeciospores of *Cronartium* spp., but they function as teliospores germinating with a basidium and basidiospores to reinfect the same or adjacent pines. No alternate hosts are involved (Hiratsuka 1969).

**Gymnoconia peckiana** (Howe) Trotter, 0 I on *Rubus pubescens* Raf. early in the season appearing systemic on young leaves with pycnia on epiphyllous and acia hypophyllous, bright orange. III not collected but can be expected to appear in late July and August on this and related *Rubus* species. Moon L. Nature Trail.

**Gymnosporangium** spp., not found in the Park. One telial host, *Juniperus communis* L., was present but not common. Various species of *Gymnosporangium* are known from the Carberry sand hills, just 50 miles south, and from eastern and northern Manitoba (Parmelee 1965, 1971). Although the alternate 0 I hosts (*Crataegus* and *Ameriunchier* of the Pomoidea) occur in the Park, rust was not found, and absence is probably due to the paucity of *Juniperus*.

**Hyalospora polypodi** (Pers.) Magn. II (III) on *Cystopteris fragilis* (L.) Bernh., Moon Lake, Gorge Trail. First herbarium records from Manitoba.

**Melampsora abieti-capraearum** Tubeuf, II (III) on leaves of *Salix* spp., Muskrat L. Trail; Rolling River road; road to fire tower south of Hwy. 19. The 0 I states are known to occur on needles of *Abies balsamea* L.

**M. lini** Lév., II on leaves of *Linum lewisii* Pursh, Audy L. Unlike the other species of *Melampsora* here recorded, the flax rust completes its cycle on flax alone. The complete cycle includes 0 I II III states. Rust has caused considerable loss in cultivated varieties of flax over the years in Manitoba (Conners 1967, p. 153). The perennial *L. lewisii* may sometimes be an important reservoir host for infection of cultivated flax.

**M. medusae** Thuem., II on leaves of *Populus tremuloides* Michx., road to fire tower south of Hwy. 19. The 0 I states are known to occur on needles of *Abies balsamea* L.

**M. paradoxa** Diet. & Holw., 0 I on *Larix laricina* (Du Roi) Koch needles, Swanson Creek; II III on leaves of *Salix candida* Fluegge, Muskrat L. Trail and *Salix sp.* Wasagaming.

**Nyssopsora clavellosa** (Berk.) Arth., III on leaves of *Aralia nudicaulis* L., Ma-ee-gun Trail, Bead Lakes Trail, Moon Lake Trail, Burls & Bittersweet Trail and Grasshopper Trail. In early July telia appear on purple-red spots as small blister-like swellings which eventually rupture the epidermis. By early August these sori tend to coalesce and become dull black and powdery. As the teliospores break away, rust becomes very conspicuous on the upper surface of leaves. It was common in the Park in 1979.

**Phragmidium andersonii** Shear, 0 I II III on leaves of *Potentilla fruticosa* L. On road to fire tower south of Hwy. 19; Swanson Creek; Arrowhead Trail. Telia not formed until early August. Teliospores are rough-walled, multicelled, black and of such size that small groups can be seen with the unaided eye. All species of *Phragmidium* are autoecious.

**P. fusiforme** Schroet., (*P. roae-acicularis* Liro) 0 I on leaves and young branches of *Rosa acicularis* Lindl., Jackfish Creek; Grasshopper Trail; 17 km north of bison enclosure on Strathclair Trail; II III on *R. acicularis*, Bob Hill Lake.

**P. ivesiae** Syd., [0 I] III hypophyllous on leaves of *Potentilla gracilis* Doug. ex Hook. vars., Central Trail nr. Birdtail Valley, and, 14 km west of jct. Long Lake rd. and Central Trail. Teliospores are mainly 3-celled, each cell with 2 equatorial pores; wall of apical cell is verrucose, smooth on lower cells.

**P. potentillae** (Pers.) Karst., [0 I] II III on leaves of *Potentilla pensylvanica* L., Central Trail at Birdtail Valley. In this species, teliospores have smooth walls and are 3-5 celled, each cell with 2-4 apical germ pores. See Fungi Canadenses no. 41.

**P. speciosum** (Fr.) Cooke, 0 I III on *Rosa sp.*, Arrowhead Trail. Acia and telia on leaves or stems, both
The hypophyllous, on P. ana

*Puccinia asteris* Duby, III on *Aster* sp., north end of Audy L. campground on scrub prairie. Teliospores germinating shortly after formation impart a silvery appearance to otherwise brown telia.

*P. atrorufusca* (Dudl. & Thomp.) Holw., 0 I causes noticeable chlorosis on leaves of *Artemisia ludoviciana* Nutt. (A. gnaphalodes Nutt.), Grasshopper Trail; Strathclair Trail 0.3 km north of bison enclosure. [II III] on *Carex* spp. not found in 1979 but recorded from Ste. Rose and Brandon by Bisby *et al.* (1938).

*P. atroruncta* Peck & Clint., [0 I] on *Prenanthes* spp. not found in 1979; II III on *Zygodenus elegans* Pursh, east end of Katherine Lake. Rust was sufficiently heavy on white camass to suggest nearby presence of the alternate host.

*P. calthae* Link, [0 I] III on both surfaces of leaves of *Caltha palustris* L. Bead Lakes Trail and Moon Lake. Aecia occur early in the season and were not collected. A second species *P. calthicola* Schroet. on *Caltha* is recorded by Bisby *et al.* (1938) from the Park and is distinguished by its rough-walled, broader teliospores.

*P. caricina* DC. *sensu latissimo*. *(P. caricis* (Schum.) Schroet.), 0 I on leaves of *Ribes americanum* Mill., Brulé; Nature Trail; Jackfish Creek; L. Audy; Bead Lakes Trail; on *R. hirtellum* Michx., Strathclair Trail north of bison enclosure; Jackfish Creek; Moon L.; on *R. hudsonianum* Richards., Strathclair Trail; on *R. oxyacanthoides* L., Moon L., on *Ribes* sp., Clear Lake; on *Urtica dioica* L. Swanston Creek; Grasshopper Trail; Deep L.; Bead Lakes; *U. gracilis* Ait., Ominik Marsh; Lake Audy road at Jackfish Creek. The II III hosts include many species of *Carex*; sori become noticeable on leaves in August and September as tiny brown to black, subepidermal eruptions; on *Carex atherodes* Spreng., Muskrat Lake Trail; *C. rossii* Boott, Muskrat Lake Trail; *C. ?rostrata* Stokes, Bead Lakes. Bisby *et al.* (1938) recognized the rusts on *Ribes* and *Urtica* as varietal segregates and Savile (1973, P. 235–236) indicates that aeciospores from *Ribes* have type 5 spores and those from *Urtica* have type 3. Inoculation studies would be helpful in linking particular *Carex* species with these segregates and perhaps delimiting spore characters of the II III states to them or their specific status equivalents.

*P. circaeae* Pers., III only, on the under side of leaves of *Circaea alpina* L. as purple-brown sori in circular groups surrounded by noticeable chlorotic zone; Bead Lakes Trail; Wasagaming.

*P. conglomerata* (Str.) S.&K., III only, on underside of leaves of *Petasites palmaeus* (Ait.) Gray, as brown sori in tight circular groups reflected on the upper surface by noticeable yellow spotting. Strathclair Trail 6 km north of bison enclosure; Brulé Nature Trail; Moon L.; Swanson Creek picnic site; Maeegun Trail. See *Fungi Canadenses* no. 110.

*P. coronata* Cda., 0 I hypophyllous, fruticicolous in compact circular groups on *Rhamnus alnifolia* L'her., Whirlpool L.; Swanson Creek; L. Audy; Kinossao Trail; Bead Lakes Trail (associated with rusted *Calamagrostis* (below)); road to fire tower off Hwy. 19, adjacent II on *Calamagrostis*; Jackfish Creek; buffalo enclosure L. Audy. Also on *Shepherdia canadensis* (L.) Nurr., Hwy. 19, 4 km west of Swanson Creek; Brulé Nature Trail; Strathclair Trail 3 km north of bison enclosure (associated with rusted *Bromus* below); Arrowhead Trail; L. Katherine; Pedon Valley; very common and conspicuous in June and early July alternating in the II III states to a number of grass genera. II III on *Calamagrostis canadensis* (Michx.) Beauv.; Jackfish Creek; Swanston Creek; Bead Lakes Trail; fire tower road south of Hwy. 19; Deep Lake; Arrowhead Trail; Rolling River road; Moon Lake, associated with rusted *Rhamnus*; on *Bromus inermis* Ley.; Strathclair Trail. Based on aecial inoculation, Fraser and Ledingham (1933) recognized 4 varieties in western Canada:

- var. *avena* F.&L. (inoc. from *Rhamnus cathartica* to *Avena*)
- var. *calamagrostis* F.&L. (inoc. from *R. alnifolia* to *Calamagrostis*)
- var. *bromi* F.&L. (inoc. from *Shepherdia canadensis* to *bromus*) but note that *Shepherdia* may support a second rust *P. caricis-shepherdiae* not recorded herein.
- var. *elaeagni* F.&L. (inoc. from *Elaeagnus commutata* to *Calamagrostis*)

Crown rust was the most conspicuous rust throughout the Park in 1979. It was especially heavy on *Rhamnus alnifolia*; although *R. cathartica* L. and *R. frangula* L. are known from Winnipeg and Brandon neither were found within the Park by the author or by W. J. Cody.

*P. cerc Falloutii* Pam. & Hume, 0 I on leaves of *Symphoricarpus occidentalis* Hook. The discrete yellow spots visible on the upper side, and indicating presence of aecia on the lower surface, become necrotic as the aecia mature; Bob Hill Lake. Other species of *Symphoricarpus* attacked are listed by Arthur (1934).

*P. crepis-montanae* Magn., 0 I II III on leaves of *Crepis tectorum* L. Muskrat L. Trail; 10 km north of Deep Lake warden station; road to L. Katherine south of Hwy. 19. Urediniospores have completely echinu-
late walls with 3–4 equatorial germ pores. In contrast, 11 spores of the only other rust of *Crepis* in the region, *P. hieraci*ii, have discrete bare areas below the 2 superequatorial germ pores (Parmelee and Savile [1981]). The record of *P. hieraci*ii on *Crepis runcinata* in Bisby et al. (1938) is certainly *P. crepidis-montanae*.

**P. dlioae** Magn. (*P. extensicola* Plowr. vars.). A complex species with 0 I on Asteraceae and 11 III on *Carex* spp. The species treatment here is very broad embodying a number of varietal segregates recognized by Arthur (1934) and followed by Bisby et al. (1938). 0 I on *Agoseris glauca* (Pursh) Raf. Strathclair Trail just north of bison enclosure; Brulé Nature Trail; Pedon Valley; on *Aster ciliolatus* Lindl., Strathclair Trail 0.3 km north of bison enclosure (open prairie assoc. with *Carex* spp.); Bob Hill L.; Wasagaming campground; nr. Swanson Creek picnic area; on *Hieracium scabriusculum* Schw., Audy L.; Grasshopper Trail; Bob Hill L.; Arrowhead Trail; on *Solidago rigida* L., Bob Hill Lake; on *Solidago* spp., Strathclair Trail 2 km north of bison enclosure; Moon L.; Bead Lakes Trail; Grasshopper Trail. II III on *Carex* sp. Bob Hill L. associated with rusted (0 I) Solidago above.

*P. helianthi* Schw., 0 I [II III] on *Helianthus laetiflorus* Pers. was found only sparingly within the Park limits, Grasshopper Trail, Audy L.; but, specimens in DAOM are from throughout southern Manitoba. This rust is widespread in Canada on wild and cultivated sunflowers (see Fungi Canadenses no. 95) and has caused considerable loss in certain of the cultivated varieties. Although rust resistance was established in some cultivars, loss is still experienced in others.

*P. heucherae* (Schw.) Diet. var. *minor* Savile, III only, hypophyllous and petiolicolous on *Mitella nuda* L. Bead Lakes Trail; Strathclair Trail 6 km north of bison enclosure; Ma-ee-gun Trail. This and related rusts were discussed in detail by Savile (1973).

**P. hieraci*ii* Mart, 0 II II III. This common and widely distributed rust complex determines its cycle on various genera of Cichorieae; on *Hieracium canadense* Michx., nr. Maintenance Compound; on *H. scabriusculum* Schw., Bob Hill L.; nr. Maintenance Compound; Arrowhead Trail; Deep Lake; fire tower south of Hwy. 19; on *Taraxacum officinale* Weber, Jackfish Creek; Beaver pond, Hwy. 19. See *P. troximontis* for comparison of uredinospore characters.


**P. intermixa** Peck, 0 III systemic or III localized on *Iva axillaris* Pursh. Not collected in the 1979 season but specimens in DAOM (2 only) are from Shoal Lake and from Hamiota south of the Park. The distribution extends westward through Saskatchewan to the Peace River region of Alberta. Illustrations and description can be seen in Fungi Canadenses no. 96.

*P. linkii* Klotzsch, III only, epiphyllous and causing purple discoloration of *Viburnum edule* (Michx.) Raf., Bead Lakes Trail; Ma-ee-gun Trail. Occurs from coast to coast wherever *V. edule* is abundant.

**P. magnusiana** Koern., II III on *Phragmites communis* Trin., Mt. Agassiz rd. at gate to Park, also known from Dauphin just north of the Park and from the vicinity of Portage La Prairie. It alternates to Ranunculaceae in the 0 I states. Uredinospores have 6–8 scattered germ pores, a useful character in separating this species from *P. phragmitis* also on *Phragmites*.

**P. marilandica** Lindr., 0 I [II III] on *Sanicula marilandica* L., Arrowhead Trail. This single collection was made on 21 July by which time uredinia and telia are usually present as scattered light to dark brown sori.

**P. mcclatchieana** Diet. & Holw., 0 I unknown; II III on *Scirpus* sp. at Sugarloaf rd. & Birdtail Creek; L. Audy rd. & Jackfish Creek; Strathclair Trail & Kennis Creek; along Kennis Creek. *P. angustata* II III is also known to occur on *Scirpus* species in southern Manitoba. It has uredinospores with 2 germ pores in comparison with 3–4 pores in *P. mcclatchieana* and is known to alternate to Lamiaceae (Labiatae). These and other rusts of *Scirpus* and related plants were discussed in detail by Savile (1972).

**P. menthae** Pers., 0 II III on *Galeopsis tetrahit* L., Grasshopper Trail. The 0 I states appear early in the season. In DAOM, there are specimens of rusted *Mentha arvensis* L. from Winnipeg to Brandon and on *Monarda fistulosa* L. from Roblin and Birds Hill. These are common hosts. The *Galeopsis* collection is apparently a new host record, as there are no specimens in DAOM, nor is it given as a host in Conners' (1967) listing or in the Index of plant diseases (1960).

**P. minussensis** Thuem. [0 I] II III on *Lactuca pulchella* (Pursh) DC., Long Lake warden station; Baldhill Trail. Pycnia and acia are systemic and may be accompanied by uredinia and telia which may also be scattered. Specimens in DAOM are from Dauphin and Grandview just north of the Park boundary. See Canadian distribution in Parmelee and Savile (1981).
P. phragmitis (Schum.) Koern., not found in 1979 but there are 0 I specimens in DAOM on Rumex occultarlis Wats. and II III specimens on Phragmites communis Trin. both from Dauphin. With the 0 I states on Polygonaceae and urediniospore germ pores 4 at the equator, this rust is readily separable from P. magnusiana.

*P. pimpinellae* (Str.) Mart., 0 II (III) on leaves of Osmorhiza longistylis (Torr.) DC., Burls & Bittersweet Trail; on O. obtusa (C.&.R.) Fern. (O. depauperata Philippi), Bead Lakes Trail; Moon L. Aecia are especially conspicuous by causing discrete chlorotic spots visible on both surfaces.

*P. poae-nemoralis* Otth, (P. poae-sudeticae (West-end.) Jørstad), II (III not found) on Poa palustris L. Moon Lake; on Poa pratensis L., fire tower site south of Hwy. 19; 10 km north of Deep Lake warden station. Scattered urediniospore germ pores and capitulate paraphyses are typical for this species. Cummins (1971) gives this entity varietal status under P. brachypodii Otth, and indicates that the aecial state occurs on Berberis sp. Aecia are not known to occur in Canada, or elsewhere except in one unconfirmed inoculation. In much of its range teliospores are not formed.

*P. poarum* Niels. (P. liatrisis Bethel), 0 I on Liatris ligulistyris (A. Nels.) K. Schum., Grasshopper Trail; 1 km east of L. Audy; II [III] on Poa arida Vasey, Grasshopper Trail. These two specimens were found in association along a trail through scrub prairie. Bisby et al. (1938) record the II III states on Agrostis.

P. polygoni-amphibii Pers., II III amphigenous on Polygonum amphibium L., Ominnik Trail; Jackfish Creek; Gunn Lake on Central Trail; Audy Lake. The 0 I states, reported on Geranium, were not found in the Park in 1979. In the subspecific segregations of Arthur (1934), this rust is treated as var. persicariae (Str.) Arth.

*P. punctata* Link var. troglodytes (Lindr.) Arth.[0 I] II (III) amphigenous on Galium triflorum Michx. Ma-ee-gun Trail; Bead Lakes Trail. This autoecious full-cycled rust bear 0 I states apparently early in the season, not found in 1979. Telial soroi are smaller than those of P. rubefaciens.

P. recondita Rob. ex Desm. (P. rubigo-vera (DC.) Wint.) A complex rust in which 6 varietal segregates were set up by Arthur (1934) separated by a combination of differing aecial hosts and grass tribes. Varietal recognition is usually not readily accomplished in practice because host association is not always known or obvious. However it is apparently justifiable that some of these varieties be recognized at the specific level, viz. var. impatiens as P. impatienti-elymi, otherwise the treatment here follows that of Cummins (1971) in recognizing this as a species complex without varietal segregation. 0 I on Actaearubra (Ait.) Willd., Bead Lakes Trail; Moon L.; Grasshopper Trail at Audy L.; on Anemone canadensis L., Muskrat Lake Trail; Brulé Nature Trail; on A. cynthia a Gray, Strathclair Trail, 10 km north of bison enclosure; on A. virginica L., 8 km east of Audy Lake; on Thalictrum dasyacarpum Fisch. & Lall., Grasshopper Trail; Burls & Bittersweet Trail; on T. venulosum Trel., 1.5 km east of Swanson Creek picnic site; Audy Lake campground; 1 km east of Audy Lake. II III on grasses, with a single collection from the Park in 1979; II (III) on Poa pratensis L.; some additional collections on deposit in DAOM from just outside the Park include: Bromus sp. (Neepawa); Bromus latiglumis (Shear) Hitchc. (Brandon); Bromus ciliatus L. (Brandon); Elymus canadensis L. (Brandon); Hordeum jubatum L. (Brandon, Dauphin); Poa arida Vasey (Brandon).

P. rubefaciens Johans., III only, large dark pulvnate sori, hypophyllous causing some leaf discoloration and malformation of Galium boreale L., Audy Lake and 1 km east of Lake; Kinsao Trail; Ma-ee-gun Trail; K. Katherine; fire tower south of Hwy. 19; Bead Lakes Trail.

P. sessilis Schneid., 0 I on Smilacina stellata (L.) Desf., Gunn Creek. Specimens in DAOM are from Brandon and Sydney. Others in the Lilliaceae that are known to become rusted include Erythronium, Malanthemum, Polygonatum, Uvularia, and in the Iridaceae, Iris versicolor L. II III hosts are Phalaries spp., not collected in 1979 but a specimen of rusted P. arundinacea L. from Brandon is in DAOM.

P. sherardiana Koern., 0 III mainly hypophyllous on Sphaeralea coccinea (Pursh) Rydb. (Malvastrum c.), not collected in the Park in 1979 but there is material in DAOM from Brandon. See Fungi Canadenses no. 173 for illustrations and Canadian distribution.

P. stipae Arth. var. stipae, 0 I on Lygodesmia juncea (Pursh) D. Don, not collected within the Park but specimens in DAOM are from Shilo; [II] III on Stipa sp., Baldy Lake Ranger Station, and specimens in DAOM from Elkhorn.

P. subnitens Diet., 0 I on Plantago eriopoda Torr. and Chenopodium album L., alternating in II III states to Distichlis stricta (Torr.) Rydb. from southern Manitooba (specimens in DAOM) but not from within the Park. Bisby et al. (1938) recorded this rust as P. aristidiae Tracy but Cummins (1971) recognizes differences. P. subnitens primarily attacks Distichlis while P. aristidiae mainly infects Aristida. See Fungi Canadenses 209.
P. substerilis Ell. & Ev. (P. scaber Ell. & Ev., II only) 0
1 unknown, II on Stipa Baldy Lake ranger station. Urediospores are smaller than in P. stipae. Included with P. stipae by Bisby et al. (1938).

P. troximontis Peck (P. hieracii auct. non. (Rohl.) Mart.), O II II III amphigenous, the O II I condition is often mainly on vascular tissue in the early season. On Agoseris glauca (Nutt.) Greene, Reich., of Lake Park, 3 km north of Deep Lake warden station. Segregated from P. hieracii on differences in urediospore characters viz. 2 equatorial germ pores vs. 2 superequatorial pores, and walls completely echinulate vs. walls with a bare area below each pore (see Parmelee and Savile 1981). The records of Bisby et al. (1938) of P. hieracii on Agoseris glauca are this species, as is in part Cummins' (1978) listing of Agoseris under P. hieracii.

P. violae (Schum.) DC., O II III on Viola conspersa Reich., fire tower south of Hwy. 19; on V. rugulosa Greene, Bead Lakes Trail; Moon L. Infected plants are quickly visible in early summer due to chlorosis surrounding the acedia, but this condition is not present around the small inconspicuous uredinia and telia and these states may be easily overlooked later in the summer.

*Pucciniastrum agrimoniae* (Diet.) Tranz., 0 I not known and II (III) hypophyllous on Agrimonia striata Michx., Moon Lake Trail; Deep Lake; telia not found in these Park specimens. Pucciniastrum spp. are typically heteroecious with vs. Puccinia species.

P. arcticum (Lagerh.) Tranz., [0 I] on Picea glauca (Moench) Voss not collected. II (III) hypophyllous on Rubus pubescens Raf. Brulé Nature Trail; Bead Lakes Trail.


*P. pyrolae* Diet. ex Arth., 0 I not known; II (III) hypophyllous on *Pyrola secunda* L., Kinosao Trail. Also known from Treesbank south of the Park (DAOM). Other species of *Pyrola*, *Moneses* and *Chimaphila* become rusted elsewhere in Canada (Ziller 1974).

*Tranzschelia thalictri* (Chev.) Diet., III hypophyllous, covering large areas as small powdery sori, on Thalictrum dasycarpum Fisch. & Lall., Audy Lake. Also known on T. venulosum Trel. from the Winnipeg area.

*Uredinopsis* spp. alternating with 0 I on needles of Abies spp. and, II III on fronds of Polypodiaceae, not collected in 1979.

U. struthiopteridis Stormer, II III on Mattucia struthiopteridis (L) Todaro var. pensylvanica (Willd.) Fern (Pteritis nodulosa) (Michx.) Nieuwl is known (DAOM) from Dauphin and Winnipeg (St. Adolphe).

Uromyces acuminatus Arth., 0 I on Lilicaceae and other families, not collected; II III on Spartina spp., *S. pectinata* Lk., Brandon (DAOM). See Fungi Canadenses no. 203.

U. alopecuri Seymour, 0 I on Ranunculus macounii Britt. (DAOM); II III on Alopecurus aequalis Sobol (A. geniculatus L. p.p.) from R. macounii Britt., inoculated by W. P. Fraser at Brandon (DAOM).

U. coloradensis Ell. & Ev., 0 I III on Vicia americana Muhl. 1 km east of Audy Lake; fire tower south of Hwy. 19; Strathclair Trail 3 km north of bison enclosure; Mt. Agassiz Ski Lodge. The 0 I states are systemic.


U. glycyrrhizae (Rabenh.) Magn., 0 II I III all states systemic or III localized on Glycyrrhiza lepidota (Nutt.) Pursh, known from north (Swan River) and south (Morris) of the Park but not collected in the Park itself.

*U. hedysari-obscuri* (DC.) Car. & Picc., 0 I III as localized infection on leaves of Hedysarum alpinum L., Audy Lake campground; fire tower south of Hwy. 19; Onanole just outside of south boundary; also DAOM records on H. boreale Nutt. from Foxwarren and Binsearth southwest of the park, and, from Rapid City to the south.

U. juneci (Desm.) Tul., 0 I on Cirsiurn spp. alternating in II III states to Juncus spp.; not collected in the Park but specimens in DAOM on Cirsiurn foedmanii (Ryd.) Arth. and Juncus balticus Willd. from Brandon support the records in Bisby et al. (1938).

U. lineolatus (Desm.) Schroet., (U. scirpi Burr.), 0 I on Slum cicutaefolium Schr. Rapid City south of the Park (DAOM) alternating in II III on Scirpus maritimus L.; not found in the Park. See Savile (1972) for differences from *U. americanus* also on Scirpus.

U. perigynus Halst., 0 I on Rudbeckia laciniata L. Not collected in the Park but there are DAOM specimens from Dauphin, Brandon, Douglas and Dropmore. II III are reported on Carex spp. but there are no records from Manitoba.
U. plumbarius Peck, 0 I systemic and II III localized on leaves of Gaura coccinea Pursh. Not collected in the Park but there are DAOM specimens from Wawanesa. Other hosts include Oenothera biennis L. from Lac du Bonnet.

U. polygoni-aviculatis L. (P. polygoni (Pers.) Fuckel), 0 I II III localized on Polygonum aviculare L., fire tower south of Hwy. 19. Other hosts include: P. erectum L. at Carman, P. ramosissimum Michx. at Katrine.

U. punctatus Schrot., 0 I systemic on Euphorbia spp., but not known in N. America. II III amphigenous on Oxytropis splendens Doug., Muskrat Lake Trail; on O. sericea Nutt. var spicata (Hook.) Barney. Not collected within the Park but known (DAOM) from Birtle (SW Dauphin); on Oxytropis spp. Lake Katherine; Wasagaming; Audy Lake road; on Astragalus sp. road to Mt. Agassiz. For distribution in Canada see Fungi Canadesis no. 24.

*U. viciae-fabae* Schrot., (U. fabae deBary) 0 I II (III). Amphigenous and cauliculous with the 0 I states in small groups on Lathyrus venosus Muhl., Burls & Bittersweet Trail; Deep Lake; 4 km west of Swanson Creek on Hwy. 19; Muskrat Lake Trail; Whitewater Lake camp area; on Vicia americana Muhl., Strathclair Trail 3 km north of Central Trail; on Vicia cracca L., north side of Clear Lake.

EXOBASIDIALES (Agaricales sensu Bisby et al.)

*Exobasidium vaccinii-uliginosi* Bond., on Ledum groenlandicum Oeder, Swanson Creek picnic site.

**FUNGI IMPERFECTI**

**HYPHOMYCETES (MONILIALES)**

*Cercospora circumcissa* Sacc., on Prunus virginiana L., Bead Lakes Trail; Deep Lake. Causes conspicuous necrotic spots and resulting shot-hole.

*Glomopsis corni* (Peck) Henderson (Glomerularia corni Peck) on Cornus canadensis L., Moon Lake; Swanson Creek. A conspicuous leaf spot with conidia, white in mass, on the undersurface.

G. lonicerae (Peck ex Gould) Henderson (Glomerularia lonicerae (Peck) Dearn. & House), on Lonicera, is known (DAOM) from Birds Hill, Morden, Portage La Prairie, but was not found in the Park in 1979.

*Ovularia pulchella* (Ces.) Sacc., on Bromus sp., causing small leaf spots, Scott Creek. One additional specimen on Agropyron in DAOM from Saskatchewan.

**COELOMYCETES (MELANCONIALES and SPHAEROPSIDALES)**

*Gloeosporium cladosporioides* Ell. & Halst., on Hypericum virginicum L., Jet Trail, Pencil Lake; acervuli dark, amphigenous on necrotic areas.

*Gloeosporium psoralaeae* Peck, on *Psoralea argophylla* Pursh, Grasshopper Trail near Audy Lake; black acervuli, epiphyllous on very small necrotic spots.

Marssonina potentillae (Desm.) Magn., st. conid. of Diplocarpon earliana (Ell. & Ev.) Wolf, on *Potentilla palustris* (L.) Scop., Brulé Trail near west end of Hwy. 19; acervuli mainly epiphyllous, causing chlorosis.

Phleospora anemones Ell. & Kell., on Anemone virginiana L., 8 km east of Audy Lake. Pycnidia scattered over entire undersurface of leaf and causing general chlorosis but not discrete leaf spotting. In this collection, leaves invaded also by *Puccinia*.

*Placospheria punctiformis* (Fuckel) Sacc., st. conid. of Leptotricha verrucosa (Wallr.) Schüepp. (Pseudopeziza repanda (Fr.) Karst. sensu Bisby et al. (1938)). Acervuli widely scattered on leaf under surface and causing general chlorosis.

*Septoria sonchi-arvensis* Dearn. & Bisby, on Sonchus sp., Rolling River road at junction Hwy. 19. Pycnidia epiphyllous on discrete necrotic spots.

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Mitella
  Puccinia heucherae var. heucherae

Monarda
  Puccinia menthae

Monolepis
  Albigo bliti

Oenothera
  Uromyces plumbarius

Oryzopsis
  Phyllochora oryzopsisidis
  Puccinia pygmaea

Osnotricha
  Puccinia pinnellae

Oxypopsis
  Uromyces punctatus

Petasites
  Puccinia conglomerata

Phalaris
  Claviceps purpurea
  Puccinia sessilis

Phragmites
  Puccinia magnusiana
  see Puccinia phragmitis

Picea glauca
  Chrysomyxa arctostaphyli
  Chrysomyxa ledi
  Chrysomyxa ledicola
  Chrysomyxa weirii
  see Pucciniastrum arcticum

Pinus
  Coleosporium asterum
  Coleosporium viburni
  Cronaritium comandrae
  Endocronaritium harknessii

Poa
  Erysiphe graminis

Puccinia poae-nemoralis
Puccinia recondita
Ustilago striiformis

Polygonum
  Erysiphe polygoni
  Puccinia polygoni-amphibii
  Uromyces polygoni-avicularis

Populus
  Melampsora medusae
  Uncinula adunca

Potentilla
  Marssonina potentillae
  Phragmidium andersonii
  Phragmidium invesiae
  Phragmidium potentillae

Prenanthes
  Puccinia atropuncta

Prunus
  Apiosporina morbosa
  Cercospora circumsissa
  Podosphaera clandestina
  Taphrina communis

Psoralea
  Gloeosporium psoraleae

Pteris
  Uredinopsis struthiopteridis

Pyroa
  Chrysomyxa pirolata
  Pucciniastrum pyroae

Ranunculus
  Uromyces alopecuri

Rhamnus
  Puccinia coronata

Ribes
  Drepanopeziza ribis
  stat. conid. Gloeosporium ribis
  Puccinia caricina

Rosa
  Phragmidium fusiforme
  Phragmidium speciosum

Rubus
  Gymnoconia peckiana
  Pucciniastrum arcticum

Rudbeckia
  Uromyces perigynius

Salix
  Melampsora abieti-capraearum
  Melampsora paradoxa
  Uncinula adunca

Sanicula
  Puccinia marilandica

Scirpus
  Puccinia mcclatchieana
  Uromyces lineolatus
Shepherdia
   Puccinia coronat
Siim
   Uromyces lineolatus
Smilacina
   Puccinia sessilis
Solidago
   Coleosporium asterum
   Puccinia dioicae
Sonchus
   Septoria sonchi-arvensis
Spartina
   Uromyces acuminatus
Sphaeralcea
   Puccinia sherardiana
Stachys
   Erysiphe galeopsisd
Stipa
   Puccinia stipae
   Puccinia substerilis var. substerilis
Symphoricarpos
   Puccinia crandallii
   Rhizogene impressa
Taraxacum
   Puccinia hieracii
Thalictrum
   Puccinia recondita
   Tranzschelia thalictri
Urtica
   Puccinia caricina
Vaccinimum
   Pucciniastrum goeppertianum
Viburnum
   Puccinia linkii
Vicia
   Uromyces coloradensis
   Uromyces viciae-fabae
Viola
   Puccinia violae
   Sphaerotheca macularis
Zygadenus
   Puccinia atropuncta

Literature Cited

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Abundance, Habitat, Reproduction and Morphology of Forest-dwelling Small Mammals of Nova Scotia and Southeastern New Brunswick

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Data on the relative abundance, habitat, reproduction, external and cranial morphology of small mammals collected in forested habitats at 10 localities in Nova Scotia and southeastern New Brunswick during July 1978 and 1979 are analyzed. Sixteen species and 378 specimens were collected in 5699 trapnights. The four most abundant species were the Woodland Jumping Mouse (Napaeozapus insignis), Southern Red-backed Vole (Clethrionomys gapperi), Smoky Shrew (Sorex fumeus), and Deer Mouse (Peromyscus maniculatus) with 100, 92, 68, and 45 specimens, respectively. The survey provided the first records of the Rock Shrew (Sorex dispar) from New Brunswick and only the third locality for the Rock Vole (Microtus chrotorrhinus) from Nova Scotia. Shrews (Soricidae), mice and voles (Cricetidae), and jumping mice (Zapodidae) constituted 28.3%, 41.5%, and 26.7% of the sample, respectively. The percentage of individuals evincing reproductive activity was higher among cricetid and zopid rodents (65.4%) than shrews (25.7%). Analysis of external and cranial variation in five species revealed significant differences between the sexes in only the Smoky Shrew (3 of 10 characters) and the Southern Red-backed Vole (weight). Significant sexual variation in the frequency of moulting was observed in the Woodland Jumping Mouse.

Key Words: small mammals, abundance, reproduction, Nova Scotia, New Brunswick, Sorex dispar, and Microtus chrotorrhinus.

We sampled forest small mammals at 10 localities in Nova Scotia and southeastern New Brunswick during July 1978 and 1979 in an attempt to determine the distribution and status of the Gaspé Shrew (Sorex gaspensis). Although we failed to capture any Gaspé Shrews, we did collect 378 small mammals representing 16 species in 5699 trapnights (TN) at localities which by and large had not previously been sampled for small mammals (Peterson 1966; Fred Scott, Nova Scotia Museum, personal communication). These specimens and associated data represent a significant contribution to the biology of the forest-dwelling small mammals of this region.

Methods and Materials

Sampling was concentrated in the habitats and microhabitats from which the Gaspé Shrew has been reported. These include rocky mixed deciduous/ coniferous forests (Roscoe and Majka 1976) and along the edges of small, rocky forest streams (Anthony and Goodwin 1924; Peterson and Symansky 1963). The sampling effort was apportioned among three major habitats as follows: 3421 TN (60.0%) — within 5 m of streams in mixed deciduous/ coniferous forests; 2028 TN (35.6%) — in mixed deciduous/ coniferous forests, usually on rocky, moderate slopes; 250 TN (4.4%) — in mixed deciduous forests. In the analyses of habitat preference, these percentages were used in calculating expected \( \chi^2 \) values. For each trapline, three break-back traps baited with chewed rolled oats were set at each station, and traplines were run for either two or three days. The habitats sampled appeared to be typical of the upland forests of the region, and our sample of small mammals is likewise representative, although there may be a bias towards geophilous (rock loving) and hygrophilous (water loving) species. Because our traps were generally too small to hold squirrels and were set primarily at sites where the probability of capturing squirrels was low, capture data for the three species of sciurids (Tamias striatus, Tamiasciurus hudsonicus and Glaucomys volans) should not be used to evaluate their abundance or distribution.

The cranial measurements for shrews and rodents were defined by van Zyll de Jong (1980) and DeBlase and Martin (1980), respectively. Cranial measurements were taken with a dial micrometer (0.05 mm calibration) and with the aid of a dissecting microscope. Only adults were used in the analyses of morphological characteristics. The criteria for determining relative age (adult vs. non-adult) varied among taxa but included growth and wear of dentition, degree of closure of cranial sutures, size, pelage and condition of reproductive organs. External measurements and weights were taken in the field and recorded on specimen labels. The specimens were...
divided between the mammal collections of the Fish and Wildlife Service, National Museum of Natural History, Washington D.C. (BS) and the Vertebrate Museum, Shippensburg State College (SSC).

Localities Sampled
Eight localities in Nova Scotia and two in New Brunswick were sampled, as follows (numbers preceding parentheses are referenced in Table 1): NOVA SCOTIA: 1) Colchester Co., Truro, 23.0 km N, 2.0 km W, West North Creek, altitude 245 m; 2) Colchester Co., Truro, 25.0 km N, 7.4 km E, altitude 120 m; 3) Cumberland Co., Oxford, 17.1 km S, 5.0 km E, Sugarloaf Mountain, altitude 240 m; 4) Inverness Co., Margaree Valley, 7.5 km N, 2.0 km E, altitude 130 m; 5) Kings Co., Kentville, 9.5 km N, 18.0 km W, Canada Creek, altitude 45 m; 6) Kings Co., Kentville, 10.5 km N, 18.0 km W, altitude 30 m; 7) Pictou Co., Trenton, 30.0 km E, altitude 160 m; 8) Victoria Co., Enlishtown, 5.0 km SE, SE slope Kelly's Mountain, altitude 100 m. NEW BRUNSWICK: 9) Albert Co., Riverside-Albert, 5.3 km N, 3.5 km W, altitude 140 m; 10) Albert Co., Riverside-Albert, 6.1 km N, 4.0 km W, altitude 200 m. These localities are represented by the corresponding numbers in Figure 1.

Results and Discussion
Shrews — Soricidae
Shrews comprised 28.3% of the small mammals collected (Table 1). The Smoky Shrew (Sorex fumeus) was the most abundant of the five species of soricids and was captured at 8 of 10 localities sampled. It was not taken at the two localities on Cape Breton Island.

![Figure 1. Map of the 10 sampling localities in Nova Scotia and New Brunswick. Localities are represented by circles; reference points used in locality descriptions are represented by triangles. Numbers are those used in Localities Sampled section.](image-url)
Table 1. Summary of captures of small mammals at eight localities in Nova Scotia and two localities in New Brunswick. Locality numbers refer to those in Localities Sampled.

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**TOTALS** | 81 | 58 | 19 | 25 | 12 | 6 | 55 | 17 | 98 | 7 | 378

**SAMPLING EFFORT (TN)** | 600 | 600 | 200 | 625 | 300 | 300 | 700 | 600 | 1574 | 200 | 5699

(nos. 4 & 8). Roscoe and Majka (1976) failed to capture the Smoky Shrew in the Cape Breton Highlands National Park, and the only specimen previously reported from Cape Breton Island (Peterson 1966) has been reidentified as a Masked Shrew (*Sorex cinereus*) (C. G. van Zyll de Jong, National Museum of Natural Sciences, personal communication). In this study, the Smoky Shrew showed a slight but statistically insignificant preference for sites adjacent to streams (48 of 68 specimens; \( \chi^2 = 2.51, .25 < p < .50, 2 \text{ df} \)). Most specimens were taken in traps set under rocks, logs and stumps.

In spite of being collected at nine of 10 localities, the Short-tailed Shrew (*Blarina brevicauda*) was not abundant, being represented by only one or two specimens at seven localities (Table 1). Short-tailed Shrews evinced no statistical difference in abundance in the three habitats sampled (\( \chi^2 = 1.55, .50 < p < .75, 2 \text{ df} \)). The other three species of shrews, the Rock Shrew (*Sorex dispar*), Water Shrew (*Sorex palustris*), and Masked Shrew, were uncommon to rare. The two Rock Shrews taken at the same locality in Albert County, New Brunswick represented the first two specimens of this species from the province. The habitat and characteristics of the first specimen taken in July 1978 have previously been described (Kirkland et
al. 1979). The second specimen, a subadult male, was trapped in July 1979 in an open talus slide on a mixed coniferous/deciduous forest hillside. All seven Water Shrews were collected adjacent to streams. The low abundance of Masked Shrews in the study (0.14/100 TN; 2.1% of total catch) contrasted with Roscoe and Majka's (1976) sampling in Cape Breton Highlands National Park, where Masked Shrews had an abundance of 4.4/100 TN and comprised 28.7% of the specimens collected.

The level of reproductive activity was much less in shrews than the cricetid and zapodid rodents (Table 2). The only indications of reproduction in females were four embryos in one Short-tailed Shrew and four placental scars in one Water Shrew. External and cranial measurements of adults of the five species are presented in Table 3. Only the Smoky Shrew had a sufficient number of adult specimens of both sexes to permit statistical comparisons of the sexes. The sexes differed significantly in 3 of 10 characters. Males were larger in total length and weight; females were larger in P4-M3 length.

**Mice and Voles — Cricetidae and Muridae**

The 157 specimens of five species of cricetid rodents comprised 41.5% of the small mammals collected. Most common was the Red-backed Vole (*Clethrionomys gapperi*) with 92 specimens; however, its numbers varied considerably among the localities (Table 1). The occurrence by habitat of 89 specimens was 30 at streamside, 54 in mixed deciduous/coniferous forest, and 5 in mixed deciduous forest, indicating a significant preference for mixed deciduous/coniferous forests ($\chi^2 = 26.25, p < .001$, 2 df). Red-backed Voles may spend considerable amounts of time below the surface, for 71 of 89 specimens were trapped under rocks, logs, roots and stumps. The Deer Mouse (*Peromyscus maniculatus*) was the second most frequently captured cricetid rodent and was the fourth most common species overall (Table 1). Its abundance did not vary significantly among the habitats. The Meadow Vole (*Microtus pennsylvanicus*) is normally associated with herbaceous habitats, and in this study, 9 of 12 were taken in dense grasses and forbs along stream edges. Three were trapped at the forest edge in areas of dense herbaceous ground cover. The two male Rock Voles (*Microtus chrotorhinus*) captured in Inverness County on Cape Breton Island are the ninth and tenth specimens taken in Nova Scotia, and this new locality is only the third for this species in the province (Roscoe and Majka 1976; Prescott, W. H. 1980). The mammals of Cape Breton Highlands National Park, 3 vols. Unpublished manuscript, Canadian Wildlife Service, Sackville, 494 pp.). Both were taken among rocks and adjacent to streams in mixed deciduous/coniferous forests, habitat that is typical for this species (Kirkland and Knipe 1979).

All six Southern Bog Lemmings (*Synaptomys cooperi*) collected were from mixed deciduous/coniferous forests. Although none were taken in boggy habitats, all were trapped at sites having at least 50% herbaceous ground cover (within 2 m of trap). Two

<table>
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<th>Species</th>
<th>Number Males</th>
<th>% Sexually Active Males</th>
<th>Testses Size in Sexually Active Males (mm)</th>
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<td>3</td>
<td>31.6</td>
<td>9.2 × 5.5 N = 6</td>
<td></td>
</tr>
<tr>
<td>Eastern Chipmunk</td>
<td>1</td>
<td>0</td>
<td>0.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red Squirrel</td>
<td>0</td>
<td>1</td>
<td>0.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Northern Flying Squirrel</td>
<td>1</td>
<td>5</td>
<td>0.0</td>
<td>20.0</td>
<td></td>
</tr>
<tr>
<td>Deer Mouse</td>
<td>18</td>
<td>25</td>
<td>94.4</td>
<td>11.2 × 8.4 N = 17</td>
<td></td>
</tr>
<tr>
<td>Red-backed Vole</td>
<td>58</td>
<td>31</td>
<td>75.9</td>
<td>12.4 × 7.4 N = 44</td>
<td></td>
</tr>
<tr>
<td>Meadow Vole</td>
<td>7</td>
<td>5</td>
<td>71.4</td>
<td>15.2 × 9.2 N = 5</td>
<td></td>
</tr>
<tr>
<td>Rock Vole</td>
<td>2</td>
<td>0</td>
<td>100.0</td>
<td>11.5 × 7.5 N = 2</td>
<td></td>
</tr>
<tr>
<td>Southern Bog Lemming</td>
<td>2</td>
<td>4</td>
<td>100.0</td>
<td>7.5 × 5.0 N = 2</td>
<td></td>
</tr>
<tr>
<td>Meadow Jumping Mouse</td>
<td>2</td>
<td>2</td>
<td>0.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Woodland Jumping Mouse</td>
<td>58</td>
<td>43</td>
<td>31.0</td>
<td>9.2 × 4.4 N = 18</td>
<td></td>
</tr>
<tr>
<td>House Mouse</td>
<td>1</td>
<td>0</td>
<td>0.0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

221 146
were taken in conspicuously rocky sites. Banfield (1974) indicated that, in Canada, Southern Bog Lemmings are found mostly in bogs, grassy marshes, or damp mixed forests surrounding bogs, although they may move into drier wooded slopes during the severest winter weather. The distribution of captures in this study suggests that the Southern Bog Lemming may have a broader ecological distribution than has been previously thought, in as much as all six specimens were sexually active, presumably resident, adults and not dispersing subadults.

The one House Mouse (Mus musculus) was trapped near an old refuse dump adjacent to a stream and about 2 km from the nearest permanent human habitation.

High percentages of all species of cricetid rodents collected were sexually active (Table 2). Small mammal abundance (6.63/100 TN), particularly that of cricetid rodents (2.75/100 TN), was low during the two years of sampling. An inverse relationship between small mammal abundance and the percentage of rodents exhibiting sexual activity has been observed over a 10 year period in New York State's Adirondack Mountains (Kirkland, unpublished data).

Cranial and external measurements of adults of all species of cricetid rodents are presented in Table 4. Comparisons of sexes were made for three of the species, and the results indicated little sexual dimorphism. One significant difference was noted; female Red-backed Voles weighed significantly more than males. This difference might reflect the high percentage of pregnant females in our sample.

**Jumping Mice — Zapodidae**

The Woodland Jumping Mouse (Napaeozapus insignis) was the most frequently captured species, with 101 specimens composing 26.7% of the total (Table 1). The distribution of captures by habitat was 70 within 5 m of the streams, 20 in mixed deciduous/coniferous forests, and 11 in mixed deciduous forests, revealing a significant preference for the first and third habitats ($\chi^2 = 18.47$, $p < .001$, 2 df). Of the 93 specimens for which ground cover (within 2 m of trap) was recorded, 68 (73.1%) were taken at sites with more than 50% herbaceous ground cover. Throughout its range, Napaeozapus prefers stream sides and sites with abundant herbaceous ground cover (Connor 1960; Whitaker 1963; Brower and Cade 1966; and Wrigley 1972). The four Meadow Jumping Mice (Zapus hudsonius) taken were all subadults trapped in dense streamside vegetation.

Wrigley (1972) found the sex ratio among 2351 museum specimens of the Woodland Jumping Mouse to be 57% males and 43% females. In this study, the

<table>
<thead>
<tr>
<th>Species</th>
<th>Total Length</th>
<th>Tail Length</th>
<th>Cranium Length</th>
<th>Greatest Width of Skull</th>
<th>Width of Maxillary Width</th>
<th>Width of Interorbital Width</th>
<th>Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Masked Shrew (7)</td>
<td>110.8-117</td>
<td>45.3-47</td>
<td>16.2-17.2</td>
<td>3.2-4.9</td>
<td>8.2</td>
<td>16.3</td>
<td>7.8</td>
</tr>
<tr>
<td>Smoky Shrew (1)</td>
<td>113.1</td>
<td>46.3</td>
<td>16.2</td>
<td>3.2</td>
<td>8.2</td>
<td>16.3</td>
<td>7.8</td>
</tr>
<tr>
<td>Smoky Shrew (4)</td>
<td>115.4</td>
<td>45.5</td>
<td>16.5</td>
<td>3.2</td>
<td>8.2</td>
<td>16.3</td>
<td>7.8</td>
</tr>
<tr>
<td>Water Shrew (1)</td>
<td>105-120</td>
<td>44.5</td>
<td>16.5</td>
<td>3.2</td>
<td>8.2</td>
<td>16.3</td>
<td>7.8</td>
</tr>
<tr>
<td>Short-tailed Shrew (6)</td>
<td>131.0</td>
<td>29.5</td>
<td>20.4</td>
<td>2.0</td>
<td>22.3</td>
<td>23.4</td>
<td>12.4</td>
</tr>
<tr>
<td>Roe Shrew (1)</td>
<td>122</td>
<td>27.3</td>
<td>16.3</td>
<td>2.0</td>
<td>22.3</td>
<td>23.4</td>
<td>12.4</td>
</tr>
</tbody>
</table>

* Differences between sexes significant at $p < .05.$
Table 4. Means and ranges for 10 measurements of adult rodents from Nova Scotia and southeastern New Brunswick. Lengths in millimeters and weights in grams. Comparisons of sexes with Student's t-test.

<table>
<thead>
<tr>
<th>Species (n)</th>
<th>Total Length</th>
<th>Tail Length</th>
<th>Hind Foot Length</th>
<th>Weight</th>
<th>Condylar Basal Length</th>
<th>Condylar Basal Length</th>
<th>Least Inter-Orbital</th>
<th>Zygomatic Breadth</th>
<th>Maxillary Tooth Row</th>
<th>Diastema</th>
<th>Cranial Breadth</th>
</tr>
</thead>
<tbody>
<tr>
<td>Northern Flying Squirrel (2 ♂♂)</td>
<td>264.5</td>
<td>114.0</td>
<td>37.0</td>
<td>69.9</td>
<td>32.80</td>
<td>6.68</td>
<td>21.75</td>
<td>6.90</td>
<td>8.28</td>
<td>17.05</td>
<td></td>
</tr>
<tr>
<td></td>
<td>264-265</td>
<td>111-117</td>
<td></td>
<td></td>
<td>32.4-33.2</td>
<td>6.55-6.80</td>
<td>21.50-22.00</td>
<td>6.75-7.05</td>
<td>7.95-8.60</td>
<td>16.9-17.2</td>
<td></td>
</tr>
<tr>
<td>Deer Mouse (13 ♂♂)</td>
<td>183.1</td>
<td>93.5</td>
<td>21.4</td>
<td>20.0</td>
<td>22.82</td>
<td>3.85</td>
<td>12.66</td>
<td>3.55</td>
<td>7.00</td>
<td>11.61</td>
<td></td>
</tr>
<tr>
<td></td>
<td>163-194</td>
<td>83-104</td>
<td>21-22</td>
<td>15.0-25.0</td>
<td>21.55-24.35</td>
<td>3.70-4.25</td>
<td>12.00-13.65</td>
<td>3.30-3.80</td>
<td>6.30-7.35</td>
<td>11.4-11.8</td>
<td></td>
</tr>
<tr>
<td>Deer Mouse (18 ♂♀)</td>
<td>187.7</td>
<td>94.6</td>
<td>21.2</td>
<td>22.3</td>
<td>22.82</td>
<td>3.80</td>
<td>12.87</td>
<td>3.52</td>
<td>7.08</td>
<td>11.75</td>
<td></td>
</tr>
<tr>
<td>Meadow Vole (5 ♂♂)</td>
<td>164.6</td>
<td>48.0</td>
<td>21.0</td>
<td>43.6</td>
<td>26.21</td>
<td>3.71</td>
<td>15.00</td>
<td>6.63</td>
<td>7.95</td>
<td>11.45</td>
<td></td>
</tr>
<tr>
<td></td>
<td>153-184</td>
<td>40-54</td>
<td>20-22</td>
<td>36.0-54.5</td>
<td>25.25-27.2</td>
<td>3.60-3.90</td>
<td>14.00-15.7</td>
<td>6.20-7.25</td>
<td>7.45-8.25</td>
<td>10.70-12.05</td>
<td></td>
</tr>
<tr>
<td>Meadow Vole (5 ♂♀)</td>
<td>166.0</td>
<td>45.6</td>
<td>20.6</td>
<td>46.9</td>
<td>25.59</td>
<td>3.60</td>
<td>14.78</td>
<td>6.28</td>
<td>7.73</td>
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<tr>
<td></td>
<td>155-180</td>
<td>41-51</td>
<td>19-22</td>
<td>37.0-63.0</td>
<td>23.75-27.45</td>
<td>3.45-3.80</td>
<td>13.80-16.00</td>
<td>5.90-6.70</td>
<td>7.15-8.25</td>
<td>10.80-12.20</td>
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</tr>
<tr>
<td>Rock Vole (2 ♂♂)</td>
<td>146.0</td>
<td>41.5</td>
<td>21.0</td>
<td>30.6</td>
<td>25.45</td>
<td>3.93</td>
<td>14.50</td>
<td>6.28</td>
<td>7.55</td>
<td>11.75</td>
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<tr>
<td></td>
<td>141-151</td>
<td>40-43</td>
<td></td>
<td>29.2-32.0</td>
<td>25.00-25.95</td>
<td>3.85-4.00</td>
<td>14.35-14.65</td>
<td>6.10-6.45</td>
<td>7.35-7.70</td>
<td>11.6-11.9</td>
<td></td>
</tr>
<tr>
<td>Red-backed Vole (16 ♂♂)</td>
<td>146.1</td>
<td>42.7</td>
<td>19.3</td>
<td>27.0*</td>
<td>23.30</td>
<td>4.03</td>
<td>13.11</td>
<td>4.85</td>
<td>7.25</td>
<td>11.15</td>
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</tr>
<tr>
<td>Red-backed Vole (15 ♂♀)</td>
<td>147.7</td>
<td>42.9</td>
<td>19.1</td>
<td>31.5*</td>
<td>23.02</td>
<td>3.98</td>
<td>12.91</td>
<td>4.98</td>
<td>7.08</td>
<td>11.10</td>
<td></td>
</tr>
<tr>
<td>Woodland Jumping Mouse (29 ♂♂)</td>
<td>243.9</td>
<td>150.4</td>
<td>32.0</td>
<td>25.6</td>
<td>21.30</td>
<td>4.96</td>
<td>12.57</td>
<td>3.68</td>
<td>6.26</td>
<td>10.52</td>
<td></td>
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<tr>
<td></td>
<td>230-262</td>
<td>142-162</td>
<td>30-34</td>
<td>21.5-29.5</td>
<td>20.70-22.0</td>
<td>4.70-5.30</td>
<td>11.90-13.10</td>
<td>3.55-3.85</td>
<td>5.95-6.55</td>
<td>10.2-11.05</td>
<td></td>
</tr>
<tr>
<td>Woodland Jumping Mouse (28 ♂♀)</td>
<td>242.4</td>
<td>149.2</td>
<td>31.2</td>
<td>26.3</td>
<td>21.21</td>
<td>4.96</td>
<td>12.59</td>
<td>3.68</td>
<td>6.20</td>
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<tr>
<td></td>
<td>231-253</td>
<td>139-157</td>
<td>30-33</td>
<td>21.5-36.0</td>
<td>20.55-21.80</td>
<td>4.70-5.20</td>
<td>12.10-13.50</td>
<td>3.45-3.95</td>
<td>6.00-6.60</td>
<td>10.2-10.85</td>
<td></td>
</tr>
</tbody>
</table>

* Differences between the sexes significant at p < 0.05.
sex ratio of the 101 specimens was 57.4% males and 42.6% females, suggesting that the bias (not significant) in favor of males was typical for the species. Using Wrigley's (1972) criterion for sexual activity in males of testes length of 7 to 11 mm, 54 (93.1%) of the males collected were sexually active. However, in this study, the criteria for sexual activity included coiled epididymis and large seminal vesicles in addition to testes size, and only 18 males (31.0%) were judged sexually active (Table 2). Thirty-three of 43 females (76.7%) were classed as sexually active on the basis of carrying embryos or possessing recent placental scars. No females had both. Only six of the reproductively active females were pregnant, and these carried a mean of 5.3 embryos (Table 2). This value is higher than the mean of 4.6 embryos reported for 80 litters for this species by Whitaker and Wrigley (1972). Although the larger mean in this study may be an artifact of the small sample size, it may also indicate clinal variation in litter size in *Napaeozapus* (McLaren and Kirkland 1979). However, the mean placental scar count for 27 females based on cursory macroscopic examinations of the reproductive tracts was 2.92, which is substantially lower than the mean value of 4.3 in 45 tracts reported by Wrigley (1972).

Significant sexual variation in the frequency of moulting was observed in this study. Of the 83 specimens for which moult data were recorded, 41 of 53 males (77.4%) and five of 30 females (16.7%) were moultng ($Z = 9.85, p < .0001$) Wrigley (1972) stated that gender apparently is not a factor in differences observed in the onset of moult in this species; however, our data suggest that male Woodland Jumping Mice initiate moulting earlier than females. The retardation of moult may be due to the energetic considerations of reproduction.

Analysis of external and cranial measurements revealed no significant sexual difference in Woodland Jumping Mice for the 10 characters measured (Table 4).

**Acknowledgments**

We are grateful to The Explorers Club of New York City for their support of this research in the form of two research grants. We also acknowledge the assistance of Charles M. Knipe who accompanied us in the field during July 1979. Michael A. Bogan and Michael D. Carleton reviewed an earlier draft of this paper and provided many valuable suggestions.

**Literature Cited**


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Status of Sandhill Cranes, *Grus canadensis*, in Central Ontario

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Ontario Ministry of Natural Resources District Offices confirmed that Sandhill Cranes, *Grus canadensis*, were breeding in three areas of central Ontario: Fort Frances, Hearst, and near Sault Ste. Marie. We censused cranes in the Sault Ste. Marie area (Sault Ste. Marie — Wabos — Espanola) in 1978 and 1979, and estimated that about 225 cranes were in the area during summer including about 40 breeding pairs. This population, very likely composed of Greater Sandhill Cranes (*G. c. tabida*), probably originated from northern Michigan, and is increasing and expanding eastwards.

Key Words: Sandhill Cranes *Grus canadensis*, central Ontario, subspecies.

Reports of Sandhill Cranes (*Grus canadensis*) in central Ontario (herein defined as the area from Kenora and Rainy River in the west to Cochrane and North Bay in the east) are limited to scattered sightings north of Hearst-Cochrane (Lumsden 1971, personal communication), close to Lake of the Woods (Lumsden 1971), and one report of breeding (young seen) near Sault Ste. Marie (Goodwin 1977). In 1977, we contacted all Ontario Ministry of Natural Resources (OMNR) District Offices in central Ontario to request information about summer sightings of Sandhill Cranes. Six Districts: Blind River, Espanola, Sault Ste. Marie, Wawa, Hearst, and Fort Frances, were reported to have nesting cranes. The first three of these Districts, which are contiguous, reported the highest numbers of cranes. We selected the southern, more accessible parts of these districts for a study to determine the status, distribution and population size of Sandhill Cranes; the research was done during 1978 and 1979.

**Study Areas and Methods**

We censused cranes in a 4000 km² area bounded by Wabos (north), Sault Ste. Marie (southwest) and Espanola (southeast) (Figure 1). The northern portion of St. Joseph Island and the southern portion of the north shore of Lake Huron are primarily farmland while the remaining sections of the study area are relatively unpopulated and forested. The northern part of the area is Precambrian rock (Collins 1925). Farmland in the central and southern parts is stratified clay deposited in the post-glacial periods of Lake Huron (Collins 1925). Much of the wooded area is climax forest, primarily Red Maple (*Acer rubrum*), Sugar Maple (*A. saccharum*), and Beech (*Fagus grandifolia*). Rivers, streams, and lakes, many with marsh edges, are common throughout the area.

We obtained information about the numbers and distribution of Sandhill Cranes in three ways. First, landowners throughout the study area were contacted in 1978 for information. If an individual had seen cranes on or near his property, we asked for information concerning numbers, presence of young, and the number of years that cranes had been observed. Second, data cards were sent to 925 persons on rural mail routes in the study area during July 1978. We requested the usual information and we sought late summer sightings of cranes with young as a way to locate nesting areas. Any sightings of equal size groups of cranes that were within 3.2 km (2 miles) of each other were considered to be of the same group unless two groups were seen simultaneously. Only reports which were subsequently verified by observing the cranes were used. Finally, we spent considerable time searching for cranes.

In northern Michigan, paired adult cranes return in early April and set up feeding territories within a 2-4 km radius of the wetland they will use for nesting (W. E. Taylor, personal communication). Local landowners and OMNR field personnel were asked in late April of both years for information on crane sightings during that month. We checked wetlands thought to contain cranes by listening for calls during the two hours after dawn and before sunset. In 1979, a Sanyo auto cassette-player with two 8 ohm speakers was mounted on a vehicle for auditory censusing (Bennett 1978a). The calls were played after dawn and before sunset at the access point nearest each wetland. This method was used daily before nesting began as that is when cranes are most vocal.

Ground searches for nests began on 6 May 1978 and 3 May 1979, when we estimated that cranes had been nesting for at least a week. This was based on observations of single adults on feeding territories previously occupied by a pair. Ground censusing was done by walking back and forth across a wetland until the
incubating crane flushed. On 5 and 6 May 1979, all wetlands on St. Joseph Island, the north shore of Lake Huron and the Dayton-Iron Bridge area were checked for nesting cranes by flying low (about 75 m) over them in a Bell 47-G helicopter. The location of each nest was marked on a 1: 50 000 topographical map.

**Results and Discussion**

A total of 157 cranes was observed in 1978 and 147 were seen in 1979. Many of these birds were in groups of three or more and were apparently either subadults or non-breeding adults. Some parts of the study area were inaccessible, some were inadvertently missed, and some reports which could not be verified were likely true. Thus, we think that about 225 cranes used the area during those summers.

Single nests were found in four wetlands in 1978; three of these wetlands contained nests in 1979, when nests were also found in another 11 wetlands. Two of the wetlands were shallow marshes and the remainder were sphagnum bogs. For details about precise locations and descriptions of wetlands, and of nest site characteristics see Tebbel (1981). Thirteen other pairs, with non-flying young, were observed elsewhere in the study area in 1978 and 1979, for a total of 27 known breeding pairs. All crane families moved from the nest wetland to adjacent upland clearings or agricultural fields within a week after the young hatched. The locations of known breeding pairs and non-breeding birds are shown in Figure 2. Based on unverified reports from local residents and OMNR personnel, we estimated that there were at least 14 other breeding pairs in the study area.

The number of breeding pairs in the study area is relatively small given the amount of apparently suitable habitat available. We found only 14 nests in the 97 wetlands we searched. Bennett (1978b) reported that up to 50 percent of the wetlands in some counties of southwestern Wisconsin contained two or more crane nests.

Sightings by local residents and OMNR personnel suggest that the population is relatively new and is increasing. Two local residents in the western part of the area remembered seeing cranes for 19 or 20 years. Both had lived in the area more than 30 years. Personnel at the Sault Ste. Marie OMNR District Office recalled that the first reports of cranes in that district were about 1970. A total of 52 landowners had seen Sandhill Cranes on their lands, and for most the first sighting was after 1974 (Table 1). The large number of recent initial sightings suggested that a substantial increase in the population has occurred. Apparently, the population is spreading eastward as cranes have been seen, on average, for more years in the western half of the study area than in the eastern half.

We observed few cranes in the northern part of the study area. Much of the area is heavily wooded with few natural or man-made openings, and most lakes
have rocky shores with little or no emergent vegetation. Thus, much of the area may be unsuitable for cranes, as they most often nest in emergent vegetation or on the floating mats of bogs in Michigan (Walkinshaw 1965) and require upland meadows or agricultural fields for feeding when they have young (Littlefield and Ryder 1968). However, our coverage of the northern area was hampered by its more inaccessible nature.

There are Sandhill Cranes north of our study area, however. Cranes have been recorded in Lake Superior Provincial Park since 1972 (Wawa OMNR, personal communication) and the Canadian Pacific Railroad staff operating between Sault Ste. Marie and Wawa have seen cranes since about 1970. We predict that cranes will increase in that area but probably will not reach the density associated with the agricultural area in the south.

We hypothesize that the cranes in our study area are part of the Great Lakes population of Greater Sandhill Cranes (G. c. tabida) which winter in Florida (Drewien et al. 1975; Nesbitt and Williams 1979). We suggest that the population originated from the upper peninsula of Michigan (Figure 1). The eastern section of the Hiawatha National Forest in Michigan, where over 20 crane nests were found in 1979 (W. E. Taylor, personal communication), is less than 100 km from the eastern part of our study area. Also the staging areas near Rudyard and Fibre-Dryburg, Michigan, where up to 1800 cranes flock in October (W. E. Taylor, personal communication) are between the two populations. That cranes were first observed in the western part of the study area (see above) also suggests an eastward dispersal by Michigan birds.

Acknowledgments

We gratefully acknowledge the field assistance of Dave Martin and Sandy Newton. The Ontario Ministry of Natural Resources (OMNR) and the Canadian Wildlife Service (CWS) are thanked for their interest and participation, as is W. E. Taylor, Hiawatha National Forest, U.S. Forest Service, for his advice and unpublished data. The people living in the area, many of whom knew about the cranes long before we

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**Figure 2.** Locations of breeding pairs (determined by the presence of a nest or non-flying young) and of non-breeding adults and/or subadults in 1978 and 1979.
did, made the field work especially rewarding. This project was funded by the OMNR, CWS, the Department of Indian and Northern Affairs, and ELSA Canada. This paper is dedicated to Stosh.

Literature Cited


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Reproductive and Hunting Behaviour in Peregrine Falcons, 
*Falco peregrinus*, in Southern Quebec*

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1Macdonald Raptor Research Centre scientific contribution no. 20

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After an unsuccessful attempt in 1979, Peregrine Falcons, *Falco peregrinus*, nested at a site in southern Quebec in 1980. The pair, made up of an apparent wild *anatum* male and captive-bred-and-released female, produced two young, the first known to fledge from a cliff site in eastern Canada south of the tree line, excluding Labrador, since 1961. Hatching appeared to take place on 6 July 1980, the young male and female fledged on 10 and 17 August, and were last observed at the site on 19 and 27 September, respectively. Over both years, 69 of 197 hunting attempts by the male were successful for a success rate of 35%. Of 218 hunting attempts by both sexes, 78% took place between 0500 and 1000 h. An attack with more dives at the prey was more likely to be successful. The principal prey species was Blue Jays (*Cyanocitta cristata*) up to 7 June, replaced by blackbirds and swallows after that date.

**Key Words:** Peregrine Falcon, *Falco peregrinus*, reproductive success, hunting success rate, southern Quebec

The status of the Peregrine Falcon (*Falco peregrinus*) has been closely monitored since its documented decline (Hickey 1969). The most recent North American survey indicated that in Canada in 1980 it no longer bred east of the Rocky Mountains south of the boreal forest, except for the site discussed herein (C. White and R. Fyfe, in preparation). The disappearance of breeding birds in the east has been attributed mainly to reproductive failure induced by DDT (Pea-kall 1976). In 1980, as a result of Cornell University’s efforts to restore the peregrine in the eastern USA through a captive breeding and reintroduction program, two pairs, using man-made towers, produced young in the wild. The Cornell breeding stock is from California, Chile, Queen Charlotte Islands, Scotland, Spain, and Nearctic tundra and taiga origins (T. J. Cade, unpublished data). Already in 1979, an active, although unsuccessful, pair of apparently wild stock peregrines occupied a cliff in southern Quebec. In 1980, the wild male of this pair successfully mated with a Cornell-released female and fledged two young. Since foraging attempts and reproductive behaviour could be easily observed in these birds without disturbing their behavioural patterns, we undertook to record this information for peregrines nesting in southeastern Canada. Data are available for 1979 and 1980 only, as the site was unoccupied in 1981.

**History of Study Area**

To minimize possible human interference to falcons using this site, the actual location of the cliff will not be revealed here; suffice it to say that this cliff over-looks a lake in southern Quebec. The first record of activity at this site was in 1961 when R. Ouellet (personal communication) noted two falcons on 18 June, and a nest containing two eggs on 6 July. On 19 and 20 August, and again on 27 August, three peregrines were seen (R. McNeil, personal communication). Hatching must have occurred shortly after 6 July to account for more than two birds on 19 August. Until the departure of the observers on 9 September, the falcons were seen almost daily. Prior to 1980, this was apparently the most recent successful nesting record for peregrines in eastern North America (Hickey 1969; Cade and Fyfe 1970; Fyfe et al. 1976). One local resident claimed the eyrie was occupied intermittently for 10 to 20 years prior to 1961.

Other records at this site included sightings of single falcons in the springs of 1962 (R. Ouellet, personal communication) and 1976 (J. Burton, personal communication). No birds were sighted during the 1970 North American peregrine survey (Cade and Fyfe 1970), but the site unfortunately was not checked in the 1975 survey. At least one bird was seen in 1977 and 1978 (P. Boily, personal communication).

In 1979, an adult male was present at the site from at least 23 April to 27 September. A female was recorded there from 8 to 21 May only. The lack of any leg band showed that the male was not captive-bred-and-released, and its colouration suggested that it was a mature specimen of *anatum* stock. The female in 1979, also unbanded, had a brown immature plumage with some graying on its back, indicating a bird in its first year. In 1980, the male’s distinctive moustachial strip,
as well as behavioural characteristics, i.e. perch use, facilitated its certain identification as the 1979 male. The 1980 female, this time in mature plumage, was wearing two bands, one aluminium and the other an aquamarine blue plastic band. Cornell University has released a number of peregrines wearing this band combination as near to the site as New Hampshire. A genetic abnormality, i.e. both alulas stretching downwards, known in a few Cornell birds (J. D. Weaver, personal communication), and the colour bands confirmed that the 1980 female was a Cornell-released falcon. According to T. J. Cade (unpublished data), this female was either of tundra parental stock or a tundra-taiga mixture. Interestingly, another successful nesting of peregrines occurred in 1980 at a cliff site in eastern Maine where an unbanded male paired with a female apparently not from the Cornell program successfully fledged two young. (Vickery 1980).

**Methods**

Between 26 May and 25 July 1979, observations of the falcons at this site were evenly distributed with a daily average of 7.7 daylight hours, totalling 460 logged hours. In 1980, the cliff was watched for a daily average of 6.6 daylight hours from 29 May to 27 September (when falcons were present) for a total of 657 h, but observations were uniformly distributed only up to 21 August. The distribution of observations throughout the daylight period for 1979 and 1980 is summarized in Table 1. An additional 21 hours of observations and searching were conducted in the period from 28 September to 12 October 1980, after the falcons had departed.

Foraging by the male was mostly within 0.8 km of the cliff, which facilitated the recording of hunting success. We defined an “attempt” as any observed hunting effort involving one or more dives by the falcon on a given prey item, resulting in its capture or escape into cover. Behaviour on the cliff face was observed with the assistance of binoculars and a telescope. Unfortunately, in 1979 few observations were recorded when both birds were present.

**Result**

**Reproductive Behaviour**

On 10 May 1979, four prey captures and two attempts were made in less than 2 h (0555 to 0740), each of the former followed by a food transfer in the air from the male to the female. On 16 May, two captures in less than 1 h were followed by similar food transfers. A normal sequence of food transfer occurred as follows: the male returning close to the cliff with prey called to attract the female. The female flew a few feet beneath the male and grasped the prey dropped by the male with her feet by quickly and partially rotating her body while sustaining flight. On one occasion when the male killed a Belted Kingfisher (*Megaceryle alcyon*) over the water and was unable to pick up the wetted bird, the female flew from the cliff and retrieved the prey. This female was observed twice caching intact prey items, behind a bush and inside a crack in the cliff, respectively. Food-caching has been previously recorded for both sexes of peregrines by Beebe (1960) and Nelson (1970).

In 1979, on 8, 9, and 16 May the male flew to several potential nesting ledges which the female visited simultaneously. On one occasion, the male transferred prey to the female. The only copulatory behaviour observed in 1979 occurred around 1400 on 16 May. The male returned to the cliff with a captured Tree Swallow (*Iridoprocne bicolor*) and the female flew to him, but no food transfer took place. The female returned to her perch calling to the male. The male then came to the ledge, transferred his prey to her, flew off briefly and returned to copulate twice in less than 15 seconds. The female proceeded to eat the prey while the male flew to another perch on the cliff. Although our observations were sporadic at this time, the female did not appear very active, with no apparent hunting behaviour and only brief flights about the

| Observation periods | 0401 | 0501 | 0601 | 0701 | 0801 | 0901 | 1001 | 1101 | 1201 | 1301 | 1401 | 1501 | 1601 | 1701 | 1801 | 1901 | 2000 | Totals |
|---------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| Observation hours   | 27   | 62   | 84   | 90   | 95   | 94   | 87   | 92   | 89   | 93   | 82   | 77   | 66   | 52   | 41   | 21   | 1142 |
| observed attempts   | 6    | 49   | 42   | 40   | 21   | 21   | 7    | 4    | 2    | 4    | 5    | 2    | 2    | 4    | 5    | 4    | 218  |
| captures            | 3    | 15   | 15   | 11   | 8    | 6    | 1    | 3    | 2    | 3    | 1    | 0    | 2    | 1    | 2    | 1    | 74   |
| % success           | 50   | 31   | 36   | 28   | 38   | 29   | 14   | 75   | 100  | 75   | 20   | 0    | 100  | 25   | 40   | 25   | 34   |
cliff. The female was no longer observed at the cliff after 21 May in 1979.

In 1980, the male and female were first observed on 8 May and 19 May, respectively, but they may have arrived earlier. On 24 May, the first observed food transfer took place in the air. Courtship activities, e.g., escorting flights, power dives by the male, bowing of the pair at the nest (Nelson 1970), continued up to 7 June. Copulations were observed twice on 29 May, three times on 1 June, twice on 2 June, and once each on 3, 5, 6 and 7 June. All of these took place within approximately 50 m of the nest but only one on the nest ledge. From 9 to 13 June, unusual behaviour was noted, i.e., female running to the male, male diving on the female, female continually chittering to the male, possibly indicating inexperience associated with breeding for the first time. It was not possible to record clutch size and laying dates. Although the incubation was shared by both sexes, the female incubated for the most part. Distinctive behavioural changes in both birds suggested that hatching took place on 6 July. During the first week after hatching, food was brought to the nest on average three to four times daily. The female assumed the responsibility of feeding the two young. Food remains were cached outside the nest by the female. The female brooded the young almost continuously until 18 July, after which her presence on the ledge decreased and the young became more active. By 17 July, the young were able to stand and move around on their tarsi. Pinfeathers showed in one youngster by 27 July, and two days later they were able to defecate outside the nest ledge.

The two young were banded on 1 August and at this time a fresh break was noted in the left leg of the female parent, cause unknown. By 4 August, the female could not land without crashing on her belly. Although the female more frequently hunted after 17 July, bringing prey to the nest, the male resumed the role as sole provider of food for both the female and the young, who by this time could pluck their own prey. The young with a more developed plumage was a male whose down disappeared by 9 August. This male first flew on the following day, to a lower ledge some 8 m away, and remained there for two days, being fed by the parents. By 13 August, he was able to fly after the female parent. The young female became more active on the original nest ledge during this time and finally fledged on 17 August.

The adult female vacated the cliff site on 19 August, but was identified by her bands and broken leg the following day some 43 km away at a municipal dump where she captured a pigeon. From that day forth, the male assumed all the duties of feeding the young. The young male was last seen at the site on 19 September, and both the adult male and the young female on 27 September.

On 5 September, both young were observed walking in a grassy open field catching insects. Similar behaviour has been noted in captive-bred-and-released peregrines (D. M. Bird, unpublished data) and two wild immature females (Dekker 1980).

The adult male was heavily involved with interspecific conflict, particularly with a pair of Common Ravens (Corvus corax) nesting on the same cliff. In 1979, aggression towards the ravens was observed as early as 26 April during their incubation period. Aggressive behaviour toward these birds was noted on 52 occasions. This behaviour usually consisted of a full-speed stoop resulting in near misses or actual removal of some feathers. Adult ravens responded by flipping over on their backs and presenting their feet. As the ravens fledged their young and vacated the cliff area, the male responded by taking over other perches on the cliff. The main roost continued to be a wind-protected recess in the centre of the cliff. As dusk approached each night, the male would settle on a rocky perch facing the cliff wall. In 1980, the ravens were forced by the pair of falcons to seek an alternative nesting site, and in the end they abandoned even their second nesting attempt.

In addition to the ravens, the male displayed aggressively toward Ospreys (Pandion haliaetus), Turkey Vultures (Cathartes aura), Sharp-shinned Hawks (Accipiter striatus), Broad-winged Hawks (Buteo platypterus), Red-tailed Hawks (Buteo jamaicensis), Marsh Hawks (Circus cyaneus), American Kestrels (Falco sparverius), Common Crows (Corvus brachyrhynchos), and Great Blue Herons (Ardea herodias). One kestrel was killed and dropped into the woods by the male. However, aggression did not always occur with the above species, and a Sharp-shinned Hawk and a Buteo sp. each attacked the male once.

Wing-moulting appeared to have begun on 20 June in the male. Sunbathing was noted on three occasions. This consisted of the male flattening himself out on a wind-protected ledge with his tail and wings fully spread. Once this continued for 12 minutes but lasted under 1 minute on the other occasions.

**Hunting Behaviour and Prey**

Of 218 hunting attempts by both sexes, 78% took place between 0500 and 1000 (Table 1). In 1979, 44 of 131 solo attempts by the male (34%) were successful. In 1980, the success rate for 66 solo attempts by the male was 37%. In total, 69 of 197 attempts (35%) were successful. During the late nesting stage, the 1980 female was successful in capturing prey only once in 5 solo attempts. She was only observed hunting twice during courtship, incubation and early nesting stages. The success rate in 15 attempts by the 1980 pair hunting together was 20%. The fastest capture rate by the
The male was 4 captures in 5 attempts in 70 minutes. No seasonal pattern of hunting success was readily apparent.

If a hunting attempt allowed for more dives at the prey, the falcon was more likely to be successful (Table 2). Attempts involving only one dive were less than half as likely to be successful as those involving two or more dives. The increase in success was about 10% with each additional dive.

Approximately 72% of the 137 hunting attempts in both years where locations were recorded took place over the lake immediately in front of the cliff. In 1980, 35% of 58 attempts over water were successful as were 20% of 15 attempts over land. Of 49 hunting attempts followed from the start in 1980, 30 originated from a cliff perch, 7 from a tree perch, and 12 from flight.

The cliff, 300 m high and 400 m long, overlooked the lake. Favoured perches were roughly 200-250 m high. Altitudes of the prey crossing lake varied greatly. A typical hunting pattern was as follows: upon sighting prey, the male left his perch, flew along the cliff face for 50 to 100 m and then aimed directly towards the prey crossing the lake, maintaining a higher altitude than the prey with a rapid flapping flight. Diving nearly vertically or obliquely on the prey over water, the male either (a) grasped the prey directly, (b) struck the prey and fished it out of the water, or (c) used repeated stoops to push it into the water where the wet bird was seized. This latter technique, seen several times, was also observed by Cade (1960). Soon after grasping the prey, the falcon reached beneath and pulled at the neck of the prey, presumably to kill it.

The prey species selected by the peregrines in 1979 and 1980 are summarized in Table 3. Blue Jays appeared frequently in the diet up to 7 June, but were replaced by swallows after this date. Blue Jays were captured readily, while blackbirds and swallows appeared more difficult to catch. Consumption time for a given prey item ranged from under 10 to 27 minutes. The male once plucked and ate a sparrow-sized prey item held in the claws while in flight. Dekker (1980) also reported male peregrines eating prey on the wing. Favourite eating perches consisted of trees in 20 cases and rocks in 5 others. A dry spruce stub standing at mid-cliff was used in at least 10 of the 20 observations.

Discussion

Although copulation occurred in 1979, the failure of the pair to complete the reproductive cycle may have been due to the immaturity of the female, the presence of nesting ravens already well established on the cliff, human disturbance, an accident involving the female, or any combination of the above. In 1980, all of those factors were negligible. The female was fully mature, and the falcons ousted the ravens from their previous territory. Diligent efforts by wardens kept climbers off the cliff, although picnickers used the cliff top.

The lateness of all recorded nesting attempts at this

Table 3—Prey selected by Peregrine Falcons within 0.8 km of nesting cliff in 1979 and 1980.

<table>
<thead>
<tr>
<th>Species</th>
<th>No. captured</th>
<th>No. missed</th>
<th>No. attacked</th>
</tr>
</thead>
<tbody>
<tr>
<td>Blue Jay</td>
<td>17</td>
<td>7</td>
<td>24</td>
</tr>
<tr>
<td>(Cyanocitta cristata)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Blackbirds*</td>
<td>8</td>
<td>12</td>
<td>20</td>
</tr>
<tr>
<td>Swallows*</td>
<td>6</td>
<td>8</td>
<td>14</td>
</tr>
<tr>
<td>Common Snipe</td>
<td>2</td>
<td>0</td>
<td>2</td>
</tr>
<tr>
<td>(Capella gallinago)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Common Flicker</td>
<td>0</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>(Colaptes auratus)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>American Robin</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>(Turdus migratorius)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Killdeer</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>(Charadrius vociferus)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rock Dove</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>(Columba livia)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mourning Dove</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>(Zenaida macroura)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Belted Kingfisher</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>(Megaceryle alcyon)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Eastern Kingbird</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>(Tyrannus tyrannus)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Warblers</td>
<td>1</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Common Grackle</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>(Quiscalus quiscula)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lepidoptera</td>
<td>2*</td>
<td>0</td>
<td>2*</td>
</tr>
<tr>
<td>Unidentified Aves</td>
<td>31</td>
<td>95</td>
<td>126</td>
</tr>
<tr>
<td>TOTAL</td>
<td>71</td>
<td>128</td>
<td>199</td>
</tr>
</tbody>
</table>

* including Red-winged Blackbird (Agelaius phoeniceus)
* including Tree Swallows (Iridoprocne bicolor)
* not included in hunting success computations in text.
site is puzzling. In 1961, eggs were still in the nest as late as 6 July. In 1979, the female appeared at the site on 8 May with copulation occurring on 16 May. In 1980, a different female arrived even later, around 19 May, and hatching occurred on 6 July. According to Bent (1938), peregrines usually arrive in this region in spring around the third week of March. Eggs were usually laid by the Sun Life falcons in April (Hall 1970). Although the status of the 1961 female is not known, one could attribute late nesting to immaturity or sexual inexperience of the females. The 1980 female, originating from tundra or tundra-taiga parents, may have been responding to a longer day length as experienced by birds nesting in northern regions. However, based on five nestings over two years by three females released by Cornell University in the New England states (T. J. Cade, unpublished data), their timing or reproduction corresponded with that reported by Bent (1938) for this area.

Dekker (1980) and Ratcliffe (1980) provided excellent reviews of hunting strategies and success of migrating and breeding peregrines, respectively. Our observation of a 35% success rate over both years fits well with previous findings. Treleaven (1961) and Dekker (1980) calculated values of 35.8% and 40.0%, respectively, for breeding adults, although the latter’s observations were limited to five hunting attempts, three of which were cooperative between the sexes. Treleaven (1977) distinguished between low and high-intensity chasing, reporting a 60% success rate in 45 high-intensity hunts. We are inclined to agree with Dekker (1980) that peregrines that forage for a mate or young are more motivated to hunt in earnest and that some adult peregrines have likely acquired more specialized skills than others. Familiarity with the habit, as well as prey habits, would certainly facilitate a higher success rate. The high success rate of the Quebec male in catching Blue Jays over water is probably not unlike that of the peregrines studied by Cade (1960) and Herbert and Herbert (1965).

In summary, success rates of hunting peregrines with young to feed are distinctly higher than those of migrating falcons and are not comparable.

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Literature Cited


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Winter Waterfowl around Pickering Nuclear Generating Station

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The distribution of waterfowl in the area of Pickering Nuclear Generating Station was studied between 17 September 1979 and 16 April 1980. Dabbling ducks were most abundant in shoreline marshes when these were ice-free. Large concentrations of Mallards, *Anas platyrhynchos*, Black Ducks, *A. rubripes*, Common Mergansers, *Mergus serrator*, Greater Scaup, *Aythya marila*, and Redheads, *A. americana*, were present around the station when the marshes were frozen. The station offers warmer water, protection from wind, and food for the waterfowl wintering in the area.

Key Words: waterfowl, distribution, cooling water, nuclear generators.

Large quantities of water are used for industrial cooling, including the cooling of condensers at generating stations, which results in the discharge of heated effluent back into lakes or rivers. The effects of heated effluent on the distribution and abundance of aquatic organisms have been reviewed by Coutant and Talmage (1975) and Talmage and Coutant (1979). The influence of heated effluent on the distribution of waterfowl has received less attention, but an increase has been noted in the numbers of waterfowl overwintering in some areas not previously utilized (Sugden et al. 1974, Goodwin et al. 1977, Prach and Surrendi 1978, Smith and Prach 1980). Those increases were associated with increased availability of food and open water at those locations during the winter.

The purpose of the present study was to document the extent of use by waterfowl and other water birds of the heated discharge at Pickering Nuclear Generating Station (PNGS) during the winter in order to assess the future environmental impacts of a second generating facility on that site.

**Study Area and Methods**

PNGS is situated on the north shore of Lake Ontario between Toronto and Oshawa (Figure 1). It utilizes a once-through cooling system in which water removed from the surface of the lake passes through the station and is returned to the lake, with an increase in temperature of from 5 to 11°C in the winter when ambient lake water ranges from 0 to 5°C.

The study area (Figure 1) extended approximately 9 km from Rouge River to Ajax. Six observation sites were initially chosen, two (A and B) at the generating station and four (D-G) along the shoreline. An additional site (C) was added on 1 February 1980. Three locations (D-F) allowed observation of adjacent marshes.

Observations were made with binoculars and telescopes twice monthly from 17 September 1979 to 16 April 1980. On each date, the numbers and species of waterbirds observed during each of six consecutive 10-min intervals were recorded for each location. From 1 February 1980 onward, observations at locations B and C consisted of three consecutive 10-min intervals rather than six. All observations were made between 0900 and 1500. Two adjacent sites were sampled simultaneously by different observers and the sequence of visits to each pair of adjacent sites was altered on each sampling date. All the waterfowl which landed on the water during the observation period were included in the counts and the locations of large groups were mapped.

**Results and Discussion**

Approximately 55,000 water birds (including loons, grebes, and coots as well as ducks and geese) representing 28 species were recorded during this study. The species recorded in greatest numbers were Mallard (*Anas platyrhynchos* 30%), Red-breasted Merganser (*Mergus serrator* 22%), Black Duck (*A. rubripes* 11%), Canada Goose (*Branta canadensis* 10%) and Common Merganser (*M. merganser* 8%) (Table 1).

The distribution of waterfowl in the study area changed appreciably in mid-January when ice covered most nearby marshes. Consequently the data were partitioned into two sets corresponding to periods when the marshes were ice-free, 17 September 1979 to 2 January 1980, and 1 to 16 April 1980, and when the marshes were ice-covered, 16 January to 16 March 1980.

When the marshes were ice-covered the numbers of water birds observed at the station increased from 77 to 288 birds per 10-min interval (*p < 0.01*, Mann-Whitney U-test), with numbers on a single date as high as 3000 birds, while the numbers observed at the non-station locations dropped from 91 to 55 per interval (*p < 0.01*) concurrently (Table 1). The three abundant
Figure 1. Location of observation sites along the north shore of Lake Ontario near Pickering Nuclear Generating Station.
The distribution patterns of the diving ducks varied. Red-breasted Mergansers were observed in substantial numbers only during the spring and fall migrations, and there was no significant difference between numbers at station and non-station locations. Common Mergansers, which remained in the study area throughout the winter, were observed more frequently at the station than along the shoreline when ice was present in the marshes. Similarly, Redheads (*Aythya americana*) and Greater Scaup (*A. marila*) were observed in substantial numbers only at the station locations (Table 1).

When ice was absent the greatest densities of dabbling ducks and geese were in the marshes with smaller concentrations around the station and in the area of Ajax. When ice covered the marshes, however, the largest concentrations were at the generating station. At the station, largest concentrations were observed inside the intake groins and on the eastern side of the intake with lower densities in the area of the discharge (see Figure 1). Density was also relatively high at Frenchman Bay, offshore from the station and at Simcoe Point. Ice had little influence on the distribution of diving ducks except that concentrations were substantially larger at the station and closer to shore during the period when the marshes were frozen. At the station the distribution of divers was similar to the dabbling ducks except for Common Goldeneye (*Bucephala clangula*) which were generally farther from shore.

In other studies of this nature, ducks were attracted to the warm water discharge of generating stations on western Lake Erie (Reed, L. W., 1971, unpublished Technical Report No. 18, Thermal Discharge Series, Institute of Water Research, Michigan State University) and on a lake in Alberta (Smith and Prach 1980), where these provided areas of open water in otherwise ice-covered situations. In contrast, on a lake receiving heated effluent in Georgia, fewer waterfowl were observed in the heated area of the lake than in the non-heated areas (Brisbin 1974). During our study, Lake Ontario did not freeze so the presence of open water per se did not appear to be a limiting factor.

Reasons for the attraction of waterfowl to the Pickering Station are not precisely known although their distributions suggest a few possibilities. Ice on the marshes apparently drives dabbling ducks out onto the lake. Their distribution around the station with concentrations inside and on the lee side of the intake groins suggests that protection from the wind is important. Warm water from the discharge recircu-

### Table 1 — Numbers (total and average per 10-min interval) of the most abundant waterfowl species observed at the Pickering Nuclear Generating Station and at non-station locations with respect to the presence of ice in the marshes

<table>
<thead>
<tr>
<th>Species</th>
<th>Ice present&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Ice absent&lt;sup&gt;b&lt;/sup&gt;</th>
<th>All dates</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Station</td>
<td>Non-Station</td>
<td>Station</td>
</tr>
<tr>
<td>Mallard</td>
<td>6 577</td>
<td>10&lt;sup&gt;c&lt;/sup&gt;</td>
<td>2 373</td>
</tr>
<tr>
<td>Red-breasted Merganser</td>
<td>15</td>
<td>&lt;1&lt;sup&gt;c&lt;/sup&gt;</td>
<td>23</td>
</tr>
<tr>
<td>Black Duck</td>
<td>4 102</td>
<td>68&lt;sup&gt;d&lt;/sup&gt;</td>
<td>718</td>
</tr>
<tr>
<td>Canada Goose</td>
<td>1 486</td>
<td>25</td>
<td>1 839</td>
</tr>
<tr>
<td>Common Merganser</td>
<td>1 629</td>
<td>27&lt;sup&gt;c&lt;/sup&gt;</td>
<td>187</td>
</tr>
<tr>
<td>Redhead</td>
<td>1 334</td>
<td>22&lt;sup&gt;c&lt;/sup&gt;</td>
<td>5</td>
</tr>
<tr>
<td>Greater Scaup</td>
<td>1 186</td>
<td>20&lt;sup&gt;c&lt;/sup&gt;</td>
<td>190</td>
</tr>
<tr>
<td>Common Goldeneye</td>
<td>379</td>
<td>6</td>
<td>244</td>
</tr>
<tr>
<td>Bufflehead&lt;sup&gt;e&lt;/sup&gt;</td>
<td>231</td>
<td>4</td>
<td>183</td>
</tr>
<tr>
<td>Other Species</td>
<td>323</td>
<td>5</td>
<td>828</td>
</tr>
<tr>
<td>All Species</td>
<td>17 262</td>
<td>288&lt;sup&gt;c&lt;/sup&gt;</td>
<td>6 590</td>
</tr>
</tbody>
</table>

<sup>a</sup> 16 January to 16 March, 1980.
<sup>b</sup> 17 September 1979 to 2 January 1980 and 1 to 16 April 1980.
<sup>c</sup> Significant difference, station vs non-station (p < 0.01, Mann-Whitney U-test).
<sup>d</sup> Significant difference, station vs non-station (p < 0.05).
<sup>e</sup> Significant difference, ice present vs ice absent (p < 0.01).
<sup>f</sup> Significant difference, ice present vs ice absent (p < 0.05).
<sup>g</sup> *Bucephala albeola.*
lates into the intake and also moves across the front of the station, allowing for year round growth of attached filamentous algae along the armour stone in those areas. Filamentous algae are not considered important food items for most dabbling ducks and geese, however, in one study (Serie and Swanson 1976) attached algae comprised approximately one-quarter of the diet of Gadwall (Anas strepera) in wetlands where its abundance was relatively high. No data are available on the feeding habits of the ducks at PNGS, but the warm water, and possibly the presence of food, may help to attract dabbling ducks to the station.

The distribution of diving ducks was similar except that they moved farther offshore. Densities of many fish species have been shown to be higher in the area of PNGS than in surrounding areas of Lake Ontario from May through November (Ontario Hydro Research Division unpublished reports). Although detailed fish distribution studies during the winter are lacking, limited sampling and impingement records at PNGS suggest the presence of substantial numbers of forage fish, especially Alewife (Alosa pseudoharengus) and juvenile Gizzard Shad (Dorosoma cepedianum). Consequently the area of the station should provide adequate food for piscivores such as mergansers. Although the bottom in the area of the station is composed of compacted sediments, not ideal for benthic feeders, the presence of the attached algae and associated benthic organisms may provide an adequate food source for the Redheads and Greater Scaup.

Attraction of waterfowl to the station is thus not simply owing to the presence of open water; protection from the wind, the presence of warm water and food availability also may be important factors.

Acknowledgments
We thank L. S. Gray and D. Schneider for their assistance in the field.

Literature Cited

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Coyote Population Fluctuations and Spatial Distribution in Relation to Wolf Territories in Riding Mountain National Park, Manitoba

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Observations of competition between Wolves (Canis lupus) and Coyotes (C. latrans) were recorded in Riding Mountain National Park, Manitoba, from July 1974 to March 1979. Twenty-two Wolves and 34 Coyotes were radio-collared and radio tracked. Home range overlap of four Coyotes and three Wolves were studied. Abundance indices obtained from howling surveys indicated that as Wolf densities declined Coyote increased. Seven known or suspected wolf-killed Coyotes were examined. Two of four radio-collared Coyotes in one Wolf pack territory were killed by Wolves, and two Coyotes may have been killed by Wolves. Average survival from time of capture for the four radio-collared Coyotes was 145 days (range 71 to 265 days). Wolves did not consume Coyotes. Coyote survival along Wolf territory edges was greatest at moderate Wolf densities.

Key Words: Coyote, Canis latrans, Wolf, C. lupus, population fluctuations, spatial distribution, Manitoba

Competition between Wolves and Coyotes was given as a reason for the extirpation of Wolves on Isle Royale (Mech 1966; Krefting 1969; Allen 1979). Mech (1966: p. 160) stated that "since coyotes and wolves are closely related, and since wolves are strongly territorial, it is not unlikely that on a limited range such as Isle Royale, wolves would chase and probably kill every coyote encountered." Killing of Coyotes by Wolves has been reported (Seton 1929; Young and Goldmann 1944; Munro 1947; Stenlund 1955; Berg and Chessness 1978). The co-existence of Wolves and Coyotes in Riding Mountain National Park is therefore of interest, and this paper describes the relationship between the two species. Hoskinson and Mech (1976) and Mech (1977) observed that Wolf territoriality may be in buffer zones between pack territories where prey is less likely to be killed. They reasoned that Wolf territory boundaries served as sanctuaries to prey if neighboring packs avoided these areas in order to reduce fatal intraspecific strife.

Fuller and Keith (1981) indicated that the home range of one radio-collared Coyote and capture site of four others were along edges of Wolf pack territories. Higher survival of Coyotes at the periphery of Wolf territories could be attributed to either (1) resident Coyotes avoiding Wolves, and this was easiest at the edge of Wolf territories or, (2) Wolf packs being less likely to frequent peripheral areas (Mech 1977). This relationship can best be studied by monitoring radio-collared animals of both species occupying the same range. Information reported in this paper is preliminary, as data were collected secondarily to Wolf studies. However, results obtained did provide insights into the relationship between the two species. To investigate Wolf/Coyote relationships further, movements of four Coyotes within the territory of the BL-78 Wolf pack were studied.

Study Area

The BL-78 Wolf pack ranged in the central portion of RMNP (Figure 1). The 2944 km^2 park is located in southwestern Manitoba. A unique feature of the park is its isolation as a wilderness area completely surrounded by agricultural land. The park falls within the general aspen parkland region which is a transition zone between grasslands (prairie) to the south and boreal forests to the north.

Water bodies are important features in RMNP. The western southcentral and central portions of the park contain slow flowing, sluggish streams and poorly drained areas. The eastern portion of the park is deeply incised with gullies formed by fast running, often seasonal streams that run down the Manitoba escarpment.

Relief, drainage and fire history are important factors that determine the plant cover in the park. Vegetation is predominantly aspen-forest, interspersed with upland fescue-prairie, wetlands (sedge-willow plant cover), upland grassland and coniferous forest.

The climate of southwestern Manitoba is characteristic of the dry interior continental climate of the prairie provinces. Summers are warm, and on the plateau in the eastern portion of the park, the climate is affected by local turbulence because of updrafts from the lowlands.

Methods

Coyotes and Wolves were trapped in #4 and #14 steel traps along park trails (Mech 1974). During the study 22 Wolves and 76 Coyotes were captured but
only 21 Wolves and 34 Coyotes were collared. This paper discusses only home range overlaps of Coyotes (n = 4) and Wolves (n = 3) whose home ranges were sympatric. Animals were immobilized with Sernylan (phencyclidine hydrochloride) and Sparine (promazine hydrochloride). Dosages used were similar (1 mg of each drug per kg of Coyote weight) to those used for Wolves (Carbyn 1981 unpublished CWS report). Radio-collared animals were monitored from the air with a Maul (M5) fixed-wing aircraft.

Locations of instrumented animals were plotted on topographic maps (scale 1:50 000). Detailed movements, predation rates, prey consumption, and hunting sequences of the BL pack were monitored from 23 October 1978 to 13 March 1979. Because monitoring flights were usually less than 1.5 hours long, fixes were obtained in order of proximity of animals to one another. An H.P. 9830 desk computer was used to plot radio locations, to calculate distances between them and to delineate territories. Radio signals that
came from a stationary source were evidence that animals were dead. Carcasses were examined as soon as possible. Dead animals were located on the ground using a receiver and a hand-held loop antenna.

Indices of canid abundance were obtained from nocturnal howling surveys along major trails in the park at 1.6 km intervals (Pimlott 1960). Responses from Coyotes and Wolves were elicited through human imitations of Wolf howls. Attempts were made to cover portions of all trails in a two-week cycle during July and August, 1974–78. Locations of all canid responses were mapped, and Coyote responses and sightings were superimposed on Wolf territory delineations from the previous winter.

Results

1. Coyote/Wolf spatial relationship in BL pack territory

Three members from a pack of eight Wolves (BL pack) were captured 1, 24 October and 21 November 1978. Movements of this pack were recorded to 31 March 1979. When territory size was plotted against the number of radio locations an asymptote occurred for the BL Wolf pack at the first 19 fixes. Total radio fixes was 64, so that the BL Wolf pack territory boundaries were well delineated. Within the BL Wolf pack territory four radio-collared Coyotes had home ranges (Figure 1). Details about the radio-collared Coyotes were as follows:

Coyote G-19, a yearling male, was captured 28 March 1978. Its movements were monitored to 18 December 1978. Signal was stationary thereafter and the carcass recovered on 24 January 1979. Cause of death was unknown as the carcass was found largely consumed by scavengers. The Coyote ranged for at least 265 days within a portion of the BL-78 pack territory (Figure 1). Of the 265 days, 79 days covered a period of time (fall and winter) when there is a possible increase in vulnerability (Carbyn 1981 unpublished CWS report) of Coyote mortality to Wolves. The home range of G-19 overlapped with B-14.

Coyote B-14, an adult female, was captured 16 September 1978. During 165 days of monitoring (148 days of which were during the period when vulnerability was possibly increased) its movements were entirely within the BL-78 pack territory (Figure 1). A Coyote (presumably B-14 or another member of a pair) was heard to howl near an American Elk (Cervus canadensis) carcass on 25 February 1979. A ground check on 26 February revealed that B-14 and a second Coyote had scavenged there and that four Wolves had converged on the bedded Coyote. Chest and neck regions were severely mangled. Postmortem examination revealed that the posterior region and uterus were partially destroyed. The Coyote was in fair physical condition and weighed 15.5 kg at death; kidney fat at its widest point measured 14 mm.

Coyote G-18, an adult male, was captured 14 October 1978. His movements, during the period when Wolf movements were monitored, were entirely within the central portion of BL-78 pack territory (Figure 1). Movements of G-18 overlapped home ranges of B-14, G-19, and B-23. G-18 survived in the territory of BL-78 Wolf pack for at least 80 days from the date of capture. He died between 11 and 18 January of unknown causes.

Coyote B-23, an adult female was captured on 14 October 1978. Movements of this Coyote were entirely within the BL-78 pack territory. The animal was found dead on 23 January 1979, after the signal was recorded as stationary on 23 December 1978. The Coyote lived for 71 days after capture within the BL-78 pack territory. Postmortem of the animal indicated that it almost certainly was killed by Wolves. Rib-cage muscles exhibited bite wounds similar to those of B-14, but genitalia were not affected.

The average survival, after capture, of Coyotes trapped in fall was 105 days. When the one spring capture was included, average survival time was 145 days. Two of the four radio-collared Coyotes found dead in BL Wolf pack territory were known or suspected Wolf kills and two may have been. During the study three other, non-collared Coyotes in the park were also found killed by Wolves in mid to late winter.

2. Coyote family group responses in relation to Wolf territories

Location of summer Coyote sightings and howling responses (Table 1) during 1974 to 1978 have been plotted for each year (Figures 2 and 6). Delineation of Wolf territories began in 1975/76 and these are shown also. During the 3.5 years of study a total of 21 Wolves were radio-collared and their movements studied. Wolf densities were highest in winter 1975/76 (1 wolf/25 km²) and decreased in 1976/77 (1 wolf/40 km²) and 1977/78 (1 wolf/57 km²) with slight increases recorded for 1978/79 (1 wolf/47 km² — Carbyn 1980 unpublished CWS report). Coyote responses were high in the year before intensive Wolf studies (Figure 2). No data on Wolf abundance is available for that year. Howling response indices suggested that as Wolf numbers decreased Coyote numbers increased. The number of responses, and sightings of Coyotes, was low to moderate in 1975, the year of increasing Wolf numbers (Figure 3) and lowest (Figure 4) in 1976 the winter after the highest recorded Wolf densities. In fact, the only known denning Coyotes that year were recorded in a fenced Bison (Bison bison) pasture (Figure 4). Wolves sometimes crawled under the fence, but packs were seldom in the
area. Other Coyote sightings and responses, with one exception in 1976, came from Wolf territory edges or outside known territories (Figure 5). In 1977 and 1978 the Wolf population was low and Coyote numbers increased appreciably.

The Audy Lake Wolf pack in 1978 consisted of only three animals that ranged widely, and Coyote responses and sightings were made throughout the pack territory. However, Coyote family groups were recorded only along the territory edge (Figure 6).

**Discussion**

Wolves often kill Coyotes, but in RMNP, unlike the Isle Royale situation (Mech 1966; Krefting 1969), the interaction has not resulted in extirpation of Coyotes. The fact that Wolves kill, but rarely consume Coyotes is an interesting phenomenon, an explanation of which requires further study.

An analysis of distances between Wolves and Coyotes in this study did not result in convincing evidence that Coyotes consistently avoided Wolves,

**Table 1—Results of Coyote howling responses during howling surveys conducted during July and August periods from 1974 to 1978 in Riding Mountain National Park, Manitoba**

<table>
<thead>
<tr>
<th>Year</th>
<th>Total distance covered in surveys</th>
<th>Status of Wolf population (Carbyn 1981)</th>
<th>Coyote Responses and sightings</th>
<th>Total Number per 1000 km</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Responses</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Group</td>
<td>Single</td>
</tr>
<tr>
<td>1974/75</td>
<td>Not recorded</td>
<td>increasing</td>
<td>15</td>
<td>10</td>
</tr>
<tr>
<td>1975/76</td>
<td>1100 km</td>
<td>high densities</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>1976/77</td>
<td>964 km</td>
<td>declining</td>
<td>0¹</td>
<td>3</td>
</tr>
<tr>
<td>1977/78</td>
<td>1240 km</td>
<td>low</td>
<td>11</td>
<td>21</td>
</tr>
<tr>
<td>1978/79</td>
<td>77 km</td>
<td>low</td>
<td>13</td>
<td>6</td>
</tr>
</tbody>
</table>

¹Figure does not include Coyote groups and single responses within Bison enclosure — an artificial situation and dealt with separately.

**Figure 2.** Coyote responses and sightings in Riding Mountain National Park in the year prior to increase in Wolf numbers (summer, 1974).
Figure 3. Coyote responses and sightings in Riding Mountain National Park during the year of increase in Wolf numbers (summer, 1975).

Figure 4. Coyote responses and sightings in the summer of 1976, a year after Wolf populations had increased. Territories of radio-collared Wolf packs during the previous winter are shown in Riding Mountain National Park, Manitoba.
Figure 5. Coyote responses and sightings in Riding Mountain National Park during a year of population decline (summer, 1977). Territories of radio-collared Wolf packs during the previous winter are shown.

Figure 6. Coyote responses and sightings during summer 1978 (a year of low Wolf numbers) in Riding Mountain National Park, Manitoba. Territories of radio-collared packs during the previous winter are indicated.
but it did suggest that Coyotes more often avoided Wolves in mid to late winter than was the case in early winter. Two factors could contribute to this process: 1) snow conditions in mid to late winter may differentially affect the species, and 2) avoidance may partly be a learned process. The results of a preliminary analysis are presented here in the hope that it might stimulate further research along these lines.

In thick, soft snow, Coyotes were more restricted in their movements than were Wolves (personal observations in RMNP and in Jasper National Park). R. Leonard (personal communication) also noted that in RMNP during severe snow conditions (1978/79) Coyotes were reluctant to leave snowmobile tracks when approached on foot. Two of three Coyotes that I found killed by Wolves in previous studies (in Banff and Jasper National Parks) were killed on snowmobile trails. Follow-up work is required to examine the effects of snow thickness on canid mobility in greater detail. In both RMNP and in Jasper National Park, Coyotes often trailed Wolves through thick snow. Similar observations were made by John Kansas (personal communication) in various Canadian Rocky Mountain National Park locations. The reason may be either convenience of travel or anticipation of scavenging on Wolf kills. Thus, it appears that even though Coyotes may avoid Wolves, after a "refractory period", they may actually trail them at a safe distance in search of food. Evidence, therefore, is not clear as to when Coyotes trail Wolves or when they avoid them and it is conceivable that it is a learned response.

Different behavior and activity patterns of Wolves and Coyotes probably are important and should be further studied. Wolf packs often rest in mid-day and there are suggestions (Carbyn 1981 unpublished CWS report, as per G. Bergeson personal communication) that Wolves avoid areas close to humans during daylight hours. Coyotes may then also adjust their movements in relation to Wolf activities. The ability to do so, however, could be related to snow thickness, as animals less capable of avoiding Wolves would perish first. According to Mech's 1977 hypothesis one would expect Wolves more often to kill Coyotes in core areas of Wolf territories than at the periphery. Furthermore, observations of Hoskinson and Mech (1976) that buffer zones between Wolf packs provide greater prey survival than core areas would be particularly applicable to present circumstances if Coyote movements are more restricted in mid to late winter. A factor not discussed before, however, is whether differential vulnerability of prey in core areas varies with Wolf densities. Presumably, at high Wolf densities Wolves would use peripheral areas more often than during low densities.

Mortality of radio-collared Coyotes within the BL pack territory showed that they could not always avoid being killed by Wolves through occupation of buffer zones. However, even though some Coyotes did get killed in buffer zones, overall Coyote survival appeared to be greater there, particularly in years of moderate Wolf densities.

Wolf pack territories in RMNP are more flexible from year to year than is the case for unexploited, stable Wolf populations. However, prey biomass and prey availability is high (Carbyn 1981 unpublished CWS report). Contrasting with the general situation was the Whitewater Lake pack whose southern boundary was stable. Accordingly, Coyote responses from year to year were higher in that area, supporting the buffer zone concept.

Wolf-related Coyote mortality in RMNP was highest when Wolf densities were high, and indicators are that regardless of their location in the Wolf territory, Coyotes can be affected under such conditions. However, when the Wolf population is at a moderate level, chances of survival of at least a few Coyotes appear greatest at the Wolf pack territory edges. At peak Wolf populations, Coyote survival was very low, especially in summer of 1976. Summer responses to howling along roads show that the number of Coyote family groups in such areas probably provide a good indication of the distribution of the overwinter survival of Coyotes. The summer after the Wolf population was highest (summer 1976), the only Coyote family recorded along roads was within a "protected" area (Bison enclosure). In this study Coyote howling response surveys were limited to available roads and may have biased the results. Sightings and responses of single Coyotes were common within a large territory of the small (3-member) AL Wolf pack, probably because winter mobility of this small pack was more restricted.

Acknowledgments
The study was funded by Parks Canada, and I am grateful for their involvement in all phases of the work. Park wardens C. Allen, T. Hoggins, G. Pylypuik, and technician D. Patriquin assisted in field work. Student assistants A. Kennedy, H. Samoil, T. Trottier, J. Tutt (deceased), and K. Whaley conducted the howling surveys and assisted in winter field work. Personnel from Dauphin Air provided us with the necessary fixed-wing aircraft support. F. Anderka assembled radio-collars. R. Leonard, L. D. Mech and E. Telfer provided critical review of the paper.

References


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Cyperaceae New to Canada from Long Point, Norfolk County, Ontario

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Cyperus flavescens var. poaeformis, Carex alata, and C. nigromarginata are added to the native flora of Canada on the basis of collections made on Long Point, Lake Erie, in 1979 and 1980. All of these taxa have an extensive eastern United States distribution and are at their northern limit on Long Point. Cyperus flavescens and Carex alata occur in adjacent portions of Ohio and Michigan. Carex nigromarginata is a more isolated disjunct, the nearest occurrences being in southern Ohio and possibly northwestern Pennsylvania. Cyperus flavescens occurs locally in moist, sandy calcareous meadows from the base of Long Point to the tip. Carex alata was found on a rotting log in Red Maple woods near Squires Ridge. Carex nigromarginata occurred locally in dry, acid sandy substrate on knolls under Red Oak from Squires Ridge to a point 5 km eastward. Additional ecological data is provided and characteristics separating the species from their nearest relatives in the Canadian flora are discussed and illustrated.

Key Words: Cyperaceae, Cyperus flavescens var. poaeformis, Carex alata, Carex nigromarginata, floristics, new records, phytogeography, Canada, Ontario, Long Point.

A floristic survey of Long Point, Norfolk County*, a 35.5 km (22 mile) long sand spit jutting out into Lake Erie, has disclosed three species of Cyperaceae new to Canada. These records are of considerable interest as additions to the native Canadian flora, and also as species to be considered in current work on rare and endangered plants.

Cyperus flavescens L.

This Umbrella Sedge was first noticed in the vicinity of the lighthouse near the tip of Long Point where it was abundant in a few moist sandy meadows, 21 September 1979, A. A. Reznicek 5334 and P. M. Catling (CAN, DAO, MICH, TRTE). Subsequently it was found occasionally on damp, more or less bare sand on beach strands along most of Long Point. It was locally abundant in somewhat disturbed situations along roads and about campsites in Long Point Provincial Park. The most frequent associates included Rhynchospora capillacea (Beak-rush), Scelaria verticillata (Nutrush), Triglochin palustris (Arrowgrass) and Cyperus rivularis (Umbrella Sedge).

This is the first Canadian record of Cyperus flavescens, a pan-tropical species that occurs northward throughout most of the eastern United States to southeastern New York and Michigan (Fernald 1950; Gleason and Cronquist 1963). It is “very local” in Michigan (Voss 1972) and listed as rare in Michigan’s endangered and threatened species program (Wagner et al. 1977).

Cyperus flavescens resembles C. rivularis and C. diandrus in its habitat, general appearance and possession of two-cleft styles and lenticular achenes. It differs in having more or less translucent, yellowish scales usually less than 2 mm long, and in its black achenes with transverse ridges whitened at maturity (Figure 1). Our collection is referable to var. poaeformis (Pursh) Fernald, the North American representative of this wide-ranging species.

Carex nigromarginata Schuw.

This sedge was found on dry knolls in open Quercus rubra (Red Oak), Acer rubrum (Red Maple) woodland (Figure 2) at the northern end of Squires Ridge, about 21 km (13 miles) from the base of the point, 25 May 1980, A. A. Reznicek 5496 and P. M. Catling (DAO, MICH, TRTE); 15 June 1980, A. A. Reznicek 5648 and P. M. Catling (DAO, TRTE). A small population was also found in a similar habitat about 25.5 km (16 miles) from the base, 15 June 1980, A. A. Reznicek 5636 and P. M. Catling (MICH). The plants occurred only in open, dry areas receiving much light due to the open marsh or pools surrounding the small knolls and the absence of shrubs and saplings in the woodland (due to browsing by deer). Dominant associates included the mosses Leucobryum albidum, Polytrichum ohiense and Dichranum scoparium and a relatively sparse cover of vascular plants including Carex artitecta (Sedge), Danthonia spicata (Poverty

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*Walsingham twp., extending from Lat. 42°32'20" to 42°36'40" and from Long. 80°28'30" at the base to 80°02'30" at the tip, now included in the Regional Municipality of Haldimand-Norfolk.
Grass), Panicum linearifolium (Panic Grass) and Poa compressa (Canada bluegrass). Also present were Carex muhlenbergii (Sedge), Carex pensylvanica (Sedge), Panicum latifolium (Panic Grass) and Panicum oligosanthes (Panic Grass). The rooting medium of Carex nigromarginata had a pH of 4.6 and included the upper 2 cm of substrate comprised of coarse sand mixed with much organic material. At 5 cm depth the substrate was almost pure sand with a pH of 5.0.

The occurrence of Carex nigromarginata on Long Point is of considerable phytogeographical interest. It is a southern and eastern species, occurring north to southern Connecticut (Seymour 1969), southeastern New York (Fernald 1950), eastern and southernmost Pennsylvania (Bright 1930; Jennings 1953), southern Ohio (Braun 1967) west to southernmost Illinois and adjacent Missouri (Mohlenbrock and Ladd, 1978). An isolated station in Crawford County, northwestern Pennsylvania, noted by Bright (1930) and Jennings (1953), is the closest reported site to the equally isolated Long Point populations but no specimens confirming this occurrence have been found (C. S. Keener in litt.).

Gleason and Cronquist (1963), Boivin (1967) and Scoggan (1978) consider Carex emmonsii Dewey, C. artitecta Mack. and C. peckii Howe to be varieties of C. nigromarginata; as var. minor (Boott) Gl., var. muhlenbergii (Gray) Gl., and var. elliptica (Boott) Gl. respectively. Although each of the above taxa has been found in Canada, the more southern C. nigromarginata s. str. (C. nigromarginata var. nigromarginata) is reported here for the first time. While C. emmonsii and C. artitecta are very similar and difficult to separate (Voss 1972), C. peckii and C. nigromarginata s. str. appear more sharply distinct. Carex nigromarginata may be distinguished from other similar northeastern North American members of the section Montanae by the following combination of characters: the culms are shorter than the stiff blades and of varying lengths but concentrations of peduncled pistillate spikes at the very base of the plant are lacking; the leaf sheaths are strongly fibrillose with age and the plants are esposite, without elongate stolons; the perigynia are mostly 3-4 mm in length with the body definitely longer than wide and are more or less concealed by dark purplish-margined scales approximately equal to the perigynia in length (Figure 3).

Carex alata Torrey

A single clump of this sedge was found growing on a rotted log in a swampy opening in Acer rubrum (Red Maple) woodland near the south beach, 18.5 km (11.5 miles) from the base of Long Point, 2 August 1980, A. A. Reznicek 6034, P. M. Catling and P. A. Keddy DAO, MICH. It is of interest here that Deam (1940) also noted that "frequently only one or two plants can be found at a station".

Carex alata was reported for Canada (New Brunswick and Manitoba) by Macoun (1888, sub C. strami-

*Carex alata* but his reports are far beyond its presently known range. *Carex alata* is primarily a southern and eastern species but ranges north to Massachusetts (Mackenzie 1931) and inland in glaciated territory in northwestern Pennsylvania (Bright 1930; Jennings 1953), northern Ohio (Braun 1967), northwestern Indiana (Deam 1940) and north well into Michigan (Voss 1972). Vouchers for Macoun’s Canadian reports have not been found and identifications were probably revised and the specimens re-filed. A report from Lambton County (Dodge 1914; repeated by Soper (1949) and Scoggan (1978)) represents a more likely occurrence. However, a search of MICH, MSC, TRT, CAN, NY and DAO disclosed no Dodge voucher, as has been the case with many interesting Dodge records for southwestern Ontario. This species is not reported for Canada by Boivin (1967).

*Carex alata* is one of the more distinctive members of the notoriously difficult section *Ovales*. Apart from *C. hormathodes*, a coastal marsh species occurring in the maritime provinces, *C. alata* is the only Canadian member of the *Ovales* with awn-tipped pistillate scales. The combination of this feature with a relatively short perigynium beak, more or less dense, stiff and erect infructescence, and perigynium body widest above the middle separate this from all other similar species (Figure 4).

**Acknowledgments**

We would like to thank Howard Crum and David Lane for determining our bryophyte collections, and G. B. McKeating and the Canadian Wildlife Service for their extensive and kind help with our field work. W. J. Crins and P. W. Ball kindly examined our specimens of *Carex* section *Montanae*. C. S. Keener provided us with helpful information on the occurrence of
C. nigromarginata in Pennsylvania and examined our specimens of C. nigromarginata. S. R. Kephart checked MSC for Dodge vouchers of C. alata.

Literature Cited


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Production of Young in a Dense Nesting Population of Yellow Warblers, *Dendroica petechia*, in Manitoba

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The reproductive success and productivity of a dense nesting population of Yellow Warblers (*Dendroica petechia*) were studied during the breeding seasons of 1974 through 1976 on the forested dune ridge along the south shore of Lake Manitoba, Manitoba. Spring temperatures influenced clutch commencement. The mean clutch size for all years was 4.5. Five-egg clutches prevailed during the first part of the breeding season; 4-egg clutches were laid (many in re-nests) later. Annual and seasonal variations in clutch size were not significant. Nest success ranged from 40% (1976) to 64% (1974); it was 48% for all years combined. Higher nests were not more successful than low nests. Nest success increased as the breeding season advanced. Five-egg clutches gave rise to the most young. Fewer young were produced per pair on the study area compared to the production of young Yellow Warblers in less dense populations, but more young were produced per unit of habitat. Predation caused most of the failures. About 25% of the active Yellow Warbler nests were parasitized by the Brown-headed Cowbird (*Molothrus ater*). Cowbird parasitism decreased reproductive success.

Key Words: Yellow Warbler *Dendroica petechia*, breeding biology, dense population, clutch size, reproductive success, Manitoba.

The Yellow Warbler (*Dendroica petechia*) nests at unusually high densities in the forested dune ridge that separates Lake Manitoba and the Delta Marsh, Manitoba, as do several other insectivorous passerines (Sealy 1980a; MacKenzie et al. 1982). Studies of the factors that promote high-density nesting by birds in this community have been underway since 1974. As the Yellow Warbler is comparatively easy to study and is the most abundant breeder on the ridge, with up to about 20 pairs nesting per ha, we studied its breeding biology, productivity and population ecology. We addressed several questions regarding the Yellow Warbler, keeping in mind that the food supply for this population and community may not be limiting its numbers (Busby and Sealy 1979; Sealy 1980a; Bermann and Sealy 1982): (1) is clutch size lower as a result of the high nesting density, or higher despite this density? (2) is the higher clutch size in the area related to the food supply, or to the high latitude? and, (3) are more young reared per pair in this dense population? We have attempted to answer these questions in the present paper.

The few published studies of the Yellow Warbler's breeding biology are relatively incomplete (see Goossen 1978, for literature review). Reproductive success generally has been based on small samples (Schrautz 1943; Young 1949; Batts 1961; Kammeraad 1966). Our study reports on 300 nests from a northern population. Our data provide a useful baseline for further studies of the species, here and in other areas.

Study Area and Methods

This study was conducted during the breeding seasons of 1974, 1975 and 1976 on a 3-km portion of the forested dune ridge that runs westward from the Assiniboine River Diversion (see map in Sealy 1980b: 155). The village of Delta (50° 11'N, 98°19'W), Manitoba, is approximately 5 km east of the study area. The woody vegetation has been described by MacKenzie (1982). Major trees include Manitoba Maple (*Acer negundo*), Green Ash (*Fraxinus pennsylvanica*), Peach-leaved Willow (*Salix amygdaloides*) and Eastern Cottonwood (*Populus deltoides*). The major shrubs are Red-berried Elder (*Sambucus pubens*) and Sandbar Willow (*Salix interior*), with some Red Osier Dogwood (*Cornus stolonifera*) and cherry (*Prunus sp.*). The dominant herb was Stinging Nettle (*Urtica dioica*), and the main climbers were Wild Cucumber (*Echinocystis lobata*) and Hops (*Humulus lupulus*).

Temperature and precipitation for May through August 1974-76 were summarized by Goossen (1978: 7). The 1974 breeding season was cool and wet in May, dry in June and normal in July. In 1975, May was wet with normal temperatures, June was normal, and July warm. May 1976 was warm and unusually dry, June was normal except for one cool spell and July was drier than normal.

Nests were checked by Goossen almost daily in 1974 and daily in 1975 and 1976. Nest contents were recorded on each visit.

The duration of the breeding season was based on the dates of clutch initiation (Myres 1955; Seel 1968)
for nests of known age. Exact dates were determined for 81% of the 320 clutches. Approximate dates were obtained by back-dating. One egg was laid each day with nine days between laying of the last egg and hatching of the first nestling, and eight days between the hatching and the fledging of the first young. Robertson's (1973) method of determining nesting synchrony was used to examine annual variation in the timing of breeding. Dates of clutch initiation were used rather than clutch completion since this excludes variation due to clutch size (Caccamise 1976).

Clutch size was determined in nests, found before the last egg had been laid, in which laying occurred on consecutive days and where there was no change in the number of eggs one day after clutch completion. Clutches parasitized by the Brown-headed Cowbird (Molothrus ater) and those in which a lapse of laying occurred were omitted. Reproductive success and mortality factors were determined for nests found before clutch completion.

An active nest is one in which at least one Yellow Warbler egg was laid. A "hatched nest" is one in which at least one Yellow Warbler egg hatched. A successful nest is one in which at least one Yellow Warbler nestling was fledged. Both parasitized and unparasitized nests were used in analysis of reproductive success. Only unparasitized nests were used in examining the relationship between clutch size and nest success. Data from renests and possibly second clutches were analysed together with data from first nests.

Statistical tests used included linear regression, analysis of variance, chi-square and z-test. The level of significance used was $P < 0.05$.

**Results**

**Timing of Breeding**

The breeding season extended from late May or early June until early July (Figure 1). The period in which clutches were initiated varied from 24–42 days (Table 1).

Nesting synchrony was greater and the length of the laying period less in the late spring of 1974, when 50% of the clutches were initiated in 2 days and egg-laying extended over 24 days. Both 1975 and 1976 data reflected more favourable spring conditions with less synchrony within the population and longer laying periods (Table 1). Laying dates of the first egg differed by 14 days between 1974 and 1976, but initiation of the last clutch varied by only 5 days between years.

The beginning of the laying period was earlier in warm springs ($r = -0.99$) (Figure 2). The start of laying in May was positively correlated with rainfall ($r = 0.78$), although this relationship was not statistically significant ($P > 0.95$).

**Clutch size**

One egg was laid per day until the clutch was completed. Occasionally a day was skipped. The mean of 144 completed clutches was 4.5 eggs (Table 2). Annual variation in clutch size was not significant (ANOVA). Clutch size decreased as the breeding season progressed (Table 3), but the difference was not significant (ANOVA). Five-egg clutches were the most common up to 7 June; 4-egg clutches predominated thereafter. Smaller clutch sizes possibly resulted from re-nesting by pairs whose first nests failed. Second broods were rarely attempted (see Goossen 1978).

**Reproductive Success**

Success of active nests found before the last egg was laid varied from 40% in 1976 to 64% in 1974 (Table 4). The overall difference between those active nests found before the last egg was laid and those found after the last egg was only 1.1%. The overall nest success for all active nests thus was 47.9%.

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**Table 2. Clutch size of Yellow Warblers in the dune-ridge forest, Delta Marsh, 1974–76.**

<table>
<thead>
<tr>
<th>Year</th>
<th>3 eggs</th>
<th>4 eggs</th>
<th>5 eggs</th>
<th>Total</th>
<th>Mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1974</td>
<td>1</td>
<td>15</td>
<td>17</td>
<td>33</td>
<td>4.5 ± 0.10</td>
</tr>
<tr>
<td>1975</td>
<td>0</td>
<td>27</td>
<td>25</td>
<td>52</td>
<td>4.5 ± 0.07</td>
</tr>
<tr>
<td>1976</td>
<td>4</td>
<td>25</td>
<td>30</td>
<td>59</td>
<td>4.4 ± 0.08</td>
</tr>
<tr>
<td>Total</td>
<td>5</td>
<td>67</td>
<td>72</td>
<td>144</td>
<td>4.5 ± 0.05</td>
</tr>
</tbody>
</table>

**Table 3. Seasonal variation in clutch size of Yellow Warblers.**

<table>
<thead>
<tr>
<th>Time interval</th>
<th>3 eggs</th>
<th>4 eggs</th>
<th>5 eggs</th>
<th>Mean ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>25 May–7 June</td>
<td>0</td>
<td>19</td>
<td>46</td>
<td>4.7 ± 0.06</td>
</tr>
<tr>
<td>8–21 June</td>
<td>1</td>
<td>38</td>
<td>26</td>
<td>4.4 ± 0.06</td>
</tr>
<tr>
<td>22 June–5 July</td>
<td>4</td>
<td>10</td>
<td>0</td>
<td>3.7 ± 0.13</td>
</tr>
</tbody>
</table>
Figure 1. Clutch initiation by the Yellow Warbler in the dune-ridge forest, Delta Marsh 1974, 1975 and 1976. Arrows indicate mean date of clutch initiation in each year.
Among 974 eggs from 227 active nests, annual hatching success varied little, with a combined success of 56.1% (Table 5). The proportions of eggs laid which gave rise to fledged young varied from 26.7% in 1976 to 41.7% in 1974. The overall fledging success, based on eggs laid, was 34.9%.

Nestling survival from hatching to fledging varied from 47.8% in 1976 to 74.7% in 1974 (Table 5). The overall fledging success from eggs that hatched was 62.3%.

Table 6 illustrates the clutch success in two-weekly intervals for clutches found before the last egg was laid. Clutches were not necessarily complete, since some failed before all eggs had been laid. For the three breeding seasons combined, clutch success increased from 37% during 25 May to 7 June to 56% during 22 June to 5 July, but the difference was not significant ($x^2$).

Three categories of nest height were recognized (Table 7), reflecting the herb, shrub and tree strata,

| Table 4. Yellow Warbler nest success, 1974–76. |
|---|---|---|---|---|
| | 1974 | 1975 | 1976 | Total |
| | No. of active nests | No. of successful nests | % successful | No. of active nests | No. of successful nests | % successful | No. of active nests | No. of successful nests | % successful |
| Nests found before last egg laid | 44 | 28 | 64 | 98 | 47 | 48 | 93 | 37 | 40 | 235 | 112 | 47.7 |
| Nests found after last egg laid | 7 | 3 | 43 | 20 | 9 | 45 | 53 | 27 | 51 | 80 | 39 | 48.8 |
| All active nests | 51 | 31 | 61 | 118 | 56 | 48 | 146 | 64 | 44 | 315 | 151 | 47.9 |

| Table 5. Egg and nestling success of active Yellow Warbler nests found before the last egg was laid, 1974–76. |
|---|---|---|---|---|---|---|---|---|
| | 1974 | 1975 | 1976 | Totals |
| No. of active nests | 36 | 98 | 93 | 227 |
| No. of nests with eggs hatched | 23 | 60 | 65 | 148 |
| No. of successful nests | 20 | 47 | 37 | 104 |
| No. of eggs laid | 156 | 402 | 416 | 974 |
| No. of eggs hatched | 87 | 227 | 232 | 546 |
| Mean number of eggs per active nest | 4.3 | 4.1 | 4.5 | 4.3 |
| Percent of eggs laid that hatched | 55.8 | 56.5 | 55.8 | 56.1 |
| No. of fledglings | 65 | 164 | 111 | 340 |
| Percent of eggs hatched that gave rise to fledged young | 74.7 | 72.2 | 47.8 | 62.3 |
| Percent eggs laid that gave rise to fledged young | 41.7 | 40.8 | 26.7 | 34.9 |
| Mean no. of fledglings per active nest | 1.8 | 1.7 | 1.2 | 1.5 |
| Mean no. of fledglings per successful nest | 3.3 | 3.5 | 3.0 | 3.3 |
Table 6. Success of Yellow Warbler clutches in relation to date of initiation, 1974-76.

<table>
<thead>
<tr>
<th>Year</th>
<th>25 May-7 June</th>
<th>8-21 June</th>
<th>22 June-5 July</th>
</tr>
</thead>
<tbody>
<tr>
<td>1974</td>
<td>0</td>
<td>58% (22/38)</td>
<td>0</td>
</tr>
<tr>
<td>1975</td>
<td>45% (24/53)</td>
<td>46% (15/33)</td>
<td>46% (5/11)</td>
</tr>
<tr>
<td>1976</td>
<td>30% (20/67)</td>
<td>41% (9/22)</td>
<td>71% (5/7)</td>
</tr>
<tr>
<td>1974-76</td>
<td>37% (44/120)</td>
<td>50% (46/93)</td>
<td>56% (10/18)²</td>
</tr>
</tbody>
</table>

¹Sample size.
²Includes one clutch after 5 July, 1975.

respectively. Differences in nest success were not significant ($X^2$).

Table 8 illustrates the relationships between clutch size and nest success for 118 clutches. The number of young fledged per active nest increased with increasing clutch size. No significant differences were found for the parameters examined ($X^2$ or ANOVA) when large clutches (5 eggs) were compared to smaller clutches (3 and 4 eggs).

The overall incidence of cowbird parasitism in active nests was about 25%. Unparasitized nests were more successful in all respects than parasitized nests (Table 9).

Mortality

Of the 227 active (parasitized and unparasitized) nests, 123 (54%) were unsuccessful. Predation accounted for 63% of the nest failures (Table 10), and desertion for 15%. Of the 19 deserted nests, 9 were deserted apparently because of cowbird parasitism. Nest failure attributed directly to the cowbird was 9%. Of 121 active nests, 95% did so after the laying period (Table 11).

The major mortality factor for eggs was predation. Although only 22% of egg mortality was directly attributed to predation, another 28% of the eggs disappeared for no apparent reason (Table 12). Some of the latter may have been preyed upon or taken by cowbirds.

The major mortality factor for nestlings was also predation. Although only 17% of the nestling mortality was directly attributed to predation, another 51% of the nestlings disappeared (Table 13). Some unhatched eggs or dead nestlings may have been thrown out by the adults during hatching. Weather accounted for 7% of the nestling mortality, most during a cold spell in June 1976. Cowbirds accounted for 7% of the nestling mortality.

Predation

Predation was not directly observed at any Yellow Warbler nests. Indirect evidence of predation was seen in nests which were obviously disturbed and others in which young or eggs disappeared with no apparent disturbance to the nest. Of 50 parasitized nests in which the condition of the nest was noted, 34 (68%)...
Table 9. Egg and nestling success for parasitized and unparasitized Yellow Warbler nests found before the last egg was laid, 1974–76.

<table>
<thead>
<tr>
<th></th>
<th>Unparasitized</th>
<th>Parasitized</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of active nests</td>
<td>169</td>
<td>58</td>
</tr>
<tr>
<td>No. of nests with eggs hatched</td>
<td>121</td>
<td>27</td>
</tr>
<tr>
<td>No. of successful nests</td>
<td>90</td>
<td>14</td>
</tr>
<tr>
<td>No. of eggs laid</td>
<td>739</td>
<td>235</td>
</tr>
<tr>
<td>No. of eggs hatched</td>
<td>451</td>
<td>95</td>
</tr>
<tr>
<td>Average no. of eggs per active nest¹</td>
<td>4.4</td>
<td>4.1</td>
</tr>
<tr>
<td>Percent of eggs laid that hatched²</td>
<td>61.0</td>
<td>40.4</td>
</tr>
<tr>
<td>No. of fledglings</td>
<td>301</td>
<td>39</td>
</tr>
<tr>
<td>Percent of eggs hatched that gave rise to fledged young²</td>
<td>66.7</td>
<td>41.1</td>
</tr>
<tr>
<td>Percent of eggs laid that gave rise to fledged young²</td>
<td>40.7</td>
<td>16.6</td>
</tr>
<tr>
<td>Average no. of fledglings per active nest²</td>
<td>1.8</td>
<td>0.7</td>
</tr>
<tr>
<td>Average no. of fledglings per nest with eggs hatched²</td>
<td>2.5</td>
<td>1.4</td>
</tr>
<tr>
<td>Average no. of fledglings per successful nest¹</td>
<td>3.3</td>
<td>2.8</td>
</tr>
</tbody>
</table>

¹Differences not significant (P > 0.05).
²Differences significant (P < 0.05).

Table 10. Causes of nest failure in active Yellow Warbler nests found before the last egg was laid, 1974–76.

<table>
<thead>
<tr>
<th>Causes of Failure</th>
<th>No. of nests that failed</th>
<th>Parasitized</th>
<th>Unparasitized</th>
<th>Total</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predation</td>
<td>15</td>
<td>62</td>
<td>77</td>
<td>63</td>
<td></td>
</tr>
<tr>
<td>Desertion of eggs</td>
<td>13</td>
<td>6</td>
<td>19</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Cowbird</td>
<td>10</td>
<td>1</td>
<td>11</td>
<td>9</td>
<td></td>
</tr>
<tr>
<td>Weather</td>
<td>1</td>
<td>6</td>
<td>7</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Human disturbance</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Nest position</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Poor nest</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Starvation of</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Young</td>
<td>3</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>44</td>
<td>79</td>
<td>123</td>
<td>101</td>
<td></td>
</tr>
</tbody>
</table>

Table 11. Frequency of Yellow Warbler nesting failures in various stages of nesting cycle.

<table>
<thead>
<tr>
<th>Nesting Stage</th>
<th>No. of nests that failed</th>
<th>Parasitized</th>
<th>Unparasitized</th>
<th>Total</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Laying</td>
<td>12</td>
<td>16</td>
<td>28</td>
<td>23</td>
<td></td>
</tr>
<tr>
<td>Incubation</td>
<td>18</td>
<td>31</td>
<td>49</td>
<td>41</td>
<td></td>
</tr>
<tr>
<td>Nestling</td>
<td>13</td>
<td>31</td>
<td>44</td>
<td>36</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>43</td>
<td>78</td>
<td>121</td>
<td>100</td>
<td></td>
</tr>
</tbody>
</table>

Table 12. Factors contributing to egg mortality in active Yellow Warbler nests found before the last egg was laid.

<table>
<thead>
<tr>
<th>Causes of Failure</th>
<th>No. of eggs lost in nests</th>
<th>Unparasitized</th>
<th>Parasitized</th>
<th>Total</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disappeared</td>
<td>104</td>
<td>16</td>
<td>120</td>
<td>28</td>
<td></td>
</tr>
<tr>
<td>Predation</td>
<td>66</td>
<td>26</td>
<td>92</td>
<td>22</td>
<td></td>
</tr>
<tr>
<td>Deserted</td>
<td>33</td>
<td>32</td>
<td>65</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Unhatched</td>
<td>38</td>
<td>10</td>
<td>48</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>Cowbird</td>
<td>2</td>
<td>31</td>
<td>33</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Weather</td>
<td>19</td>
<td>2</td>
<td>21</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Human disturbance</td>
<td>12</td>
<td>2</td>
<td>14</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>On ground</td>
<td>8</td>
<td>5</td>
<td>13</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Buried</td>
<td>0</td>
<td>13</td>
<td>13</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Poor nest</td>
<td>5</td>
<td>0</td>
<td>5</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Construction</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>&lt;0.5</td>
<td></td>
</tr>
<tr>
<td>Nest position</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>&lt;0.5</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>288</td>
<td>140</td>
<td>428</td>
<td>100</td>
<td></td>
</tr>
</tbody>
</table>
Table 13. Factors contributing to nestling mortality in active Yellow Warbler nests found before the last egg was laid.

<table>
<thead>
<tr>
<th>Causes of Failure</th>
<th>Unparasitized</th>
<th>Parasitized</th>
<th>Total</th>
<th>Percent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Disappeared</td>
<td>79</td>
<td>25</td>
<td>104</td>
<td>51</td>
</tr>
<tr>
<td>Predation</td>
<td>34</td>
<td>2</td>
<td>36</td>
<td>17</td>
</tr>
<tr>
<td>Weather</td>
<td>14</td>
<td>1</td>
<td>15</td>
<td>7</td>
</tr>
<tr>
<td>Cowbird</td>
<td>0</td>
<td>14</td>
<td>14</td>
<td>7</td>
</tr>
<tr>
<td>On ground</td>
<td>7</td>
<td>2</td>
<td>9</td>
<td>4</td>
</tr>
<tr>
<td>Human disturbance</td>
<td>6</td>
<td>2</td>
<td>8</td>
<td>4</td>
</tr>
<tr>
<td>Dead in nest</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>Starvation</td>
<td>5</td>
<td>0</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Nest position</td>
<td>2</td>
<td>3</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>Deserted</td>
<td>0</td>
<td>3</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Caught in nest</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0.5</td>
</tr>
<tr>
<td>Total</td>
<td>150</td>
<td>56</td>
<td>206</td>
<td>100.0</td>
</tr>
</tbody>
</table>

had no apparent nest disturbance. J.L. Morgan and S.G. Sealy (unpublished data) have noted that nest predation by Red Squirrels (*Tamiasciurus hudsonicus*) on the study area is accomplished with no nest disturbance.

Discussion

The results of our study of Yellow Warbler breeding biology can be summarized as follows: (1) the mean clutch sizes on and off our study area at northern latitudes were higher than elsewhere, (2) clutch size varied within but not among the years, (3) the greatest number of young fledged from the largest and most frequent clutch (5 eggs), (4) nest success (48%) was near the mean in open-nesting altricial species (49%), as studied by Nice (1957), (5) fledging success of nestlings was lower than that in other studies of the Yellow Warbler, but nevertheless more young were fledged per unit area of habitat because of the high nesting density in the dune-ridge forest, and (6) predation was the major cause of nest failures. These findings are discussed in the two subsections that follow.

Clutch size

Natural selection for clutch size in birds has been studied more intensively than almost any other aspect of a species' ecology, but shaping of clutch size is complex and still not well understood. Klop (1970) broadly reviewed clutch-size determination in birds and noted that mean clutch size has been reported to vary with food supply, habitat, population density, age of breeders, egg-laying dates during the season, latitude, longitude, heredity, and other factors. Lack (1954) contended that clutch size and ultimately breeding densities are controlled by density-related food conditions (see also Gibb 1960; Yom-Tov 1974). Lack argued that mean clutch size in birds has been adjusted by natural selection to produce the maximum size of brood that the parents can nourish.

In order to determine whether the higher clutch size of the Yellow Warbler on our study area reflected merely the higher latitude or was a response to abundant food, we examined the literature for clutch size data from other populations (Table 14). Generally, clutch size increased with increasing latitude, although the mean of 4.2 eggs from Kansas was an exception. The mean size of 23 completed clutches from Alberta and Manitoba (outside our study area) was 4.4 eggs (4 of 3 eggs, 7 of 4, 12 of 5). Thus the clutch size of the dune-ridge population of Yellow Warblers was no larger than that found elsewhere at comparable latitudes.

We also looked at the causes of variation in clutch size. In all of these studies, including the Canadian prairie data, clutches ranged from 3 to 5 eggs. The numbers of females that do not nest, i.e., whose clutch sizes are 0, were generally not known. Such information is crucial to determining realistically the mean clutch and its variation in a population. Since we found brood patches on all of the hundreds of females handled for banding during the breeding seasons of 1974 to 1981, we believe that all females in our study area do breed. Lack (1966) argued that clutch size is

Table 14. Clutch size of the Yellow Warbler in relation to breeding density and latitude.

<table>
<thead>
<tr>
<th>Location</th>
<th>Latitude</th>
<th>Density (prs/ha)</th>
<th>Mean Clutch size</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manitoba</td>
<td>50°</td>
<td>19.1</td>
<td>4.5</td>
<td>This study</td>
</tr>
<tr>
<td>Alberta,</td>
<td>49°-55°</td>
<td>—</td>
<td>4.4</td>
<td>PNRS¹</td>
</tr>
<tr>
<td>Manitoba</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>North Dakota</td>
<td>46°-49°</td>
<td>—</td>
<td>3.6</td>
<td>Stewart (1975)</td>
</tr>
<tr>
<td>Iowa</td>
<td>43°</td>
<td>—</td>
<td>4.0</td>
<td>Schrantz (1943)</td>
</tr>
<tr>
<td>Michigan</td>
<td>43°</td>
<td>2.1²</td>
<td>2.9</td>
<td>McGee (1972)</td>
</tr>
<tr>
<td>Wisconsin</td>
<td>43°</td>
<td>3.5</td>
<td>3.5</td>
<td>Young (1949)</td>
</tr>
<tr>
<td>Michigan</td>
<td>42°</td>
<td>0.2</td>
<td>3.8</td>
<td>Batts (1961)</td>
</tr>
<tr>
<td>Utah</td>
<td>42°</td>
<td>5.5-8.2²</td>
<td>3.9</td>
<td>Frydendall (1967)</td>
</tr>
<tr>
<td>Kansas</td>
<td>37-40°</td>
<td>—</td>
<td>4.2</td>
<td>Johnston (1964)</td>
</tr>
</tbody>
</table>

¹Calculated using 23 complete clutches in the Prairie Nest Records Scheme (Manitoba Museum of Man and Nature).
²Calculated by Busby (1978).
adapted seasonally to match the efforts the parents
must make to obtain food, and Klomp (1970), among
others, stressed the role of the physiological condition
of the female. Hussell (1972) speculated that seasonal
changes in clutch size are related to the probability of
adult survival. Our data revealed no significant differ-
ences in mean clutch sizes among the years of our
study (Table 2), and this trend has continued through
1981 (Sealy, unpublished data). The differences we
found within each season can be explained by any one
of the above arguments, but we lack critical support-
ing evidence. It seems unlikely, however, that food
quantity (Busby and Sealy 1979) and quality (Bier-
mann and Sealy 1982) in the dune-ridge forest
changed markedly as the seasons progressed. Nolan
(1978) concluded from his analysis of clutch size in the
multi-brooded Prairie Warbler (D. discolor), that
advancing date was associated with reduction in mean
clutch size, but probably without respect to the extent
of the female's previous reproductive efforts. Nolan
(1978) found also that larger clutches tended to occur
in years when the early part of the egg-laying period
was warm. Clutch size in our study showed no such
relationship (Figure 2, Table 2); the proportion of
5-egg clutches was about 50% each year, even in the
cold spring of 1974 (Figure 2). According to Lack's
(1954) hypothesis, the most frequent clutch size
should be the most productive (see Murray 1979). The
various studies reviewed by Klomp (1970), however,
have produced mixed results. We found in our study
that the most frequent and largest clutches (5 eggs)
produced the most fledglings (see also Biermann and
Sealy 1982). Our results, in fact, are not in keeping
with several recent studies (Charnov and Krebs 1974;
Perrins and Moss 1974; Middleton 1979). In those
studies, and others on passerines (Crawford 1977;
Brown 1978; Smith 1981), it was shown that young
birds (= 1st year) were less efficient than older birds in
rearing young from the fewer eggs that they laid.
Biermann and Sealy (1982) found on our study area
that Yellow Warblers fed young in broods of four
more food by weight than broods of five and three, but
each load brought to young in broods of five was more
nutritious. Breeding performances by female Yellow
Warblers of different ages are currently being studied
by Sealy; data are also needed on the variation in
quality of individual territories.

Second broods are rarely attempted by Yellow
Warblers on our study area (Goossen 1978), or else-
where in its range. This is in contrast to Prairie
Warblers in Indiana which lay, on average, 11 eggs in
three clutches each year (Nolan 1978). The clutch size
in the Prairie Warbler is smaller but the annual pro-
duction is greater, compared to the Yellow Warbler.
Williams (1966) and Tinkle (1969) considered that
laying several clutches per season was a greater repro-
ductive effort than laying a single clutch. Spencer and
Steinhoff (1968), on the other hand, assumed the
reverse. Murray (1979) believed that whether females
lay a single clutch or several clutches per season will
depend on the advantage each alternative has in par-
ticular environmental conditions. The probabilities of
survival and reproduction by individual Yellow
Warblers, crucial in such a discussion, are being gen-
erated on our study area.

Clutch sizes of other dense nesting passerines on
our study area also are large compared to those
determined elsewhere (Sealy, unpublished data). The
mean clutch size of Northern Orioles (Icterus galbula)
increased when the food supply, usually chironomids,
was enhanced during an outbreak in 1976 and 1977 of
the forest tent caterpillar (Malacosoma disstria). Also
the nesting density of these orioles doubled in 1977
(Sealy 1980a; unpublished data). Increased clutch size
associated with locally abundant food resources has
been reported also in some parulids (MacArthur 1958;
Zach and Falls 1975; Sealy 1979). However, Yellow
Warblers did not respond to the presence of tent
caterpillars on our study area in 1976 or 1977 by
increasing their clutch sizes or population density
(Sealy, unpublished data).

Clutch size in passerines may vary inversely with
breeding density (Perrins 1965; Klomp 1970; Krebs
1970). Perrins (1965) found that when the Great Tit
(Parus major) population doubled in size, the mean
clutch size was reduced by 2.02 eggs. In all, 69% of the
variation in clutch size was accounted for by the
effects of laying date and density. Perrins suggested
that laying fewer eggs at a higher density had been
selected as a result of individual birds producing,
under these circumstances, more surviving young
from small than from large clutches. In the Yellow
Warbler (Table 14), the trend (between areas) was for
clutch size to be directly related to breeding density.
Clearly, more work needs to be done on this aspect.
However, variation in food supply at the various
study sites, and latitude (Lack 1954), may also influ-
ence the sizes of clutches laid.

Reproductive success

Nest success of the Yellow Warbler ranged from
42% to 75% (Table 15); the success of nests in our
study (48%) fell within that range. Nest success in
open-nesting altricial birds ranged from 38% to 77%
with a mean of 49% (Nice 1957). Those figures must be
used with caution since the procedures were not out-
lined in 17 of 35 studies, and some may have included
nests found after clutch completion which would bias
them toward success (Woolfenden and Rohwer 1969).
Several studies of parulids have attempted to reduce
Table 15. Reproductive success of the Yellow Warbler.

<table>
<thead>
<tr>
<th>No. of nests</th>
<th>Nest success</th>
<th>Hatchings success (%)</th>
<th>Fledging success (%) (eggs)</th>
<th>Fledging success (%) (nestlings)</th>
<th>Productivity¹</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>41</td>
<td>—</td>
<td>71</td>
<td>54</td>
<td>76</td>
<td>2.2</td>
<td>Schrantz (1943)</td>
</tr>
<tr>
<td>12</td>
<td>42</td>
<td>48</td>
<td>33</td>
<td>70</td>
<td>1.2</td>
<td>Young (1949)</td>
</tr>
<tr>
<td>16</td>
<td>75</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>Kendeigh (1941)</td>
</tr>
<tr>
<td>20</td>
<td>45</td>
<td>57</td>
<td>39</td>
<td>67</td>
<td>1.5</td>
<td>Batts (1961)</td>
</tr>
<tr>
<td>15</td>
<td>—</td>
<td>84</td>
<td>38</td>
<td>—</td>
<td>—</td>
<td>Salt (1973)</td>
</tr>
<tr>
<td>262</td>
<td>69</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>McGeen (1972)</td>
</tr>
<tr>
<td>227</td>
<td>48</td>
<td>56</td>
<td>35</td>
<td>62</td>
<td>1.5</td>
<td>Kendeigh (1942)</td>
</tr>
</tbody>
</table>

¹Young fledged per nest.

Table 16. Yellow Warbler nesting densities and productivity in the Delta Beach Ridge Study area.

<table>
<thead>
<tr>
<th>Year</th>
<th>Total nests</th>
<th>Nesting density¹ (pairs/ha)</th>
<th>Productivity/ha²</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>138</td>
<td>14.4</td>
<td>21.6</td>
</tr>
<tr>
<td>1981</td>
<td>128</td>
<td>12.9</td>
<td>19.4</td>
</tr>
</tbody>
</table>

¹Nesting densities were determined by Sealy (unpublished data) during an on-going study of the dynamics of breeding in the passerine community on the forested dune ridge.
²Productivity = number of young fledged per nest = 1.5 young per nest (see Table 15). Second broods are rarely attempted (see Goossen 1978).
ple, was possibly affected by the Blackburnian Warbler (*D. fuscus*) which appeared to depress the number of the former species where they coexisted. Hence, territoriality and interspecific dominance by the Least Flycatcher may be involved in limiting the density of Yellow Warblers nesting in the dune-ridge forest. Yellow Warblers might nest even more densely on the study area if Least Flycatchers were not present.

Our studies to date indicate that food availability and abundance *per se* may not be limiting population sizes on the forested dune-ridge (but see Sealy 1980a). Food accessibility and quality, however, may vary over the habitat and this is currently being studied. The availability and distribution of nesting habitat on the study area that is selected by each species appears to be playing the major role in this regard.

**Acknowledgments**

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**Literature Cited**


Myres, M. T. 1955. The breeding of Blackbird, Song


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Notes

Nursing and Associated Behavior of Peary Caribou, *Rangifer tarandus pearyi*

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We saw 44 nursing events by Peary Caribou (*Rangifer tarandus pearyi*) cow-calf pairs between 23 June and 14 August on northeastern Prince of Wales Island, NWT. Calves initiated 88.6% and terminated 6.8% of the nursing events. Reverse parallel nursing from the side was the position taken up by all cow/calf pairs. Durations of bouts of nursing averaged 38.6 ± 21.51 (SD) seconds and ranged from 15 to 120 seconds. Attention getting behavior was exhibited 56.8% of the time by calves without prior care from their dams. Care was offered 13.6% of the time by dams without calves first beginning to suckle.

Key Words: Peary Caribou, *Rangifer tarandus pearyi*, nursing, behavior, Prince of Wales Island, Northwest Territories.

During the first months of life, a Caribou calf physically depends on its dam for sustenance, direction and protection and is psychologically dependent on her for social acceptance and a general state of well-being. Those dependencies are culminated in the formation of a strong mother-young bond which is likely focused on the act of nursing and its associated care behavior by the cow and care-soliciting or attention getting behavior by the calf. We report our limited results as there has been no documentation of nursing behavior of Peary Caribou.

**Study Area and Methods**

Observations of Peary Caribou groups by ground observers was on northeastern Prince of Wales Island, NWT. The terrain is broken by successive marine beach ridges descending from high ground to sea level. Those beach ridge formations both aid and hinder ground observers: the relief often provides prominences from which the Caribou can be watched, but at the same time, it causes ‘blind spots’ into and from which Caribou can disappear and reappear during observations.

We flew in a Bell 206B helicopter at 200-400 m above ground level to locate Caribou groups (see Miller and Gunn 1979 for details). On spotting a group in a suitable location, we turned away and landed out of sight of the group 0.4 to 1.6 km away, depending on cover afforded by surrounding terrain. Two observers walked to a prominence and used 15-60X zoom spotting scopes and 10 × 40 binoculars to observe the Caribou. Nursing and associated behavior was described on magnetic tape and subsequently transcribed onto observation forms.

**Results and Discussion**

On northeastern Prince of Wales Island between 23 June and 14 August 1977 we observed groups of Peary Caribou with calves on 22 occasions for 35 hours and 1 minute. On 11 of those occasions, we saw 44 nursings among 58 cow-calf pairs. We observed nursings during 11 observations of 28 to 333 minutes in duration and we did not see nursing take place during 11 observational periods of 6 to 125 minutes (mean ± standard deviation equals 155 ± 116.90 minutes and 36 ± 36.03 minutes respectively). Groups of caribou were of similar mean size and range during the early (X = 14.8, range = 8-25) and mid-summer (X = 14.8, range = 10-24) periods of observation and of markedly smaller (X = 8.5) mean size and less range (8-9) during the late summer period. Calves present in each group averaged 5.3 ± 2.90 (SD) calves and ranged from 3 to 12 (X = 5.5, range = 3-9) in early summer; X = 6.0, range = 3-12 in mid-summer, and X = 3, range = 3-3 in late summer).

Our observations were clumped in three time periods during the summer. Therefore, we presented our findings by those three observational periods (Table 1).

The peak of calving for Peary Caribou on northeastern Prince of Wales Island appears to be in the third week of June, based on our observations during June 1976-80. If we assume an average birth date of 18
Table 1—Summary of observations of nursing by Peary caribou cow/calf pairs, Prince of Wales Island, NWT, 1977

<table>
<thead>
<tr>
<th>Variable</th>
<th>Early summer</th>
<th>Mid-summer</th>
<th>Late summer</th>
</tr>
</thead>
<tbody>
<tr>
<td>Date (day/month)</td>
<td>23/6-2/7</td>
<td>12/7-18/7</td>
<td>7/8-14/8</td>
</tr>
<tr>
<td>Observational time (min)</td>
<td>271</td>
<td>972</td>
<td>462</td>
</tr>
<tr>
<td>Number of cow/calf pairs</td>
<td>22</td>
<td>30</td>
<td>6</td>
</tr>
<tr>
<td>Cow/calf pair time (min)</td>
<td>1133</td>
<td>6915</td>
<td>1386</td>
</tr>
<tr>
<td>Number of nursings</td>
<td>11</td>
<td>27</td>
<td>6</td>
</tr>
<tr>
<td>Observed/expected ratios</td>
<td>2.08</td>
<td>0.84</td>
<td>0.93</td>
</tr>
<tr>
<td>Initiator of nursing bout</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cow</td>
<td>1</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Calf</td>
<td>10</td>
<td>24</td>
<td>5</td>
</tr>
<tr>
<td>Terminator of nursing bout</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cow</td>
<td>11</td>
<td>25</td>
<td>5</td>
</tr>
<tr>
<td>Calf</td>
<td></td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Calf’s nursing position</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Left side</td>
<td>6</td>
<td>12</td>
<td>1</td>
</tr>
<tr>
<td>Right side</td>
<td>3</td>
<td>15</td>
<td>5</td>
</tr>
<tr>
<td>Duration of nursing bouts (sec)</td>
<td>40.6</td>
<td>41.4</td>
<td>23.3</td>
</tr>
<tr>
<td>Mean</td>
<td>26.54</td>
<td>21.47</td>
<td>6.06</td>
</tr>
<tr>
<td>Standard deviation</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

June ± 3 days, we can suggest that the calves we observed during early summer were 2-17 days old; those seen in mid-summer were 21-33 days old; and those seen in late summer were 47-60 days old. Thus, to evaluate the relative observed rates of nursing, we calculated cow/calf pair time for the three observational periods (Table 1). Total cow/calf pair time was obtained by multiplying the number of cow/calf pairs in an observation by the length of that observation and summing those values for all observations within each observational period. A one-way Chi-square test was done on the number of nursings against cow/calf pair time for each observational period. A significant difference (P < 0.05) was found between the proportional rates of nursing during the three observational periods. The observed/expected ratios obtained from the analysis (Table 1) indicate that observed nursing was relatively greater than expected in early summer and less than expected in mid- and late summer.

In total 88.6% (39) of the nursing events were initiated by calves and 93.2% (41) were terminated by cows. Calves initiated and cows terminated 86.4% (38) of the bouts of nursing; cows initiated and terminated 6.8% (3) of the bouts; cows initiated and calves terminated 4.5% (2) of the bouts; and a calf initiated and terminated 2.3% (1) of the bouts.

Reverse parallel nursing from the side was the position taken up by all cow/calf pairs. Reverse parallel nursing from the right side was slightly more common, 52.3% (23); than from the left side 43.2% (19). Two of the first nursings observed were recorded as being from the side, but which side was not differentiated.

Durations of bouts of nursing averaged 38.6 ± 21.51 (SD) seconds and ranged from 15 to 120 seconds. Bouts of nursing were of similar mean durations during early summer (X = 40.6 seconds) and mid-summer (X = 41.4 seconds) and relatively short on the average in late summer (X = 23.6 seconds).

Care-seeking or attention getting behavior associated with nursing was exhibited 56.8% (25) of the time by calves without any immediately prior care from their dams. Care was offered 13.6% (6) of the time by dams without calves first beginning to suckle. Calves solicited care from their dams on 24.0% of the occasions by nuzzling their dams; on 20.0% of the occasions by attempting to nurse; on 20.0% of the occasions by rubbing against their dams; on 16.0% of the occasions by sniffing their dams; on 12.0% of the occasions by nudging their dams; and on 8.0% of the occasions by licking their dams. All (six occasions) unsolicited care by maternal cows consisted of licking. Care-giving behavior during the nursing events consisted of mixtures of licking, sniffing, nudging, nuzzling and rubbing. Nibbling probably occurred but was not discerned.

Our finding that calves initiated most of the nursing events is in agreement with the general observation that ‘follower type’ ungulate infants, of which the Caribou is one, are likely to initiate nursing events (Lent 1974). Our finding that the reverse parallel position was always used by Peary Caribou cow/calf pairs during bouts of nursing is in general agreement with the commonness of the use of this position by ungulate infants (Lent 1974). Lent (1966), however, found that nursing from the rear was also common in
Alaskan Caribou (*R. t. granti*). We probably would have seen nursing from the rear by Peary Caribou calves, if we had obtained more observations. Our observations (unpublished data) of nursing from the rear by Canadian Barren-ground Caribou (*R. t. groenlandicus*) calves in June 1981 suggests that the position is used most often after initial attempts to nurse when the maternal cow had walked away or was walking away from her calf. Thus, nursing from the rear is most likely a position used by persistent or opportunistic calves: the survival value of which, if any, is unknown.

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**Literature Cited**


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**Response by American Goldfinches, *Carduelis tristis*, to a Severe Winter Storm**

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During the severe storm of 26 January 1978, American Goldfinches were captured and weighed at a feeding station in Guelph, Ontario. Body weight increased significantly before and during the storm period, suggesting the birds responded to the storm by fat deposition. Accompanying behavioural observations support this conclusion.

Key Words: American Goldfinch *Carduelis tristis*; winter storm; body weight; behaviour.

Inclement weather is known to affect bird populations detrimentally (Lack 1966). This may result from changes in food availability (Zumeta and Holmes 1978), restricted foraging opportunities (Bovino and Burtt 1979), or the direct impact of severe conditions (Stewart 1978; Williams 1979). Although the after-effects of storms on specific populations have been recorded (Kinsky 1968; Stewart 1978), few studies have monitored populations immediately before, during, and after storms (O’Neill and Parker 1978).

Because the occurrence of storms is unpredictable, the ability to collect information on the response by birds to them is severely restricted. As a result, such studies cannot be planned. The researcher must act opportunistically to collect data that are otherwise difficult to obtain. The resultant data are often less than ideal, and are frequently impossible to interpret by strict analytical methods.

On 26 January 1978, a severe winter storm that set record low barometric pressure for the date in several localities, accompanied by heavy rain, snow and winds, swept into southern Ontario (Anonymous 1978). The meteorological data recorded at Guelph for the 24 h period of noon 26 January — noon 27 January were: minimum barometric pressure 963.8 mb; total precipitation, 15.2 mm rain and 24.6 cm snow; mean wind speed 48.7 km/h/ maximum and minimum temperatures of 5.7° and -13.2°C respectively (data courtesy of Department of Land Resource Science, University of Guelph). During this storm an effort was made to trap and weigh American Goldfinches *Carduelis tristis*. Additionally, observations on feeding activity during the storm were made in the hope that the combined data might provide information on the direct response of the birds to the extreme weather conditions. As a result of regular
banding operations, birds were accustomed to feeding from Potter traps, baited with unshelled Sunflower *Helianthus annuus* chips and placed on a table elevated 1.5 m above the ground, while nearby was a roofed feeding table that was kept supplied with sunflower chips. This method of winter feeding by Goldfinches is now commonplace in southwestern Ontario (Middleton 1977) and must be accepted as normal behaviour.

Following trapping, each bird was sexed, aged (Middleton 1974), weighed to the nearest 0.5 g (Pesola 30 g scale), banded, and released. As Goldfinches exhibit both daily and seasonal changes in body weight (Wiseman 1975; Middleton 1977; Carey et al. 1978), any comparison of weight should ideally take both into account. However, because the timing and duration of the storm and the behaviour of the birds were beyond control, sample sizes were small and did not lend themselves to critical analysis by age group, time of day and season. As a compromise, weight comparisons were restricted to the storm period and those weights measured in the three days of banding before and after (see Table 1).

The storm of 26 January 1978 struck with intensity just before 1200, and abated during the following morning. Although the traps were operated from 0800, the first Goldfinch was not trapped until 1005 and the majority (18/24) were trapped between 1115 and 1140. From 1200 until dusk (1630), a few Goldfinches made attempts to land on the traps and feeding table, but because of the strong winds and blowing snow were unable to do so. Any feeding activity was thus restricted to gleaning spilled seed beneath the tables. Traps were set at 0730 on 27 January and were operated throughout the day. Compared to the previous day, feeding activity was less frantic, although the second heaviest male ever encountered (19.5 g) was trapped, and the previous high for a female (18.5 g) was matched. Birds of both sexes trapped during the storm period (26 and 27 January combined) were significantly heavier (ANOVA P < 0.005; $\bar{X}_M = 19.93; \bar{X}_F = 8.18$) than their counterparts trapped in the three sessions before (16-23 January) and after (30 January-6 February) the storm (Table 1).

A similar set of observations was recorded during a second, though less severe storm (Anonymous 1979) between 5 and 6 April 1979. Because sample sizes during the storm were unavoidably small ($N = 8$), the data are not presented here, but a trend to increased weight during the storm was apparent.

There are several possible ways in which Goldfinches may have responded to storm conditions. First, the frenzied feeding that preceded the storm suggested that the birds were aware of the impending storm before the direct effects were obvious to humans. Possibly one stimulus for increased feeding activity was rapidly falling barometric pressure. Migrant birds are known to respond to changes in barometric pressure (Emlen 1975, p. 186) among other environmental stimuli (Schmidt-Koenig 1979). Many species may be able to use barometric pressure accompanied by changes in wind speed and chill factor as indicators of approaching weather changes. Second, the heavier body weights encountered during the storm period suggested that the birds responded to the impending adverse conditions by rapidly increasing their body reserves, while at the same time maintaining a full gut for as long as possible. The record high weights of individual birds supported this suggestion, while showing that under extreme conditions overnight fattening may approach that of migrant species, even though King (1974, p. 20) suggested that this is uncommon. The high individual weights recorded during and following the storm may also suggest that heavy birds are in better condition to cope with the extreme conditions and may in turn have a greater likelihood of survival. However, no carcasses were found during the storm, and this suggestion could not be verified.

The importance of body reserves for overnight winter survival has been established for several species (Brooks 1968; Kendeigh et al. 1969; King 1974; Newton 1969, 1974; Biebach 1977) and is implied for the American Goldfinch (Carey et al. 1978). Newton (1974, p. 244) found that Bullfinches *Pyrrhula pyrrhula* were heavier in cold than in mild winters and in the extreme British winter of 1962-63 had the highest weights of all. Finally, Newton (1974) suggested that there is an appropriate body weight for survival at

**Table 1**—Body weights (Mean ± S.D.) of American Goldfinches recorded before, during and after a severe winter storm at Guelph, Ontario, 1978.

<table>
<thead>
<tr>
<th>Date</th>
<th>N</th>
<th>Male Weight (g)</th>
<th>Female Weight (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>16 Jan</td>
<td>10</td>
<td>16.0</td>
<td>4</td>
</tr>
<tr>
<td>19 Jan</td>
<td>23</td>
<td>15.6</td>
<td>10</td>
</tr>
<tr>
<td>23 Jan</td>
<td>1</td>
<td>14.0</td>
<td>-</td>
</tr>
<tr>
<td>26 Jan*</td>
<td>18</td>
<td>17.6</td>
<td>6</td>
</tr>
<tr>
<td>27 Jan*</td>
<td>35</td>
<td>17.0</td>
<td>22</td>
</tr>
<tr>
<td>30 Jan</td>
<td>17</td>
<td>16.4</td>
<td>4</td>
</tr>
<tr>
<td>2 Feb</td>
<td>21</td>
<td>16.1</td>
<td>10</td>
</tr>
<tr>
<td>6 Feb</td>
<td>14</td>
<td>16.3</td>
<td>3</td>
</tr>
</tbody>
</table>

*Indicates storm period.
specific temperatures. Thus, the strategies reported here for the American Goldfinch under storm conditions fit with observed cardueline patterns (Brooks 1968; Newton 1974).

Finally, previously banded birds were recaptured after the storm at rates similar to those found in other years, and no evidence of decrease in local numbers was obtained. Although winter storms may have a detrimental effect on some avian populations, it appears that resident winter populations of at least one native passerine have inbuilt mechanisms that permit them to respond quickly to impending storm conditions and thereby enhance their likelihood of survival.

Acknowledgments
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Literature Cited

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A Screech Owl, *Otus asio*, was observed to take advantage of the conspicuous and predictable behaviour of Little Brown Bats, *Myotis lucifugus*, returning to their roosting colony in attempting to capture the bats as prey. Although no conclusive proof of prey capture was obtained, the owl's activity apparently caused a temporary decline in the size of the bat colony.

Key Words: Screech Owl, *Otus asio*; predation; Little Brown Bat, *Myotis lucifugus*, nursery colony.

In June 1980, we observed the predatory behaviour of a Screech Owl (*Otus asio*) at a nursery colony of Little Brown Bats (*Myotis lucifugus*). The colony consisted of a maximum of 695 bats, mainly pregnant females, inhabiting the attic of an old farm house near Westport, Ontario. Bats entered and exited the colony at both ends of the building through gaps in the woodwork at the peak of the roof. Bats began to arrive from their winter hibernation sites at the end of April, and the owl was first observed on 4 June. It was subsequently seen on all four nights that observations were made past 2300. Although the bird was unmarked, we believe all observations were of the same individual due to its consistent behaviour.

Observations were made primarily by backlighting the animals against the sky and occasionally with the aid of a Zoomar night vision scope or the edge of a flashlight beam. The owl arrived at the colony each night between 2300 and 2400 when the bats were returning to the colony from their first feeding period to digest their food or nurse their young. The bats made short circling flights to approach the peak of the roof as they attempted to land and enter. Each individual made up to 20 attempts before managing to gain a foothold and crawl inside and there was thus a conspicuous, continual swarm of bats at each end of the house. The owl took advantage of this behaviour.

The owl used three perches from which to attempt to capture bats: a window ledge 2 m directly below each peak, and the dead branches of a maple tree 1.2 m from the rear peak. The owl sat on a perch and watched the bats for up to 5 min. It then flew to the peak and tried to capture a bat, often reaching with its feet into one of the cracks through which a bat had just crawled. The owl then either returned to its original perch or to a perch on the opposite side of the house, having obviously failed to catch a bat, or flew southward away from the house and was lost from view. On the latter occasions, it did not return for 15 to 53 min and we speculate that it had been successful in capturing prey. If so, it was successful in 5 of the 12 attempts we observed (42%).

We made a thorough search of the area to the south of the farmhouse within 1 km. Tree holes were plentiful and although we found some feathers in two large holes and some feces under one perch, we found no regurgitated pellets, food scraps or food caches (Phelan 1977). Thus, we found no incontrovertible evidence that the owl was successfully preying on the bats.

The owl's activities did seem to have an effect on the number of bats using the colony. The colony size had increased to 695 bats (counted as they emerged at dusk) by 4 June, the first night the owl was observed. By 14 June the colony had declined to 450 bats and by 16 June to only 351. On 16 June we captured the owl and released it in a conservation area 60 km away in order to reduce interference with our bat studies. After the owl was moved, the number of bats increased to 422 by 18 June and remained stable at that level until the juveniles began to fly (end of June).

Observations at two other colonies, and at the same site in previous years, revealed no similar decline in numbers. Thus, even if the owl was not successful in capturing bats, its activity appeared to cause some individuals to move to other roost sites.

Predation on bats, especially in temperate regions, appears to be opportunistic (Gillette and Kimbrough 1970) and although many species of owl eat bats, they usually constitute only a small proportion of an owl's diet (e.g. Fisher 1893; Ruprecht 1979). Ruprecht (1979) noted that the frequency of bats in owl pellets
reflected the degree of contact likely between the two, and suggested that shared occupancy of a building may be an important factor. Our observations indicate that of equal importance may be the high concentrations, predictable behaviour and conspicuousness of bats that roost in large groups in buildings (or natural sites). In the tropics, the conspicuousness and predictability of bats feeding at fruit trees allows some owls to adopt an ambush predatory strategy (Morison 1980) similar to that reported here. Although bats may also be taken while away from colonies, this is likely less common and due mainly to chance encounters between predator and prey. At colony sites and regular feeding areas a predator can be much more calculating in its pursuit of prey.

Acknowledgments
We gratefully acknowledge the valuable field assistance of P. Stys, J. McNaughton, G. Kwiecinski and F. Connor. Support was provided by Natural Sciences and Engineering Research Council of Canada Graduate Scholarships to RMRB and CET and a Grant-in-aid of Research to RMRB from the American Society of Mammalogists.

Literature Cited

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Swainson’s Hawks, Buteo swainsoni, Nesting Near Winnipeg

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Swainson’s Hawk, Buteo swainsoni, has reoccupied the eastern periphery of its breeding range near Winnipeg since 1951. A small sample from Winnipeg suggested that clutch size may be larger than, and productivity comparable to, that reported for other areas. All Swainson’s Hawks seen near Winnipeg were light phase.

Key Words: Swainson’s Hawk Buteo swainsoni, breeding range, clutch size, productivity, color phase.

Swainson’s Hawk, Buteo swainsoni, commonly breeds in southwestern Manitoba (Bent 1937, Godfrey 1966). Bent (1937) and the A.O.U. Checklist (1957) noted that this species breeds east to Winnipeg, but Godfrey found no evidence to support this assertion in and about 1951 (letter to V. H. Scott, 13 July 1967). Our purpose is to confirm that Swainson’s Hawk regularly breeds near Winnipeg and to compare nesting data from Winnipeg with those of other areas.

Swainson’s Hawk was historically an abundant summer resident near Winnipeg but declined rapidly as settlement expanded (Thompson 1890). There have been numerous sightings in the vicinity of Winnipeg recently (H. W. R. Copland, Manitoba Museum of

All nests were near the tops of trees, principally Trembling Aspen, *Populus tremuloides*. Height from top of nest to the ground ranged from 4.3 m to 11.2 m ($\bar{x} = 7.1$ m), as noted by Dunkle (1977). Thompson (1890) and Pittman (1943) stated that Swainson’s Hawks rarely nested at heights greater than 6 m on the prairies, but Sharp (1902) reported nest heights from 10.6 m to 22.7 m in California. Nest height appears to be at least partly determined by tree height.

Nest size ranged from 43 $\times$ 44 cm to 67 $\times$ 74 cm ($\bar{x} = 53 \times 56$ cm), as found elsewhere (Bent 1937, Pilz 1976). The smallest nest was newly constructed in 1981 and corresponded in size with those reported by Bowles and Decker (1934). Nest depth ranged from 24 cm to 46 cm ($\bar{x} = 32$ cm), as is typical for the species (Bowles and Decker 1934, Schmutz et al. 1980).

The 16 adults observed in the study area were light phase birds. Dark phase Swainson’s Hawks are uncommon in Manitoba (Gardner 1971), Saskatchewan (Pittman 1943), and Wyoming (Dunkle 1977), but become more abundant in Washington (Bowles and Decker 1934) and California (Sharp 1902).

Nests were monitored throughout the summer to obtain productivity data. Nests were visited as infrequently as possible and methods outlined by Bart (1977) were employed to minimize risk of increasing mammalian predation. Nest contents were first checked late in the incubation stage (20 June) because of the tendency of Swainson’s Hawks to desert nests that are visited earlier (Bent 1937, Dunkle 1977, Scott 1978).

Mean clutch size was 3.3 eggs (1c/2, 4c/3, 3c/4). Thompson (1890) stated that Swainson’s Hawk commonly laid 3 but sometimes 4 eggs, but Criddle (1915) maintained that 4 was the usual clutch size in Manitoba. Clutch size was reportedly smaller in other areas with clutches of 3 common, 2 not unusual, and 4 rare in Montana (Cameron 1913) and Washington (Bowles and Decker 1934). In Wyoming (Dunkle 1977) and California (Sharp 1902) 2 and 3 egg clutches were equally common, while 4 egg clutches were not known.

Two clutches were destroyed by predation and one was deserted prior to hatching. In both cases of predation, the nest depression was covered with a mound of fresh leaves and twigs. No material was added to nests following desertion or successful fledging of young. Swainson’s Hawks use green leaves and twigs to line their nests (Cameron 1913; Pittman 1943) but this behavior following nest predation has not been reported. We suspect that the desertion was caused by a severe storm with winds gusting to 80 kph on 17 and 18 June. The nest tree had a small diameter at the nest (3.5 cm) and condition of nest and contents on 19 June suggested that the incubating adult was unable to stay on the nest during the storm. No renesting attempts were evident.

In the five remaining nests, 15 of 16 eggs hatched (94%). Hatching generally occurred in the 4th week of June. One pair deserted four young ranging from 1 to 7 days of age when we set up a tower 30 m from the nest to observe behavior. Swainson’s Hawk thus is prone to desertion even after eggs have hatched.

Four pairs (50%) fledged a total of 7 young (0.9 young per active nest). This compares with the 1.0 young fledged per active nest in northeastern Illinois (Keir and Wilde 1976), but is lower than the 1.4 young per active nest reported for Wyoming (Dunkle 1977). Our sample is too small for statistical comparison and the desertion that we caused lowered productivity.

**Acknowledgments**

We thank D. Munro for field assistance, H. W. R. Copland, V. H. Scott, M. Dedrick, R. F. Koes, and R. W. Nero for their cooperation, and R. C. Rounds for reviewing the manuscript.

**Literature Cited**


An Ontario Range Extension for the Dorcas Copper Butterfly, Epidemia dorcas Kirby

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A population of the Dorcas Copper Butterfly, Epidemia dorcas Kirby, was discovered in the Regional Municipality of Waterloo. This southerly range extension is 120 km farther inland from the Great Lakes than any previously known record in southern Ontario, suggesting that other southerly, inland populations could exist and should be checked for in suitable habitat.

Key Words: Epidemia dorcas, Dorcas Copper, range extension, Waterloo Regional Municipality.

The Dorcas Copper (Epidemia dorcas Kirby 1837) is a butterfly of the boreal zone, often found associated with sphagnum-Black Spruce bogs (Ferris 1977, Howe 1975). The southern limit of its previously known distribution in Canada is on the northwest shore of the Bruce Peninsula, in Bruce County (Hess 1979), although in the United States it occurs in remnant bogs several hundred km further south into northwestern Ohio and southern Michigan (Ferris 1977). In 1980 a new location for E. dorcas was discovered in the southwest corner of the Waterloo Regional Municipality. This represents a southerly Canadian range extension of approximately 120 km, and is the only population of E. dorcas truly inland from the Great Lakes in southern Ontario apart from a collection near Elmwood, Bruce County (Hess 1979).

Ferris (1977) in a recent taxonomic revision of E. dorcas and the closely related species Purplish Copper, E. hellioidea Boisdruval 1852, recognized seven subspecies of E. dorcas, only one of which, E. d. enterus Ontario. The morphological similarity of E. dorcas and the more common E. hellioidea has no doubt created some identification problems in the past. E. dorcas has a usually single, orange spot on the dorsal, anal area of the hindwing, which becomes an orange, crenulate band in E. hellioidea. Occasionally the orange spot on E. dorcas can extend “...along the wing border for a few cells as loosely connected lunules” (Ferris 1977). The host plant of E. dorcas is Shrubby Cinquefoil, Potentilla fruticosa (Rosaceae), whereas E. hellioidea uses species of smartweeds, Polygonum spp., or docks, Rumex spp. (Polygonaceae). However, Shapiro (1974) has reported a southwestern (USA) population of E. hellioidea feeding and ovipositing on Ege'de's Cinquefoil, Potentilla ege'dei. The number of annual broods differs between the two species, E. dorcas being single brooded and E. hellioidea double brooded. Both butterflies are on the wing during July and August in southern Ontario.

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Life histories of *E. dorcas* and *E. helioides* have been described by Newcomb (1911) and Coolidge (1924) respectively. For a thorough treatment of the life histories and taxonomy of these two species, the reader is referred to these two papers and Ferris (1977).

The Waterloo Regional Municipality location is 2.5 km east of Ayr in North Dumfries township (43°17'30"N, 80°25'30"W). The site is a wet sedge meadow and fen surrounded on two sides by two marl lakes and on the third and fourth by Tamarack-sphagnum bog and hardwood forest. The dredging of one lake was evidenced by large mounds of marl deposits along its banks. Ohio Goldenrod, *Solidago ohioensis*, reported by Newcomb (1909) as being common at his southern Michigan station for *E. dorcas*, grows profusely on these deposits. The north sides of the lakes are surrounded by a relict conifer bog. The dominant plant in the meadow was *Potentilla fruticosa*. Other plants present were Spike Rush (*Eleocharis olivacea*), Twig Rush (*Caldium mariscoides*), Hooded Ladies-tresses (*Spiranthes romanzoffiana*), Pitcher Plant (*Sarracenia purpurea*), Kalm's Lobelia (*Lobelia kalmii*), Bladderwort (*Utricularia minor*), Bedstraw (*Galium labradoricum*) and Bog Goldenrod (*Solidago uliginosa*).

Eight specimens (six females, two males) were collected on 16 August 1980. Vouchers will be placed with the National Collection (CNC) Agriculture Canada in Ottawa and the Royal Ontario Museum, Toronto. Numerous other *E. dorcas* were seen on and about the *Potentilla* in the meadow along the lake edges. No oviposition was seen. Other Lepidoptera present were Eyed Brown (*Lethe eurydice*), Viceroy (*Limenitis archippus*) (which was driven off by *E. dorcas*), Clouded Sulphur (*Colias philodice*) (albino females predominated) and European Cabbage Butterfly (*Pieris rapae*).

Since *E. dorcas* is found in the United States far south of the Waterloo R. M. location, this butterfly should be sought in other inland, remnant bogs and fens in southern Ontario where *P. fruticosa* occurs.

Acknowledgments

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Literature Cited


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DDE Not Implicated in Cliff Swallow, *Petrochelidon pyrrhonota*, Mortality During Severe Spring Weather in Oregon

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Large numbers of Cliff Swallows (*Petrochelidon pyrrhonota*) died in late May near Burns, Oregon, during cold, wet weather. The brains of five dead birds did not contain lethal concentrations of DDE, and no PCBs were detected.

Key Words: Cliff Swallow *Petrochelidon pyrrhonota*, DDE, mortality, weather stress, weight loss.

Migrants that winter in Latin America may be carrying DDE and may die when weather-stressed. This paper reports a test of this possibility.

Van Velzen et al. (1972), on the basis of laboratory studies with Brown-headed Cowbirds (*Molothrus ater*), concluded that DDT residues present a hazard to birds that utilize stored fat during periods of stress. As birds starve, organochlorines may be released from mobilized fat and relocated in the brain. Since organochlorines act principally on the central nervous system, it is important to know the effects of starvation on the concentrations of organochlorines in the brain.

Stickel et al. (1970) concluded that minimum concentrations of 300–400 ppm of DDE in the brain (wet weight) were diagnostic for DDE-caused mortality in experimental cowbirds. For comparison, American Kestrels (*Falco sparverius*) died in laboratory studies with 213, 223, 230, 280, and 301 ppm in the brain (Porter and Wiemeyer 1972, Henny and Meeker 1981), somewhat lower than in cowbirds.

Passerine birds were collected throughout much of the western United States in 1980 to monitor pollutant burdens. Cliff Swallows (*Petrochelidon pyrrhonota*) from two Oregon sites were collected in June–July as part of this study, and 7–8 adult birds from each site were analyzed at Laltech Scientific Services, Madison, Wisconsin (DeWeese, in prep.). Pools of the whole Cliff Swallow carcasses (ppm, wet weight) showed the following: Malheur National Wildlife Refuge (NWR) (DDE 2.1, PCBs 0.11), Summer Lake Wildlife Management Area (DDE 4.0, PCBs 0.13).

Cliff Swallows suffered extensive mortality at Malheur NWR, Burns, Oregon, apparently as a result of a "cold snap" and rain for three days up to 27 May 1980. At least 45 dead and emaciated adult birds were collected in the immediate vicinity of refuge headquarters. The weight (mean ± SD) of 45 dead Cliff Swallows was 16.03 ± 1.07 g, compared with 21.16 ± 1.02 g for seven apparently normal adult birds collected in the same area on 17 July 1980 (i.e., a 24.2% difference). The minimum temperatures at headquarters ranged from 0 to 1°C for three days before the dieoff and the three-day mean maximum temperature was 8°C below normal for May (U.S. Weather Bureau 1980). We decided to test whether organochlorine pesticides might have been implicated in the Cliff Swallow mortality.

The brains of five Cliff Swallows that died at Malheur NWR on 27 May 1980 were stored frozen and analyzed for organochlorine pesticides, or their metabolites, and PCBs at the Patuxent Wildlife Research Center, Laurel, Maryland, by procedures described by Cromartie et al. (1975) and Kaiser et al. (1980). The mean DDE concentration (ppm, wet weight) was 7.4 (range 2.1–12.0), and no other organochlorines were detected. These concentrations were far below those reported as diagnostic for DDE-caused mortality in either cowbirds or kestrels.

Although Cliff Swallows collected at Malheur NWR on 17 July were survivors of the May "cold snap", and thus might have been supposed to have lower residues than those that died during May, the May brain and July body burdens were not greatly dissimilar. Only a small percentage of the DDE residue in experimentally poisoned birds is found in their brains (Stickel et al. 1970). The body burden of DDE in the July Cliff Swallow carcasses was insufficient to cause death even if it were possible to mobilize all of those residues to their brains (based on total micrograms of DDE in carcass and size of the brain). DDE did not apparently contribute to the swallow deaths in the May "cold snap". However, other North American migrants wintering in Latin America, where DDT is still used (Weir and Schapiro 1981), still may be exposed to persistent pesticides.

Acknowledgments

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B. D. Ehlers of the Malheur NWR staff for bringing the swallow dieoff to our attention. S. N. Wiemeyer and J. C. Franson reviewed an early draft of the manuscript. L. R. DeWeese kindly provided unpublished carcass residue data.

Literature Cited


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Location of Larvae of the Winter Tick, *Dermacentor albipictus* (Pack.), in Elk Island National Park, Alberta

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After reports of heavy infestations of Winter Ticks on moose in Elk Island National Park, Alberta, a search was made for the free-living tick larvae on 15 October 1980. Large aggregations were found on grass, shrubs, and the boundary fence in the northeast corner of the Park. Some larvae had ascended to the top of the fence, a height of about 2.2 m.

Key Words: *Dermacentor albipictus*, Winter Ticks, moose, game farming, Canada.

Infestations of Winter Ticks on moose in Elk Island Park sometimes exceed 10³ ticks per moose and are associated with hair loss and deaths in late winter (Samuel and Barker 1979). Since most larvae of this species emerge in the summer but do not ascend the grass until September or October at Kamloops, British Columbia (Wilkinson 1967), a preliminary reconnaissance was carried out on 15 October 1980 to investigate the distribution and behavior of the free-living larvae in the Park.

Larvae were sought by visual examination of grass tips, low shrubs, and other suitable supports, and by sweeping with a 1 × 1 m flannelette flag and a 0.5 × 0.5 m 'propashnik' sampler (Blagoveshchensky 1957). A thin layer of snow on the ground made the larvae more visible but hindered the use of the samplers by dampening the cloth.

Most of the larvae were found by visual inspection because they were in large aggregations. Many were found at several locations near and on the border fence (Figures 1 to 4) in the northeast corner of the Park where visitors had reported picking up larvae on their clothing. None were found at a salt lick north of the Park headquarters, or at the 'aspen exhibit' clearing, or on the trail inside the southern boundary fence adjacent to Highway 16. A systematic survey of the Park was not attempted.

At one of the infested sites, larvae had settled in the 'knots' in the page-wire fence (Figures 1 and 2) at 0.2–1.7 m above ground, good heights to crawl onto a moose's legs or trunk. However, a few aggregations were on the top wire about 2.2 m above ground, and thus could only transfer to a moose reaching upwards, as in some browsing activities. The larvae became
Figures 1-4. Height of ascent and aggregation of larvae of Winter Ticks. Arrows indicate sites occupied by clusters of larvae.

1. Some larvae occupied the topmost 'knots' in the boundary fence, about 2.2 m above ground (p = propashnik).
2. Tick larvae in 'knot' in boundary fence wire.
3. Clusters of larvae on grass, and displaced onto 'propashnik'.
4. Clusters of larvae on shrub that was browsed in previous years.
active on the approach of the observer, probably alerted by carbon dioxide and other olfactory stimuli. The ambient temperature was about 5°C. Winter Tick larvae have been recorded on grass at 18°F [–7.8°C] (Wilkinson 1967) and probably survive much lower temperatures. Wilkinson (1953) observed grouping of the larvae of the Southern Cattle Tick (Boophilus microplus) up to 1.2 m with individual larvae ascending to 1.7 m after the larvae were liberated at the base of a 3.3 m lath.

The aggregations of larvae along the northeast fence in the fall may be due to the use of the clearing along the earth roadway for loitering by moose in the spring, probably because it is one of the less human-frequented sunny areas in the park. The engorged female ticks would drop here in the spring and the warming of the clearing by sunshine would assist oviposition and egg development (Wilkinson 1967).

Further studies of the distribution of the larvae are desirable, to assist in planning reduction of infestation levels by habitat modification, for instance by controlled fall burns, or by arranging for annual movement of moose to alternate fenced halves of the park. The Winter Tick may become economically important if attempts are made to use aspen or boreal woodlands (Telfer and Scotter 1975) for game or 'meat-horse' farming.

Literature Cited

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An Observation of the Transportation of Pea Clams, Pisidium adamsi, by Blue-spotted Salamanders, Ambystoma laterale

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In Nova Scotia, during April 1980, Blue-spotted Salamanders, Ambystoma laterale, were observed transporting Pea Clams, Pisidium adamsi, attached to digits of their hind limbs. The significance of this as a dispersal mechanism may be minor compared to that of birds and insects, but might quickly establish populations in new ponds.

Key Words: Pea Clam, Pisidium adamsi, Blue-spotted Salamander, Ambystoma laterale.

In the evening of 16 April 1980, cattail ponds along Beecham Road, (45°55’N, 64°00’W), 10 km south of Tidnish, Cumberland County, Nova Scotia, were being investigated for migrating salamanders. The road is unpaved and has shallow cattail ponds with soft mud bottoms on both sides. Adjacent woodland, about 5 m from the road, is mixed second growth composed mainly of spruce, fir, maple and birch. At 2100 AST Blue-spotted Salamanders, Ambystoma laterale, were seen on the gravel road. At this time the sky was overcast, air temperature was 9.0°C and water temperature in the ponds 11.5°C. An investigation of the west side of the road in the immediate area revealed salamanders moving across the leaf litter in the woods, down a grassy bank and into the cattail pond. From here they proceeded out of the pond, up onto the road and across it to a pond on the east side, taking about 10–15 minutes to complete the distance. More than fifty Blue-spotted Salamanders were seen. A sample of sixteen was collected and two of these were found to have one individual each of the Pea Clam, Pisidium adamsi, (family Sphaeriidae) attached to a toe of a hind foot (Figure 1). The salamanders were brought back to the laboratory and kept in water at about 5.0°C for observation. After thirteen days the Pea Clams were still firmly attached to the
salamanders’ toes, causing swelling at the point of attachment. Most Pea Clams remain tightly closed at temperatures below 8°C and this most likely prevented separation (Mackie, personal communication, 1981). The Pea Clams were removed for further examination and identification. Shell lengths of the two specimens were 4.5 mm and 5.5 mm. The species may attain a shell length of over 7.0 mm. The specimens were believed to be mature but were not gravid. 

The Blue-spotted Salamander is terrestrial for most of the year, but it migrates to shallow ponds to spawn in the early spring. In Nova Scotia, this migration takes place in mid-April at night, following a period of rain, and many salamanders may be seen on the move together. The ponds used for spawning are usually not far from the woodland habitat. Usually, the adult salamanders stay in the ponds only for a few nights and then return to the woods.

*Pisidium adamsi* is a common species found throughout North America east of the Rocky Mountains, in a wide range of habitats which include muddy ponds with decaying vegetation (Burch, 1975). The species has been previously recorded from Nova Scotia, but there are insufficient records to assess its distribution in the province.

The various mechanisms by which Pea Clams are dispersed have been reviewed by Rees (1965) and more recently investigated by Mackie (1979). Pea Clams, particularly some species of *Musculium* and *Sphaerium*, are commonly early colonizers of new, isolated freshwater habitats. These animals are hermaphrodite and capable of self-fertilization. A population may thus be established once a single individual has been transported into a new pond. Of the dispersal mechanisms used by the Pea Clams, floating and aerial dispersal by birds and insects probably are most important. However, Mackie (1979) has indicated that fish and aquatic mammals may also play a role. Rees (1952) has reported on transportation of Pea Clams by various species of amphibians in Britain.

Studies of Blue-spotted Salamanders being carried out by one of us (J. G.) have indicated that their populations are centred primarily on aquatic breeding sites and that the distance of dispersal into the surrounding terrestrial habitat may be no more than thirty meters. When the migration begins, the salamanders travel quickly to the pond and, as has been observed, they may pass through one pond in order to reach another nearby. The 10 to 15 minutes taken by the salamanders to cross the ground between the ponds and the fact that the migration takes place in rain and at night will ensure that there is a high level of survival of the transported Pea Clams. Mackie (1979) has determined experimentally that individuals of *Pisidium casertanium* and *Pisidium variabile* in which the valves were held open with a fine wire had a 60% chance of survival after 15 minutes of suspension in the air, and that the period of time of exposure that would be lethal was considerably extended by high atmospheric humidity.

The transportation of Pea Clams by salamanders cannot be considered as important as aerial transportation by birds and insects. However, the level of mortality would probably be lower and establishment of a population in a new pond might be accomplished more rapidly. Pea Clams that become attached to salamanders when they are about to leave the pond to return to their terrestrial habitat would obviously not survive unless the salamander passed through another pond on the way. As the return trip is not carried out as a distinct migration this aspect would be difficult to investigate. This observation supports the view of Rees (1952) that amphibians play a definite role in the transportation of Pea Clams over short distances and that this mechanism can be significant in the colonization of new freshwater habitats.

**Acknowledgments**

The authors would like to thank R. Merrick for taking the photograph and Dr. G. L. Mackie for confirming the identifications of *Pisidium adamsi* and for his comments on the manuscript.
Literature Cited


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Accepted 13 November 1981

Scansorial Behavior in Woodchucks, Marmota monax

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Five instances of tree climbing by Woodchucks (Marmota monax) were observed during the summers of 1979 and 1980 in southeastern Minnesota. Four Woodchucks apparently used trees as refugia from a perceived predator when burrows were greater than 50 m away, and one Woodchuck used a forked tree as a sunning site.

Key Words: Marmota monax, scansorial, behavior, Woodchuck.

Although the Woodchuck (Marmota monax) generally is regarded as a conspicuous species in farmland regions (Cook 1945), few reports of tree climbing by Woodchucks exist (Grizzell 1955; Killingbeck 1974) except for anecdotal accounts of individuals using trees when pursued by dogs (e.g., Bowdish 1922; Medger 1922; Gianini 1925). The rarity of scansorial behavior in Woodchucks is attested to by the fact that only Grizzell (1955) reported multiple sightings over a relatively short time span (three sightings in two years). Furthermore, no data have ever been gathered regarding proximate factors influencing tree climbing by Woodchucks. During a study of Eastern Cottontail (Sylvilagus floridanus) ecology at the Rosemount Agricultural Experiment Station in southeastern Minnesota (44°43'N, 93°6'W), Woodchucks were censused while walking trap lines totalling 3.7 km. Trap lines were visited five days per week, and trapping commenced in mid-July. For each sighting of a Woodchuck in a tree, data recorded included tree species and diameter at breast height (dbh), height climbed, and behavioral characteristics of the animal. In addition, an intensive search for burrows was conducted within a 100-m radius of the tree.

I observed five instances of tree use by Woodchucks at the Rosemount Station during the summers of 1979 and 1980. Woodchucks were seen in trees (not in the act of climbing) on 17 July 1979, 1 August 1979, and 17 August 1979 and climbing trees on 3 August 1980 and on 15 August 1980. Based on visually-estimated weights of animals (Snyder et al. 1961) and distances between observation sites, five different Woodchucks were believed to have climbed trees. Two animals climbed trees in a 50-year-old, 5-row shelterbelt, two used trees in a 40-year old, sparsely-wooded waste area, and the remaining individual was observed climbing a tree on a farmstead lawn.

Four tree species were used by Woodchucks: Eastern Cottonwood (Populus deltoides), American Elm (Ulmus americana), Box Elder (Acer negundo), and Silver Maple (A. saccharinum). Tree dbh ranged from 26 to 40 cm, (X = 34 cm), and Woodchucks ascended to heights varying from 1.8 to 5.5 m (X = 3.1 m). Four of five individuals ascended only to the first large branch; they then remained motionless and allowed themselves to be approached closely. Indeed, one of the four Woodchucks moved only after being poked persistently in the hindquarters with a stick. The remaining Woodchuck, after momentarily stopping on a low-hanging branch, climbed another 2 m to a higher branch as I approached and moved frequently while I stood beside the tree.

Gianini (1925) proposed that Woodchucks far from their burrows climb trees to avoid predation, but this hypothesis has never been examined. On four occasions in the present study (all in August), tree use by Woodchucks was associated with distances of >50 m to the nearest burrow; on two occasions this distance exceeded 100 m. Presumably I was viewed as a potential predator, and my approach elicited scansorial
activity in each of these instances. Hence, Woodchucks encountering predators when substantially removed from burrows (e.g., > 50 m) may climb trees rather than attempt to flee to their dens. Interestingly, four Woodchucks released from live traps located < 30 m from burrows ran to them; in all four cases, nearby overstory trees were ignored even though they were closer to Woodchucks than the dens were. De Vos and Gillespie (1960) noted that Woodchucks traversed greater distances in midsummer, perhaps in response to changes in food availability. If foraging activity increases during August in preparation for hibernation (see Snyder et al. 1961), increasingly extensive movements away from burrows may result, thereby precluding use of burrows as escape sites and increasing the frequency with which scansorial activity occurs.

The remaining Woodchuck was located in a tree only 10 m from a burrow. Upon being prodded with a stick, this individual jumped to the ground and immediately entered the burrow. I doubt that this Woodchuck was using the tree as an alternative escape site; rather, I suspect that the animal may have been using the forked perch as a sunning site. Killingbeck (1974) observed a Woodchuck sunning in a dead Basswood (Tilia americana), and Gianini (1925) reported Woodchucks sunning on leaning trees and fence posts. I observed similar use of a fence post at the Rosemont Station during July 1979.

Thanks are extended to G. N. Back and R. H. Yahner for reviewing an earlier draft of the manuscript.

Literature Cited


Received 2 September 1981
Accepted 10 October 1981

Late Pupping by the Harp Seal, Pagophilus groenlandicus, in the Eastern Canadian Arctic

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Hammill, M. O. 1982. Late pupping by the Harp Seal, Pagophilus groenlandicus, in the eastern Canadian Arctic. Canadian Field-Naturalist 96(2): 216–217.

A partially moulted, white coated Harp Seal, Pagophilus groenlandicus, pup was collected in July off the southeast coast of Baffin Island. The pup appeared to have been born in the arctic at the beginning of July, four months after normal pupping occurs for this species at lower latitudes.

Key Words: Harp Seal, Pagophilus groenlandicus, reproduction, distribution

On 25 July 1981, I collected a partially moulted whitecoat male Harp Seal pup, Pagophilus groenlandicus (Erxleben), at Cyrus Field Bay (63°N, 64°W), southeastern Baffin Island. The seal was shot on a floating ice pan in an area where the sea surface was three-tenths covered with pack ice. The long white lanugo covered only the posterior portion of the body suggesting that if the normal moult pattern had occurred the animal was from 18–30 days old (Silvertson, 1941; Stewart and Lavigne, 1980).

The nose-tail length of this animal (95 cm) was comparable to healthy pups of only six days of age (Stewart and Lavigne, 1980) while the blubber layer over the sternum (1.8 cm) and maximum girth (70.0 cm) were indicative of an animal in poor condition.

It appears likely that this seal was born in the Arctic. Date of birth must have been at the beginning of July some four months after pupping occurs in the Gulf and Front herds during late February to mid
March (Sergeant, 1965). Some harp seal pups have been sighted in Davis Straight among Hooded Seals (Cystophora cristata) during aerial surveys conducted in late March 1978, although their numbers were very low (John Parsons, personal communication, MacLaren Atlantic Ltd., Dartmouth, Nova Scotia).

Because of the persistence of sea ice at these latitudes, the season of births might be somewhat retarded and less synchronized than in the main whelping patches much farther south. I also speculate that seals giving birth at these extreme northern latitudes might be inexperienced recently mature females. As a result, the survival of their progeny would be expected to be very low, because of inexperienced parental care and harsher environmental conditions.

Literature Cited

Received 12 November 1981
Accepted 28 February 1982

An Albino Little Brown Bat, Myotis lucifugus, from Alberta

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An albino Little Brown Bat, Myotis lucifugus, is reported from Alberta. This is the third albino specimen of this species and the first for Canada.

Key Words: albino, Little Brown Bat, Myotis lucifugus, first, Canada.

Walley (1974) reviewed albinism in bats and reported an albino Little Brown Bat, Myotis lucifugus, from Wisconsin. The latter was the second known specimen of an albino of this species. An additional albino Little Brown Bat, recently donated to the Provincial Museum of Alberta is reported here.

This specimen, prepared as a study skin and skull, PMA No. Z80.77.1, was captured 30 July 1980 in a summer cottage at Seba Beach, Alberta. Unfortunately, the person who saw the bat killed it by striking it with a broom. This resulted in a rupture of the abdominal wall and a crushed skull. When the specimen was received at the museum it was severely dehydrated and the hair was slipping. As a result the only measurements obtained were forearm 37.5 mm and foot 11 mm.

The specimen is believed to be a “true” albino in that the pelage, flight membranes, and ears are all white without any indication of dark pigmentation. Because of the nature of the specimen when it was received, it was not possible to examine the eyes. Albinism in bats is not common and for this reason any report of its occurrence is worth recording. The specimen reported here is the third albino of this species to be noted and is the first for Canada.

Literature Cited

Received 6 January 1982
Accepted 18 March 1982

1Provincial Museum of Alberta Natural History Contribution 70
Mortality of Nestling Blue Grouse Owing to Inclement Weather

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Three nestling Blue Grouse (Dendragapus obscurus) were found dead during cool, wet weather. Inattentiveness by the female may have been a factor in the deaths. Other information suggests that inclement weather usually does not affect the survival of nestling Blue Grouse in coastal British Columbia.

Key Words: Blue Grouse Dendragapus obscurus, British Columbia, nestlings, mortality, weather.

On 18 June 1981, while conducting studies on Blue Grouse (Dendragapus obscurus) on Hardwicke Island, British Columbia, we found three dead nestlings whose death almost certainly was caused by inclement weather. The nest was found on 21 May with 4 eggs present; final clutch size was 5, and estimated date of hatch (Zwickel 1977) was 17 or 18 June.

The hen, an adult, was present and relatively dry when the nest was checked at 0755 on 17 June. She ran off the nest when approached but remained close by; all eggs were pipping. At this time, wind and rain were very light and the temperature was +10°C.

Rain was almost continuous, being moderate to heavy at times, until the next check, at 1000 on 18 June, when precipitation was moderate, wind light, and the temperature +8°C. As we approach the nest, we saw two very wet, dead chicks lying close together outside the nest, approximately 15 cm from the hen. The hen was on the nest and her back was visibly soaked. When we were 1 m from her, she flushed and flew out of sight into tall dense trees approximately 200 m away. One dry chick ran from the nest and was captured. A fourth chick was wet and dead in the nest and the fifth was still hatching. We remained at the nest for one-half hour but the hen did not return. Twenty minutes later we checked the area again but could not find her. Since she appeared to have abandoned the surviving chicks we collected them for an avian study. The partly hatched chick emerged later in the day, under artificial heat.

The presence of dead young in and near the nest suggested that this female had not brooded her young attentively. Also, most hens with nestlings remain at the nest site when disturbed whereas this female flew out of the area on 18 June. On the previous day she had remained near the nest. Whether her change in behaviour was related to her being very wet on the second day cannot be determined. Lack of attentiveness probably was a contributing factor in the death of these young.

Although the direct cause of death was almost certainly cool, wet weather, poor cover at the nest site may have contributed indirectly to the mortality. This nest was at the base of a 1 m tall Western White Pine (Pinus monticola), whereas most nests in this area were under logs, stumps, or Douglas Fir (Pseudotsuga menziesii) or Western Hemlock (Tsuga heterophylla), trees which generally provide better overhead cover than Western White Pine. Sites with better cover appeared to be present in the immediate vicinity.

Much has been written on the effects of weather on survival of juvenile grouse and conclusions are variable, even within a species (e.g., Myrberget 1972, Marcstrom and Hoglund 1980). Zwickel and Bendell (1967) suggested that post-hatch weather normally is not important to the survival of young Blue Grouse, and observations of two broods for extended periods during cold, wet weather supported this conclusion (Zwickel 1967).

Young Blue Grouse usually leave the nest within a day of hatching, and our finding indicates that inclement weather can cause mortality during this period. However, another nest we found in 1981 successfully hatched on 18 June, and other broods also were known to have hatched on this day. Among over 100 nests found and subsequently hatched on Vancouver Island or Hardwicke Island (R. A. Lewis and F. C. Zwickel, unpublished data) ours was the only instance in which nestlings died as a result of adverse weather. Therefore, in most cases cool, wet weather does not affect survival of nestling Blue Grouse in coastal British Columbia.

Acknowledgments

We thank the Bendickson families and B. Murray for the hospitality they extended us during our studies on Hardwicke Island. V. Lewin and F. C. Zwickel kindly commented on the manuscript.

Literature Cited


Received 20 January 1982
Accepted 21 March 1982
News and Comment

North American Loon Fund Grants

The North American Loon Fund (NALF) announces the availability of two grant programs for support of new or current research, management, or educational projects that may yield useful information for Common Loon conservation in North America.

The first of these programs, the Robert J. Lurtsema Research Award, consists of a $1000 stipend available annually for a suitable research project focused on a member of the family Gaviidae. Preference will be given to students and independent researchers with limited availability of other funding.

The second program offers modest grants in support of research, management, or educational projects directly related to the conservation of Common Loons as a breeding species. Proposals in the range of $500 to $3000 are most likely to be considered for funding.

Further guidelines for prospective applicants are available upon request from the NALF Grants Committee. Deadline for submission of proposals is 31 January 1983. Funding awards will be announced by 15 March 1983.

Please submit guideline requests to:
North American Loon Fund Grants Committee
North American Loon Fund
Meredith, NH 03253 USA

Editor’s Report for 1981

Dr. Lorraine C. Smith resigned as Editor of The Canadian Field-Naturalist early in 1981. Lorraine’s impact on the journal is evident in the quality of her issues and documented in her Editor’s reports, editorials, and comments which together totalled over 50 published pages. Her contribution is further emphasized in Table 1 which lists the 17 editors of The Canadian Field-Naturalist and its predecessor, The Ottawa Naturalist, since 1887. In nine years Lorraine edited 20% (4509) of all pages published over 95 years (22 882). Only four other Editors of the journal (Senn, Gibson, Leechman, and Macoun) served longer terms. In 1981, Lorraine edited 95(1) mailed 20 January 1981, (2) 23 April 1981 and (3) 15 September 1981. These contained all manuscripts which she had accepted up to, and including, 6 April 1981.

The Council of The Ottawa Field-Naturalists’ Club appointed me to succeed her 8 June 1981. The summer postal strike and the rebreaking-in process slowed the review of subsequent new manuscripts and acceptance of those returned after revisions Lorraine had earlier recommended. The last issue of the volume 95(4) was not mailed until 7 April 1982. However, as this report is written (early August 1982), 96(1) has been mailed, most manuscripts for the remainder of volume 96 are in galley or in the hands of the printer, and editing for volume 97 is in progress.

The number of manuscripts submitted to The Canadian Field-Naturalist in 1981 (Table 2) is similar to that over the past six years, down from 1973-75, but up compared to the years prior to 1973. Looking ahead at 1982, 94 manuscripts have already been submitted. The proportion of manuscripts accepted of those submitted in 1981 is incomplete but appears likely to be similar to that established since 1976.

The number of manuscripts published in The Canadian Field-Naturalist volume 95(1981) is given by field of study in Table 3. The number of pages of research (43 articles and 34 notes, excluding miscellaneous) was 350 (68% of the total published). Miscellaneous material (the 10 articles noted in Table 3) plus Announcements, Thanks, News and Comment, and The Ottawa Field-Naturalists’ Club Annual Report, accounted for another 77 pages (15%), the Book Review section for 72 pages (14%) and the Index for 15 pages (3%). The number of reviews and titles in the Book Review section published by field of study was: zoology (32 + 160), botany (17 + 53), environment (15 + 110) and miscellaneous (7 + 38) for a total of 71 reviews and 361 titles. These figures indicate this section’s value to the generalist and amateur through its extensive coverage and evaluation of current natural history literature.

Table 4 compares the number of research articles and notes published over the past 14 years by volume. A recent trend toward fewer notes is evident and this is
a major factor in the drop in total manuscripts published in 1978-81 compared to 1973-1977. Such declines may be cyclical as an earlier low point for notes is evident in 1968-1971.

I owe thanks to Lorraine for her complete and meticulous records which had already been placed in Bill Cody's hands before my appointment, and to Bill for forwarding new manuscripts to Associate Editors in the interval between Editors. Thanks are also due to Roger Taylor, then President of the Ottawa Field-Naturalists' Club, for encouraging me to reconsider my initial refusal to stand for Editor; to the Council of the Ottawa Field-Naturalists' Club for the appointment; and to Ron Bedford and the other members of the Publications Committee (and to many authors) for their patience and encouragement during the year. My appreciation also goes to Associate Editors Ed Bousfield, Steve Smith, Charles Jonkel, Charley Bird, Charley Krebs and Bill Pruitt for reviews and guidance, and particularly to Tony Erskine and George La Roi who have continued to send ornithology and The Biological Flora of Canada manuscripts, respectively, to reviewers and recommendations on revisions to authors. In addition, George Argus, Stan Van Zyll de Jong, and Don McAllister gave valued advice on reviewers. Wilson Eddy has continued his efficient and comprehensive handling of the Book Review section, a task he has carried out since 1975, beginning with 89(3). Harvey Beck again compiled the Index, his third since volume 93(1979). As the Index can not be completed until the fourth number is actually in numbered page proof, Harvey has to respond to an immediate completion request and his speed in meeting such a deadline is awesome, despite the inabilities of courier services to quickly locate him. Bill Cody, who was first listed as Business Manager in 1949: 63(1) and who has continued to care for the journal's business for an unbroken 33 years, managing five Editors in the process, has been as invaluable now as he was during my previous term as editor; always efficient, continually encouraging and merciless in bringing pressure to bear when the need was perceived. The National Museum of Natural Sciences, National Museums of Canada, have been particularly supportive and I am

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¹Volumes 1-31 (1887-1918) generally had 12 issues, 32-57 (1919-1942) generally had 9, 58-66 (1943-1952) had 6, and 67-95 (1953-1981) had 4. However, there are a number of irregularities in numbers per year, sometimes involving numbers combined, sometimes fewer numbers than normal. Here combined numbers have been counted as one number. For a full treatment see W. J. Cody and B. Boivin. 1954. The Canadian Field-Naturalist and its predecessors. The Canadian Field-Naturalist 68(3): 127-132.

²No allowance has been made for the increases in page size. The journal was (in inches) 8 to 8 1/4 by 5 1/4 to 5 1/2 in 1887-1918, 9 1/2 by 6 3/4 in 1918-1969, and 9 3/4 by 7 1/4 in 1970-1981.

³A. G. Kingston was acting Editor during an unspecified length of absence of the Editor in 1895.

⁴Acting Editor during completion of volume started by predecessor.

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*This includes 10 papers and notes published in volume 95, 6 in 96(1), and 49 accepted for 96(2-4). An additional 51 have been returned to authors for revision. There are also 12 manuscripts submitted in 1980, 6 in 1979, 1 in 1978 and 1 in 1975 that are still carried on the journal's files as under consideration pending author's revisions as of August 1982. Sources: Editor's Reports in The Canadian Field-Naturalist 88(1): 111; 90(2): 202; 91(2): 197; 92(2): 203; 93(2): 201; 94(1): 97-98; 95(2): 215-216; and current Editor's files.


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*One Reports of Significant Range Extensions is included in each category for a total of three.
**Includes two papers in The Biological Flora of Canada series.
***Two Viewpoints, Introduction plus five articles in the Centennial Symposium, one Obituary, and one Editorial.


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| Totals  | 473   | 769 | 1242 |

Average per year: 33.8 Articles, 54.9 Notes, 88.7 Total
Average per issue: 8.5 Articles, 13.7 Notes, 22.2 Total

grateful for time, space, and encouragement to Henri Ouellet, Chief, Vertebrate Zoology Division; to Louis Lemieux, Director until 31 December 1981; F. Hugh Schultz, Assistant Director and, later, Acting Director; and, subsequently, to C. G. (Chuck) Gruchy, Acting Assistant Director and, later, Acting Director. I am also indebted to Emil Holst and his staff, particularly Ed Finnigan, at M.O.M. Printers for their help and guidance.

During or at the end of 1981 David Scott (Associate Editor since 1975), George La Roi (1976) and Charley Krebs (1975) asked to be released from their responsibilities as Associate Editors. The latter two kindly saw me through the balance of 1981. George has retained the responsibility for The Biological Flora of Canada series (begun in 1979) but Charley has escaped to a new academic appointment, far from The Canadian Field-Naturalist, in Australia. Ed Bousfield (an Associate Editor since 1969), Steve Smith (1972), Charles Jonkel (1972), Charley Bird (1974), Tony Erskine (1974) and Bill Pruitt (1971-1976, and again since 1979) have all accepted reappointment. In addition, Don McAllister and Stan Van Zyl de Jong have accepted appointments in 1982. Don is a former Associate Editor (1965-1972) and Stan is a former Chairman of the Publications Committee (1976-1977). Business, Book Reviews and Index continue to be handled by Bill Cody, Wilson Eddy and, hopefully, Harvey Beck, respectively, in 1982.

Although Associate Editors have always been
acknowledged in *The Canadian Field-Naturalist*, formal recognition has not been given to the outside reviewers who have made an increasing contribution to the review process. The Publications Committee has therefore recommended that their names be included in the annual Editor's Report. The following submitted review comments during the calendar year 1981 on one or more manuscripts:


Thanks are due Tony Erskine, George La Roi, Wanda Cook and Bill Cody who assisted in the compilation, and to all who have made the review process successful.

FRANCIS R. COOK
Editor
Book Reviews

ZOOTOLOGY

Small Mammals


It is always pleasant to see factual Canadian natural history presented in a form to interest and intrigue the younger mind. This colouring book gives an alternative to Bugs Bunny and Mickey Mouse. Canadian small mammals are presented in lifelike natural situations and representative habitats. The drawings are excellent, maintaining factual appearances and yet presenting eye-catching poses to attract the young artist while keeping the simple line format that allows colouring. Simple colour instructions accompany each picture.

The text also aims to hold the young naturalist’s attention. The interest is captured by first describing a live-action situation. Mice scamper to barely elude a predator’s grasp. This is followed by information on habitats, behaviour, distribution, and other factual data. I was a little surprised at the story of a possum meeting a hungry bobcat in southern Ontario.

Testing on our 10 and 12 year olds brought interesting results. Although both professed interest neither could keep it up more than half-way to the finish, in spite of prodding. The youngest claimed to be above colouring books (he can draw almost as well himself) and yet he had difficulty understanding some of the more difficult words and concepts in the text. Since he has accompanied his father on small mammal ecology investigations since birth, this was a bit disappointing.

Personally, I think this is a commendable book which should be recommended for young Canadian naturalists, probably in about the 10 year-old range. Some parental interest is required as well.

WILSON EEDY

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The Birds of Sable Island, Nova Scotia

By Ian A. McLaren. 1981. The Nova Scotian Institute of Science, Dalhousie University, Halifax. 84 pp., $7.50.

The name Sable Island conjures up a variety of images for different people. Dreaded by sailors as the “graveyard of the Atlantic” it is nevertheless much appreciated by naturalists who are becoming increasingly aware of the rich plant and bird life found on this thin sliver of an island, 160 kilometres off the eastern coast of Nova Scotia. Its wild horses have been described in articles and in a famous novel (Thomas Raddall’s The Nymph and the Lamp). During the last decade or so they have also been frequently photographed, as have the thousands of fur and harbour seals. For ornithologists the island acquired instant fame upon the discovery, in 1884, of the only known nesting ground of the Ipswich Sparrow [now known to be a “large pale race of the Savannah Sparrow”].

This volume consists of two principal sections. The first part begins with a fascinating historical account of the birds of Sable Island, and those who studied them. Especially interesting is the chapter on “The Ornithological Bouteilliers”, the three youngest children of Superintendent Robert J. Bouteiller, who was stationed on the island during the 1884-1912 period. A visit by Jonathan Dwight Jr. in 1894 had great importance for the ornithology of the island, because Dwight’s encounter with these children awakened their interest in bird study. Between 1894 and 1910 these youngsters sent over 100 bird skins to Dwight, thus supplementing the original collection the American ornithologist made during his visit to Sable Island. Many other well known visitors, among them Alexander Graham Bell and John Macoun, collected data, albeit sporadically, during the 20th century.

Other short chapters deal with the following topics, “bird habitats and bird finding”, nesting species, and regional migrants. A detailed table, for the spring and fall migrations of the 1967-79 period, for 150 “selected” species, is also included in the last section. One of the major findings of this table is that the median migration dates suggest “that migration routinely carries on much later in the spring than might be supposed for many species.” Another list, of vagrants, shows an interesting combination of western, northern, southern and European species which have turned up on Sable Island over the years. These include such “rarities” as the Roseate Spoonbill, Limpkin, American Avocet, Cave Swallow, Hermit
Warbler and Wheatear. "Unseasonable records" and "Historical changes" close this section of the book.

"Accounts of species" takes up roughly two-thirds of the book. It is based, partly, on the bird records of Mrs. Cristel Bell (1963-69) which were published in a preliminary account of The Birds of Sable Island [1972, McLaren and Bell], and partly on more recent records established by Dr. McLaren, his colleagues and students. A list provided by A. A. Richard (1974-79) is also included. The annotated list has 325 species accounts which range from a one sentence entry on the Black-backed Three-toed Woodpecker to nearly a page on the Common Tern. The longer accounts contain useful historical references. Sixteen black-and-white photographs show a sample of representative and unusual species described in the accounts. The list of references provides those interested in the avifauna of Sable Island with plenty of additional study material.

This book is an interesting combination of the old-fashioned "annotated list" and the modern "bird-finding guide." It is well researched, well written and reasonably priced. Maybe it is just as well that it is costly and difficult to get to Sable Island. This publication will definitely increase the desires of naturalists to visit this fascinating place. It is recommended.

MARIANNE GOSZTONYI AINLEY

History and Philosophy of Science Program, McGill University, Montreal, Quebec

The Audubon Society Field Guide to North American Insects and Spiders


The creation of a field guide is always a difficult task because a number of conflicting requirements are made of such books. To appeal to the broadest audience (usually one with little background in the subject) the guide must be simple to use and unencumbered by excessive technical jargon. At the same time, any field guide must be accurate, be up-to-date, and provide as much pertinent information as possible. That both of these guides come close to fulfilling the first set of requirements is due primarily to the unique format that has by now become a trademark of this series.

Colour photographs are relied on as aids to identification; the 600-700 photos of individual species comprise the first section of each guide. The various species are grouped into sections on the basis of similarities of shape and colour, and identification is easily accomplished by first locating the correct general shape and finally by combining individual photographs with morphological descriptions from the text.

The second, and major section of each guide provides, in addition to the morphological description, notes on habitat, range, food or host, life cycle, and finally miscellaneous comments, which usually take the form of systematic notes. The guide to butterflies provides, in addition, short notes on flight period and on major distinguishing features of similar species.

In the case of the volume dealing with the insects and spiders this approach, overall, has met with only moderate success. The relatively novel grouping of the colour plates, while overcoming some of the basic problems of identification guides, has also created new ones. For example, in the section dealing with bees and wasps one applauds the inclusion of the Syrphidae and other bee-like insects which are commonly mistaken for bees. Unfortunately this approach has been carried to extremes in some cases, and certain arrangements seem destiny to confuse rather than aid in identification. The inclusion of the mayflies, for example, among the Diptera assumes a simplemindedness that is unlikely to be the case since even to the novice these insects bear little resemblance to flies. Similarly, based on their overall appearance, the owflies and ant lions should have been included with the dragonflies rather than the Diptera, a fact the text itself acknowledges.

While for the most part of excellent quality, in some cases the photographs themselves hinder accurate identification. Some, such as the photographs of larvae of the blackflies (Simuliiidae) and net-winged midges (Blephariceridae), are taken from so great a distance that they are unrecognizable beyond being dark spots on a rock. A few misidentifications (e.g. *Hesperophylax* as *Grammotaullius*; a Caenidae nymph as *Baetidae*) further detract from the book.

Those anticipating a full taxonomic treatment in the text will be disappointed to find that within each order only a few families (usually those containing the larger or shower species) are mentioned. In turn, under each family heading only a few species are considered in detail. While those listed are usually the more common species, this is not always the case. In some families, for example the biting midges (Ceratopogonidae), the only species described is one of extremely local distribution. Thus the unfortunate impression is given (and remains uncorrected in the
rest of the text) that the family itself is extremely local.
These, as well as some dated classificatory arrangements, mar what is one of the best efforts yet to provide an easy to use field guide for those with little entomological background. While by no means worse than any other field guide to the insects and spiders, one final caution must be made. The temptation, easy to succumb to considering the format, to identify everything one sees to species should be firmly resisted. The incompleteness of a guide describing in detail fewer than 700 species out of a total fauna of more than 100 000 species is readily apparent.

The guide to the butterflies, by contrast, has avoided many of the problems mentioned above. Because the total fauna covered is only about 700 species, a fuller taxonomic treatment is possible. Ironically, this completeness serves to underscore many of the identification problems present in entomology as a whole. Only when trying to determine differences in two seemingly identical species of butterflies do the true difficulties of species identification become apparent.

Some basic problems with the photographs are very much in evidence. Blurriness, obscured taxonomic characters, and colour wash-out all serve to make identification of some species very difficult. Identification of some Colias species, for example, may have to be abandoned for these reasons.

One major strength of the guide lies in the inclusion of a selection of photographs of immature stages. These, coupled with an index to species of host plants preferred by the caterpillars, should assist considerably in identification of the immatures.

The adoption of a number of recent taxonomic changes in the text may meet with some initial resistance by some users who may object to the shifting of the majority of Boloria species to the genera Clossiana and Procollossiana or similarly the shifting of Pieris species to the genera Pontia and Artogeia. Widespread acceptance, however, should gradually overcome any problems.

On the whole, the completeness of the information accompanying the plates, the ease of use in the field, and the transcontinental treatment of the fauna should go a long way toward making this one of the most successful field guides to the butterflies. A success, one might add, which it works hard to achieve.

Rein Jaagumagi
Royal Ontario Museum, Department of Entomology, 100 Queen's Park, Toronto, Ontario M5S 2C6

Character Variation and Evolution of Sibling Species in the Empidonax difficilis-flavescens Complex (Aves: Tyrannidae)


This book should be perused by those naturalists wanting details of the similarities and differences between two hard-to-differentiate Empidonax species (Western Flycatcher, E. difficilis and Yellowish Flycatcher, E. flavescens). The author measured and/or analyzed body weight, color, bill, toe, feather and wing length for more than 1280 specimens during a 10-year study involving 6 years of field work. More than 200 individuals were used to prepare more than 5000 spectrographs of songs. Objective multivariate analyses are conducted regarding the variation of habitat, song and morphology among 50 populations ranging from British Columbia to Panama within these two taxa. Many passages enlighten probable relationships among other flycatchers of North America. The Dusky, E. oberholseri and Hammond's, E. hammondii, flycatchers are heavily considered.

All populations of Western and Yellowish flycatchers considered utilize shaded woodlands near flowing water for breeding. Males are slightly larger than females in both species, but E. flavescens is more sexually dimorphic than E. difficilis. Inland birds are larger than coastal birds. A see-saw pattern of deep bill depths, low song pitches, long toes, wings, and tails alternates with shallow bill depths, high song pitches, short toes, wings and tails over the geographic range of these flycatchers. Migratory populations have relatively pointed wings while non-migratory populations have rounded wings. In a comparison among the Western, Yellowish, and Hammond's flycatchers, the trend in variability for morphology at the intrapopulation level is antipodal to that at the interpopulation level.

The text is written in the style of a highly detailed scientific journal article with several sections reading like regular book chapters. Appendices include details of capture localities and comments on specimens. The text is relatively free from typographical errors and reads easily but several areas are too detailed (especially page 98). The photographic reproduction of most of the plates purporting to show habitats is of
A World List of Mammalian Species


This is a somewhat useful listing of the world’s living and recently extinct mammalian species. The ordinal name, geographical range, and habitat are listed for each species. Information is provided on feeding habits, endangered status, and whether or not the species was introduced by man to an area. Synonyms of generic and specific names and the general acceptance by professional taxonomists of a given taxonomic scheme are dealt with. The higher classification scheme (ordinal name arrangement) generally follows Simpson (1945, Bulletin of the American Museum of Natural History 85: 1-350) but deletions, additions, and changes to taxonomic relationships occur in some areas.

The text has many errors and/or omissions. For North American mammals, for example, the text does not list the Whitetail Jack Rabbit’s (Lepus townsendii) range as occurring in Canada even though the species occurs in five provinces. The North American Wolverine’s more widely encountered scientific name, Gulo luscus, is not listed as a synonym of its less widely encountered but officially accepted name, Gulo gulo, the common European name. Spermophilus elegans is not listed as a species but has been deemed a full species for several years. Pitymys pinetorum is listed even though it has been officially designated as Microtus pinetorum for some time. The entire chipmunk genus Eutamias has been changed to Tamias in the text but this change has not officially been accepted (e.g. Ellis and Maxon, 1979, Journal of Mammalogy 60: 331-334). The authors discuss recent extinct mammals but the Sea Mink, Mustela macrodon, is not mentioned. Many other errors occur throughout the text involving mammals on all continents. The bibliography is cumbersome because references are not listed alphabetically with respect to author nor are they listed in any other useful order.

Overall, this treatment on world mammals does not accord well with other treatments of its kind (e.g. Walker, E. P., 1975, Mammals of the World. 3rd edition. Johns Hopkins University Press, Baltimore, Maryland.) For these reasons, I cannot recommend this book for use by persons interested in deriving definitive, professional information on mammalian species’ scientific names, habitats, or geographic ranges but can recommend it for use as a usually correct listing of some interest. When a rigorous definitive set of taxonomic data is needed, the information contained in this text will have to be extensively checked against other references.

RICHARD M. ZAMMUTO
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A Field Guide to the Birds of Australia


The appearance of a one-volume, detailed, well-illustrated field guide to the birds of any region is usually a welcome event. Graham Pizzey’s A Field Guide to the Birds of Australia, illustrated by Roy Doyle, is a beautiful book, which promises to supersede previous guides to the avifauna of Australia. While its slightly larger format, and correspondingly heavier weight, will play havoc with pockets used to carrying one of the two volumes of Peter Slater’s earlier Field Guide to Australian Birds, the contents and illustrations of the new guide will make it worthwhile for any native or visiting field ornithologist to carry it in a shoulder bag or backpack.

The book is divided into four sections of unequal length.

1) A short introductory chapter explains how to use the guide and how to recognize birds by the use of the “Peterson system of distinguishing field marks.” It includes notes on classification, on common names of Australian birds, on expressions used (such as “eclipse plumage”), and on birds sounds. A brief discussion of the illustrations in addition to sections on habitat, range, status, subspecies, and race complete the “Introduction.”

2) The major part of the field guide contains species descriptions of all birds recorded in Australia up to December 1975. The brief introductory text to each family of birds includes notes on food, range, and number and species within the family. Species accounts include field marks, similar species, voice, habitat, breeding (where appropriate), range, and status. Each species of Australian birds has been assigned a species number by the author. This number is extensively used in cross-referencing on the plates, range maps, and in the indices. “Field marks” includes not only characteristic adult plumages but also immature, and in many cases juvenile, plumages. Outstanding field marks are italicized and characteristic behaviour patterns described. “Breeding” contains pertinent nesting data and, where information was available, the breeding behaviour of the parent bird. In the text the assigned species number and the plate number of the corresponding illustration appear in heavy print, as do English names, printed in capital letters. Scientific names are in smaller print and where several vernacular names exist “other names” are also listed.

3) The eighty-eight plates by wildlife artist Roy Doyle include 32 in black-and-white. These depict either hawks, shorebirds, ducks, swifts, and swallows in flight or those species, such as cormorants and shearwaters, “that are mostly gray, black or white.”

The author admits that these “are reproduced in monotone for economy and because recognition in flight is often based on style rather than colour.” Some of the “monotones” are striking, such as those on Boobies, Frigatebirds, and Cormorants (Plates 6, 7, and 8). The lines and contrasts are sharp and crisp. In comparison, some of the others, such as those on flight illustrations of Albatrosses (Plate 3), Petrels and Shearwaters (Plate 4), and Australian Pelican and waterfowl (Plates 9-12) seem washed out. Waders in flight (Plates 37 and 42) are also somewhat faded, which impression is further aggravated by the general crowding of these plates caused by the need to depict both breeding and non-breeding birds of the same species.

The majority of colour plates are stunning. Field marks are clearly visible. Each illustration is much more than a mere schematic representation of a bird. While crowding still occurs on some plates, the effect is not nearly as disturbing in colour as in monotone. A minor complaint concerns the green colour used for the legs of several waders which does not correspond with the description of leg colour in the text. The illustrations are reproduced on good quality semigloss paper. Plate numbers, species numbers and titles are in bold face print. A scale bar appears on each plate to be used on that plate only.

4) Distribution maps occupy the last part of the book. These are supposed to represent the “breeding distribution of all species” on the Australian continent and in surrounding waters. Further examination of the range maps reveals, however, that 38 of the 633 maps are of wintering birds belonging to the Suborder Charadrii [waders]. Moreover, in the introduction to the Charadrii the author stresses that “most species [of this suborder] found in Aus. are migrants, breeding mostly in n. hemisphere, migrants to s. hemisphere during Aug.-Oct., leaving again Mar.-Apr.” While inclusion of range maps of these regular migrants is absolutely necessary to aid Australian field ornithologists more careful proofreading should have eliminated such confusion.

No field guide will ever please everyone. As D. L. Serventy says in the “Forward”, “The virtue of a field guide is that it contains all the information necessary, in pictures and text, to identify a bird.” Graham Pizzey succeeded in producing an eminently readable, well illustrated, one volume field guide. Its minor faults should not discourage anyone interested in Australian birds.

MARIANNE GOSZTONYI AINLEY

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Bird Banding in Alberta

Edited by Martin K. McNicholl. 1981. Alberta Naturalist Special Issue No. 2. Federation of Alberta Naturalists, Box 1472, Edmonton. 73 pp., illus. $3.00 (plus $0.50 postage).

Bird Banding in Alberta, a potpourri of thirteen articles describing a variety of Alberta bird-banders and bird-banding studies, was published especially for the 1981 meeting of the American Ornithologists' Union in Edmonton. There is no introduction to explain the origin and purposes of the compilation: however, an article by editor Martin McNicholl, entitled “Banding in Alberta: an overview”, partly makes up for this. In it, McNicholl summarizes the amount of banding effort expended on various groups of birds and highlights the work of a number of individual banders in Alberta.

To some extent, the volume can be considered a tribute to the late Professor William Rowan, pioneer Alberta bird-bander; a critical but thoughtful 1928 paper by Rowan, entitled “The scientific aspects of bird-banding”, is reprinted therein. Also included are biographies of Edgar Jones and the late Ken Trann, two well-known Alberta banders, plus a rather whimsical autobiographical article (first published in 1940) by Kathleen Salt, wife of Birds of Alberta author Dr. Ray Salt. The report is dedicated to Ken Trann, whose untimely death at the age of 36 robbed Alberta of one of its most promising amateur ornithologists.

The other eight articles deal with studies of particular bird species that involve banding. These species include Ferruginous Hawk (Ray Salt); Merlin (Alan Smith); Tree Swallow and Mountain Bluebird (Donald Stiles); Ring-billed Gull (Chip Weseloh); Black-capped Chickadee (Martin McNicholl); Dipper (David Ealey); birds of prey in general (Richard Fyfe and Ursula Banasch); and a Peregrine Falcon release program (Allen Wiseley). Salt’s article is a reprint of a 1939 paper, but the others are original contributions to the scientific literature.

The volume is well edited, and typographic and other errors are few. Although its subject matter is rather specialized, it will be of interest to all bird-banders and to others interested in the ornithology of western Canada. For these persons, Bird Banding in Alberta is certainly worth its modest price.

WAYNE C. WEBER
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Aquatic Entomology: The Fishermen's and Ecologists' Illustrated Guide to Insects and Their Relatives


The recent rise in popularity of aquatic entomology can be directly measured by the number of new books that have appeared on the subject. The general increase in awareness of our environment as well as the importance of aquatic organisms in environmental studies can be deemed primarily responsible for this explosion of literature. In this latest work two of the groups most conscious of the state of our aquatic ecosystems, fly-fishermen and ecologists (i.e. naturalists and conservationists) have been targeted.

The arrangement of the book assumes little formal training in entomology and proceeds to fully educate the reader in all the basics from collecting techniques to life histories. Special attention is paid to the problems encountered in living in an aquatic environment and the resultant adaptations that have developed to overcome these problems. McCafferty also makes a commendable effort towards breaking down the traditional language barrier that has existed between entomologists and fly-fishermen by correlating the two very different systems each has employed for naming insects.

While the book deals briefly with most of the major groups of aquatic organisms, the prime emphasis is placed on the insects. To this end, picture keys (of the type commonly found in some field guides) are used to identify adults and larvae to the ordinal level. This same system is used to key larvae to the family level (adults are keyed only for Coleoptera, though adults of each family are discussed in the text). Incorporating material from most of the major entomological works, these keys are both accurate and easy to use.

The text for each section presents notes on general biology and habitat as well as including a short morphological description of all life stages for each family. In addition to this taxonomic and ecological information, a specific attempt has been made to include material of particular use to fly-fishermen such as the best time or manner in which to fish with a certain fly.

Primarily for the benefit of the fly-tier, though certain to be enjoyed by others, is a series of 16 color plates of Provonsha's stunning illustrations. One however must take exception with McCafferty's
expectation that these will prove useful for field identification. It is unlikely that a book as large and heavy (and as expensive) would ever find its way into the field more than once.

It is only in this mode of publication that one can find any major fault. That a book so obviously geared towards being a field guide should be presented in a hard-cover, over-size format severely limits its use precisely where it would have been most beneficial.

While likely to be dismissed by the serious student of entomology as merely a coffee-table book on aquatic insects, this book is excellent as a basic guide for non-entomologists. Interested amateurs seeking a single source book on aquatic insects need look no further. This book has been produced specifically for them and should provide many hours of interesting reading.

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Atlas of North American Freshwater Fishes


This massive compendium fills a gap in the literature on North American vertebrates that has been begging for attention for over a century. For the first time, freshwater fish biologists have a text available which provides comprehensive coverage of all freshwater fishes found north of Mexico, comparable to those long available to ornithologists and mammalogists. It is a treasure-trove of information on fishes, much of which was previously scattered in diverse, difficult-to-obtain publications or remained unpublished. The authors and their compilers have done a great service for students of fishes, particularly zoogeographers, who will no longer have to cover their desks with the many regional publications once needed for general work of this nature. But wait! The authors caution again and again that this is only a provisional, working volume, produced using numerous shortcuts, in order to make it rapidly available to fish biologists for continuous revision toward production of a revised edition. Therefore, pick it apart if you will, but send your criticisms to the authors so that they can correct, revise, and make available this information to all of us.

The Atlas covers approximately 775 North American freshwater fishes including 32 exotics known to reproduce successfully here, some extinct species, and about 100 anadromous, catadromous, and marine forms known to occur in fresh water. Freshwater fishes confined to Mexico were excluded for various reasons. Information on each species is provided in a standard format including Order and Family, scientific and common name, distribution map(s) and brief statements summarizing present knowledge of type locality, systematics, distribution, habitat, adult size and general biology. The fishes are arranged phylogenetically (primitive to advanced) except that within a

family, genera and species are in alphabetic order.

In general, the authors have achieved admirably the goals they set for themselves, but there are shortcomings which could have been easily overcome with just a bit more care and a little outside review. As a zoogeographer and a map-oriented person, I take exception to some of the maps used in the text. In all maps of eastern Canada, something is very wrong with the shape and size of Nova Scotia, the size of Prince Edward Island, the placement of Cape Breton, and Anticosti Island is missing. The Canadian Arctic Islands are shown in great detail on the cover illustration but on maps in the text islands north of Baffin are omitted even where there is space for them. They are important to the distribution of species such as Arctic char. On the other hand, Mexico is figured in many of the maps in the text (because distributions of some species extend south to there) but is excluded from the cover illustration except for Baja, California. Mexico is part of North America and Baja is part of Mexico, so why the discrepancy? Since maps form at least half the total page space and this is an Atlas, more care should have been taken for their accuracy and consistency. It is also probable that a bit more proof reading by external referees would have corrected many deficiencies in the distribution maps. Locality records for many well known species such as Atlantic salmon were unrepresented even when they were readily available in the literature. There is a lot more work to be done before a definitive edition of this Atlas is available.

The low-cost production method for this edition has put the price within reach of everyone and no student of North American fishes should be without a copy.

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Principles of Fishery Science

Fishery science, in the broad sense intended by the authors of this book, embraces diverse disciplines such as limnology, oceanology, meteorology, hydrology, geomorphology, nutrition, pathology, engineering, economics, sociology, political science, physiology, and ecology in the "...application of scientific knowledge to the problems of providing the optimum yield of fishery products...". Clearly then, the authors stated purpose, "...to help students and professionals reach a thorough understanding of fishery science", is an ambitious one. It is somewhat unrealistic in its assumption that persons with such capacity for understanding do indeed exist. Perhaps I am splitting hairs, but I believe that the most which could be expected is to bring fishery biologists and ecologists to the realization of how important it is to consider input from, and promote interaction with, practitioners of other relevant disciplines. This is, at best, what the book achieves.

Inextricably associated with transdisciplinary attitude to fishery management is the concept of optimal yield, which is mentioned here and there in this book. Unfortunately, the reader is pretty much left alone to figure out what it means. An inking, but only that, is given of the potential for conflict of interest in determining which aspect of fishery yield ought to be optimized. For example, the co-existence of sport and commercial fishing opportunities requires considerable compromise on both parts. Among themselves, sportfishermen may disagree as to whether a water body should be managed for trophy fishermen or those who just wish to catch a fish, regardless of size.

An extremely complex picture emerges when, as is frequently the case for river and reservoir fisheries, competing demands on water (e.g. for hydropower or pollution abatement) or on floodplains (e.g. for agriculture and construction) are considered. Large scale marine fisheries may experience similar conflicts among alternatives, for example optimizing revenue or employment, or the preservation of traditional lifestyles. These are the types of problems which a modern fishery manager may expect to encounter. Although a sense of this is given throughout the book, I would have preferred a more cogent statement at some point.

No matter what objectives are desired they must be set within the context of biological reality. In the past, definition of this reality has been the preserve of population dynamics. Fully a third of the Principles of Fishery Science has been devoted to elaborating the techniques commonly practiced in the study of fish populations. I found this to be a clear and concise treatment of what is, for many students, a difficult subject. The authors do present a trophodynamic model of a lake ecosystem as an example of the community or ecosystem approach. However, many of the recent developments in the responses of communities to exploitation, based on studies of north temperate lakes, tropical-shelf fisheries, and the Great Lakes of Africa are ignored. Whereas it is true that 'multispecies' approaches have not yet been developed to the point of general applicability, and probably will not be for some time to come, there is likely to be much activity in this area in the near future. Any text on fishery science should attempt to create a sense of excitement about its potential.

Following the chapters on population dynamics are several which are an odd assortment in that they deal with rather specific topics, mostly relating to the manipulative management of small scale freshwater fisheries, primarily recreational. Fishery scientists involved in the management of large scale commercial marine fisheries will find little here that is useful, interesting though it may be. But then, even through the chapters on population dynamics there is a distinct bias towards techniques most frequently applied in studying freshwater fish populations. For example, sequential population analysis, one of the most widely used techniques in the analysis of marine fish stocks, is not presented. In my opinion this bias serves only to emphasize the diversity of fishery situations and the difficulty of adequately treating them all in a single introductory text.

Finally, I feel some responsibility to colleagues who already have on their shelves the first edition of this book. There is evidence of updating, perhaps most extensive in Chapter two, 'Characteristics of Fisheries'. However, most of the increase in size of the volume is due to the addition of an appendix entitled 'Review of Mathematics and Statistics', which this reviewer did not attempt to assess in detail. I was disappointed to note that nowhere was the reader referred to the revised (1975) version of Ricker's 1958 monograph Handbook for Computation of Biological Statistics of Fish Populations. Similarly, the continued reference to the 1964 edition of Fish Catching Methods of the World in spite of a substantially revised 1972 version is a trivial but unnecessary disservice to the reader.
The Hawaiian Goose: An Experiment in Conservation


“What is so special about the Hawaiian Goose that a book need be written about it? The answer is that it has become a classic symbol of Man’s unconscious destruction of nature and, later, of his conscious efforts to conserve. As is so tragically typical for many island birds.” With these words Janet Kear and Andrew Berger begin an interesting and scholarly monograph summarizing the presently available information on the Hawaiian Goose (Branta sandvicensis) or Nene (nay-nay) as it is called by the Polynesians.

The Hawaiian Goose is the State bird of Hawaii. Being endemic to the island of Hawaii, it has the smallest range of any species of goose. When Captain James Cook “discovered” the Hawaiian Islands in 1778, the Hawaiian Goose population is estimated to have been around 25,000 birds. The goose population began declining shortly after “discovery” due to Man’s direct (hunting, catching live birds and eggs, and disturbance of behavior and nesting patterns) and indirect (introduction of goats, pigs, mongooses, dogs and cats; and habitat deterioration) activities. By 1952 the population was estimated at less than 30 birds. Through private and public financing, from many sources, a Hawaiian Goose restoration program was begun in 1949 and has expanded greatly since that time to include both a program in the Hawaiian Islands (especially at Pohakula) and at the Wildfowl Trust at Slimbridge, England. Starting with two geese in 1949 at Pohakula, over 1700 Hawaiian geese have been reared and re-introduced to the wild through efforts of Ah Fat Lee and Sir Peter Scott. At the time of publication of The Hawaiian Goose the population of geese has increased to an estimated 750 birds in the wild and 1250 in captivity. The Hawaiian Goose is affectionately, dedicated to Ah Fat Lee and Sir Peter Scott for their loving efforts in the Hawaiian Goose restoration program and for helping change the goose’s status (in the I. U. C. N.’s Red Data Book) from an endangered species to a rare species.

The Hawaiian Goose summarizes biological data on the species obtained in both its natural habitat and in captivity. The book is divided into two obvious sections accordingly. Differences in style indicate the portion of the book dealing with the Hawaiian Goose in England was written mainly by Janet Kear while the Hawaiian section was written by Andrew Berger. However, this difference did not detract from this monograph’s overall readable and interesting style.

I found the book to be relatively free of errors. The tables and figures are pertinent and easily understood. The photographs are of excellent quality and relevant, however, I wish they had been in color. The illustrations of Hawaiian Geese by Joe Blossom, Tim Halliday, Sir Peter Scott, John Turner and Gwyn Williams were excellent, however, I was even more impressed by the outstanding pen-and-ink drawings of Hawaiian Goose food plants by Sue Monden.

The Hawaiian Goose is closed with reflective thoughts. “The example of the Nene . . . is often quoted as one of the few instances where a species has been saved from extinction by captive breeding. The propagation programme, which has resulted in the restocking of the wild, has become something of a conservation legend. But has it been an unqualified success? . . . the species has been saved from extinction. In that aim, the programme has obviously succeeded, and succeeded extremely well.”

“Nevertheless, we are justified in asking whether the thousand and a half released birds have increased the breeding potential of the wild Hawaiian Goose . . . In restricted inbred populations, genes for deleterious characters which are generally recessive, are more likely to be brought together and their effects emerge in the offspring . . . Many natural selection pressures, as well as those imposed by inclement weather are removed during captive breeding.

“Not only can birds carry deleterious genes survive captivity, but there may be inadvertent selection of characters that stand the captive animal in good stead and yet would be disadvantageous in the wild. Only those individuals that tolerate captivity will breed, and they may do so because they have a lower reaction to sudden noises and strange objects than their fel-
lows. They are clearly 'tamer', in that they will allow human proximity during the breeding season."

"Conservation is generally expensive and it is not always easy to decide how to allocate funds that are available. Initially, money should perhaps be used to purchase reserves in which rare animals can continue to live undisturbed. These reserves may need to be vigorously protected, both from man and from his domestic and introduced animals and plants... In the case of birds, eggs may be collected, and the young raised and released at an early age into the habitat. More animals can survive to adulthood by this method than if the parents rear their own young, but it is probably only sound policy for a species with relatively little dependence on traditional learning. Only as a last resort, as with the Nene, should animals be taken into captivity, bred and released."

*The Hawaiian Goose* is a comprehensive (considering present knowledge) and scholarly monograph which should be of interest to professional biologist, bird watchers, island ecologists and waterfowl enthusiasts. I found it fascinating reading.

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**BOTANY**

**The Fossil Hunters: In Search of Ancient Plants**


This book is an extremely interesting and readable account of the history of paleobotany. It is a worthy companion-piece for Andrews' earlier book *Ancient Plants and the World They Lived In*, which portrays the kinds of plants that prevailed in past geological periods. The approach is far from being duly systematic; rather it is based on a series of pithy biographical sketches of people who have contributed most to the field. Quotations from letters, anecdotes, and well chosen photographs add to the vitality of the book. The author makes no attempt to present only the favourable side of the workers mentioned. In addition to the work of many famous scientists, Andrews emphasizes the significant contributions of keen amateurs — a group that has a special place in the hearts of all paleobiologists.

The author traces the growth of paleobotany from the late 1600s to the 1970s. He develops, in unusual detail, contributions of several late 17th and 18th century naturalists, and this is one of the great strengths of the book. Among the most influential of these naturalists are: Robert Plot, Edward Lhwyd, Martin Lister (the famous physician), and John Woodward — perhaps the most important paleobotanical collector of his time. Johann Jakob Scheuchzer of Zurich receives special praise. He carried the British work to a more advanced level. Andrews states... "if one wishes to point to any one man as the first paleobotanist, he seems deserving of the title". Scheuchzer's *Herbarium Diluvianum* of 1709 stands as the first really comprehensive and well-illustrated book on fossil plants.

Andrews then turns to the remarkable advances made in paleobotany during the 19th and 20th centuries. Chapters are devoted to important workers like Adolph Brogniart and Kaspar Sternberg. Brogniart's study of silicified seeds from Autun and St.-Etienne, is described as one of the great landmarks of paleobotanical literature. The author compares Brogniart's fine "biological sense" and excellent classification of plants (as exemplified in the *Historie*) with Sternberg's more comprehensive *Flora der Vorwelt* — the official starting point for the naming of fossil plants.

For about 40 years following the closing years of the 19th century, Sir Albert Seward was the dominant figure in paleobotany. In addition to the remarkable breadth and depth of his botanical knowledge, and his influence on students, Seward's 600-page *Plant Life Through the Ages* set his stamp on the period. The latter book reveals a particular interest in plant geography and paleoclimatology. In his chapter "The Age of Seward", Andrews comments on Marie Stopes' paleobotanical contributions. This is enlightening, because most biographies stress her books on sex and pioneering birth-control work in Britain.

Canadians will be interested in the section on one of this country's greatest naturalists, Sir J. W. Dawson. Dawson first encountered fossil plants as a schoolboy in Pictou, Nova Scotia. While digging for flakes of clay-shale to cut into pencils, he was surprised to find one with... "a delicate tracing in black, of a leaf like that of a fern... I was puzzled by the question whether they were real leaves or not, if real, how they came to be in the stone." Evidently the beginning of his important studies of Devonian plants began with a short visit from Sir William Logan (first Director of the Geological Survey of Canada) in 1843. "He showed me drawings of fossil plants he had observed,
which, for the first time, gave me the idea I afterwards followed up, that Gaspé might afford a fossil flora much older than that of the coal formation [Carboniferous]." Andrews remarks that . . . "palaeobotanists are people, and have most of the usual good and bad points". He recounts one particularly acrimonious dispute between Dawson and William Carruthers of the British Museum of Natural History over the identification of Protaxites, concluding "Most of the specimens of Protaxites that I have seen are rather poorly preserved, and I have some sympathy with Dawson’s erroneous interpretation."

After reading the Epilogue, I am left with a clear impression of the author’s wisdom, his intense interest in scientists as people, his great experience (40 years!) in the field of palaeobotany, and the extraordinary vigour with which he has pursued his subject. This book will have a broad appeal for people interested in the history of science, and will be of particular value to students of botany, palaeontology and geology. I heartily recommend it.

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The Biology of Bromeliads


The author states that the book was written to bridge the gap between the highly technical and the popular literature that is currently available on bromeliads. He notes that two audiences are addressed, the serious grower of bromeliads and the botanist.

The introduction includes a complete historical account of bromeliad knowledge. A brief review of classification includes an explanation of terms such as species, taxonomic and horticultural varieties, forms, ecotypes, and cultivars. A large portion of the book is dedicated to presenting general plant biology topics such as plant anatomy and morphology, cell biology, and plant physiology with bromeliad examples.

The sections on mineral nutrition, photosynthesis, and photosynthetic strategies are good reviews of the current knowledge of these subjects. Much of the basic research in these fields was done by the author. He uses this knowledge as a basis for speculation about the significance of pigmentation and leaf arrangement in the Bromeliaceae. Later chapters treat these topics in greater detail and offer further observations and speculations by the author about the ecological significance of bromeliad morphology, anatomy and physiology.

Cytology, genetics, reproduction mechanisms, dispersal, and photoperiodism are reviewed and discussed. The chapter on reproductive structures outlines the author’s interpretation of the tendencies of floral specialization within the Bromeliaceae and describes the floral and inflorescence diversity within the family.

Although little is known about pollination in the Bromeliaceae, the knowledge of pollination ecology and reproductive strategies in the angiosperms, in general, is used as a starting point from which to extrapolate to bromeliad examples based on what is known.

Seed development, ontogeny, and seedling development are reviewed. Neotony has previously been suggested as the method by which the “atmospheric” tillandsioids evolved from water impounding “tank” bromeliad precursors. The author discusses this possibility, and the evolutionary significance of the phenomenon as it relates to the tillandsioid bromeliads.

A final chapter addresses the horticultural significance of some of the previously described topics and offers some cultural suggestions.

This book is the most complete and authoritative text currently available on the subject of bromeliad biology. It pulls together much scattered literature and suggests gaps in our knowledge of the Bromeliaceae. Good line drawings, diagrams and tables make the text easy to follow. A number of black and white and colored photographs are used to illustrate structure and pigmentation. A shortcoming is found, however, if the goal set out in the preface is to be reached. Although the text is more technical than the popular bromeliad literature, the glossary will make the book accessible to the bromeliad grower. Some literature references are made, but a number of ideas are presented that are not clearly original with this publication, for which no literature is cited. This work would be of greater value to the botanist and student if greater attention had been given to literature citations.

The book is highly recommended as a good introduction to the family for the bromeliad grower and botany student alike.

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The Illustrated Flora of Illinois: Flowering Plants


In my second review of a book of this series (Canadian Field-Naturalist 92:413. 1978), I presented a list of the volumes that had appeared at that time, subsequently, such lists began to appear on the jackets of succeeding volumes. For the convenience of readers of the Canadian Field-Naturalist it will be useful and convenient to reproduce the latest list here as of June, 1981 (the date given on the jacket). All books are by Robert H. Mohlenbrock aided by a distinguished panel of editors which I listed in my earlier review.

Ferns. 1967. $8.19
Flowering Plants: Flowering Rush to Rushes. 1970. $10.00
Flowering Plants: Lilies to Orchids. 1970. $10.00
Grasses: Bromus to Paspalum. 1972. $11.70 (CAN)
Grasses: Panicum to Danthonia. 1973. $16.28 (CAN)
Sedges: Cyperus to Selneria. 1976. $15.00 ($19.39 CAN)
Flowering Plants: Hollies to Loasus. 1978. $16.80
Flowering Plants: Willows to Mustards. 1980. $18.00
Flowering Plants: Magnolias to Pitcher Plants. 1981. $22.95.

A total of eight volumes have been published; one on ferns, five on monocotyledonous and two on dicotyledonous plants. The treatment of Carex is yet to appear to complete the Monocotyledons.

My immediate reaction to this list was to note the escalating cost. The final volume is double the price of the first and I dread to think what the future price for the final volume will be. And, of course, with static or reduced library budgets and the current exchange of the U. S. dollar, one becomes apprehensive concerning just how our libraries are going to maintain their levels of excellence without a reverse in the inflationary trend.

In the Willows to Mustards there appears a list of superb illustrations by Paul Nelson, a Foreward by Mohlenbrock, a country map of Illinois, an introduction in which it is explained that the series is following a modified Thorne classification (modifications included use of Hypericaceae for Clusiaceae, the separation of Asclepiadaceae from Apocynaceae, the separation of Apiaceae from Araliaceae and the recognition of Phymataceae which was included in Verbenaceae by Thorne). The list is presented in its entirety with those families contained in this volume appearing in boldface. This volume covers Thorne's Orders Salicale (1 family, Salicaceae), Tamaricale (1 family Tamaricaceae with 1 monotypic weedy genus — Tamarix gallica L.) and Capparidale (3 families, Capparidaceae, Redaceae and Brassicaceae).

Each Family is described, followed by a key to genera. Each genus is described followed by a key to species (called key to taxa because lower ranks are included). Each species is provided with principle synonymy, a description, then followed by the Common Name, Habitat, Range, Illinois distribution. For each species there is a superb full page line drawing, showing habit, or portion of a branch in the case of willows, an enlargement of floral parts, and a dot map for Illinois. The dots are placed exactly in the center of each county and do not show precise location, not too serious in a map 2 x 3 cm for Illinois and for a state where most countries are about equal in size.

Keys are of the bracketed type with one indentation permitted, a device which avoids some of the confusion which arises with the use of the standard bracketed key and yet still retains the printers advantage of uniform blocks of typeset.

The willows are well-presented with clear descriptions and references to the principle willow workers as Ball, Swink, Fernald, Argus, Jones, etc. consistently referring to them in the present tense when, for some of them, past tense is more factual. Twenty-four native, adventive and commonly cultivated species and one hybrid are included. I was pleased to learn that the common pussy willow of the florist is usually Salix caprea L. the Goat Willow, but why it is called Goat is not explained. Seven species and two hybrids of Populus follow to complete the Salicaceae.

The preferred spelling of the Order Capparidales is adopted rather than the conserved Capparales, following Crosswhite and Itlis, and the use of Polanisia Raf. over Cristatella Nutt. is employed. An interesting adoption of Cleome hassleriana Chod. for the Spiderplant arises over the use of C. spinosa L. and C. speciosissima Deppe.

For the Mustards the family name Brassicaceae is employed following Thornes usage of "-aceae" endings for all families. This important group of plants consists of 38 genera, 80 species and numerous varieties in Illinois. A summary of the taxa treated in the volume follows, they are: 5 families, 44 genera, 137 species, 17 lesser taxa and 4 hybrids. There is a 4 page glossary which doesn't add much as it is too short to be very useful. A list of reference and index completes the volume.

On the whole, this is a very fine volume which brings together some of the contentious mustards into
The volume "Magnolias to pitcher plants" continues the series, using the modified Thorne system. This is the third volume on dicots and subsequent volumes will appear as they are completed rather than in strict taxonomic sequence. The plan is similar: a Foreword by the editor/author, a county map, an introduction containing the Thorne classification, the text proper, a summary of taxa (15 families, 52 genera, 110 species, 13 lesser taxa), a short glossary, literature cited and index. The volume covers the Order Annonales (Magnoliaceae, Annonaceae, Aristolochiaceae, Calycanthaceae, Lauraceae, Saururaceae), the Berberidales (Menispermaceae, Ranunculaceae, Berberidaceae, Papaveraceae), the Nymphaeales (Nymphaeaceae, Nelumbonaceae, Cabombaceae, Ceratophyllaceae) and Sarraceniales (1 family, Sarraceniacae).

The treatment of Ranunculus (with 25 species in Illinois) follows the classification of Benson's 1948 treatment but does not take advantage of the more recent study of the R. hispidus complex by Thomas Duncan (1980, University of California Publications in Botany 77: 1–125), probably because the manuscript had already gone to press, but it is a pity it could not have been followed.

I note too, that Brasenia Schreb. finds its way into the Cabombaceae, rather than the customary Nymphaeaceae, emphasizing the trend to separate families for genera that do not seem to be too closely related. This is a deliberate modification of the Thorne classification by Mohlenbrock who recognizes the Nelumbonaceae, Cabombaceae and Nymphaeaceae as distinct families rather than as subfamilies of the Nymphaeaceae, a view with which even without study, I should be inclined to agree.

The illustrations in this volume were prepared by Mrs. Meriam Wysong Myer except for one and parts of two others which were done by Mark Mohlenbrock, the author's son (and just as skillfully, too). The quality is every bit as good as those by Nelson in the preceding volume. Some, however, are not full page and the remainder of the page is filled by text. In some cases they were of such a size as to make it not worthwhile to include text, resulting in wide lower margins.

There is no doubt that this volume succeeds in its presentation of this group of species for Illinois, both in the written portion and in the illustrations.

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Moulds: Their Isolation, Cultivation and Identification


This book is intended as an introduction to the laboratory study of moulds. Its eight chapters deal with general characteristics, classification, natural occurrence, cultivation, isolation, contamination, microscopy and identification of these fungi.

Moulds are defined as mycelial fungi commonly encountered in the home or laboratory and which can be easily grown and studied. The four main phylogenetic groups that contribute to the mould flora (omycetes, zygomyces, ascomycetes and basidiomycetes), along with the imperfect fungi, are well documented and illustrated. The modern system for anamorph classification based on conidium ontogeny also is clearly presented.

The teaching experience of the author is beneficially evident in his very practical explanation of procedures for cultivation, isolation and microscopy. The author is careful to forewarn the student of the numerous pitfalls that may be encountered in using sterile techniques and when preparing microscope slides of moulds. The imaginative diversity of procedures and numerous examples should stimulate the student to work independently to select or develop specialized procedures for particular problems. In addition to the basic methodology, the author describes moist chamber, baiting and spore printing methods for isolating moulds, bridging and tunnelling techniques for decontaminating cultures, and slide culture techniques for preparing microscopic mounts. Recipes for culture and mounting media are provided.

Keys, descriptions and illustrations facilitate identifying 60 of the most commonly isolated mould genera. The dichotomous keys are easy to work and include numerous cross references to morphologically similar genera including additional genera illustrated in the preceding chapters. Generic descriptions briefly dis-
cuss diagnostic characteristics, natural habitats, anamorph-telemorph relationships and guide the reader to the more specific taxonomic literature. The illustrations of genera are more than adequate to show diagnostic characteristics, although some students may be confused initially by the lack of scales or other magnification indicators.

The author has succeeded in producing a very readable text. Nomenclature is flawlessly up to date, and the book is well referenced with close to 100 references (mostly taxonomic) published up to 1980. There is an index to the 170 genera of fungi cited in the text; however, very few technical terms and techniques are indexed. The author does not provide a glossary of mycological terms and a number of terms (e.g. gamentanga, zoosporangia, phialide, columella) are introduced in the text without adequate explanation.

In my opinion, this publication is the best instrument currently available to introduce students to laboratory work with common moulds. The binding, paper and print are appropriate for heavy use in a teaching laboratory. The chapters on methodology also may be useful to persons in professions dealing incidentally with fungi, although the identification section may be limiting when unusual moulds are encountered in specialized situations.

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Checklist of the Mosses of Canada


A checklist of Canadian mosses is an important step toward facilitating bryology in Canada. Its publication will permit bryologists in Canada to determine whether a moss is new without spending inordinate time searching the literature, and to this end additional pages are provided for adding taxa and checking off provinces.

The book lists 996 species; compared to 1170 in the 1973 North American Checklist by Crum, Steere, and Anderson, the total points to the richness of the Canadian flora. Its preparation was a major undertaking by well-recognized Canadian bryologists. The reproduction is good and the 6 1/2" x 9 3/4" size is convenient for field or office use.

The book is organized in a very practical way with a phylogenetic listing of families and genera followed by an alphabetical list of species with authors. Families can easily be located by a number following the genus name. Nomenclature usually follows Crum, Steere, and Anderson (1973), which makes it easy for most taxa to be compared with descriptions in the most recent American Floras. However, nomenclature for Sphagnum apparently follows Andrus (pre-publication?). The Mniumaceae nomenclature follows Koponen (1968). No mention is made of these sources, but a list of synonyms is provided.

The authors have made several improvements over the earlier checklist of Ontario mosses (Ireland and Cain 1975). Species lists are vertical on the page so the book does not need to be turned sideways. Where numbers were used before to denote counties, two-letter abbreviations denote provinces. The separate listing of literature reports has been combined with the species list by use of open and closed circles with ? denoting probable misrepresentations and * denoting new records for North America (many of which are combined with ?).

Of the 70 taxa with * that were verified by the authors, implying that they are new to the North American list, some are clearly just different interpretations of taxa by Crum, Steere, and Anderson. This is most evident in Mnium and Sphagnum. The authors have treated taxa such as Sphagnum angustifolium as new to North America, when in fact Crum, Steere, and Anderson have considered it to be S. recurvum var. tenue, which is listed by Ireland et al. among the synonyms, and clearly is already known in North America by that name. Pseudomnium magnifolium (= Mnium punctatum var. elatum) is treated as new, but Mnium thomsonii (= Mnium orthorrhynchum) is not. Yet both species are listed by Crum, Steere, and Anderson under the synonyms shown above. Some * taxa are clearly errors, such as Fontinalis antipyretica var. gigantea. It therefore requires considerable effort to determine what is really new to the North American list. It would have been useful if the authors had distinguished the taxa truly new to North America from those which are different interpretations of the Crum, Steere, and Anderson taxa.

These problems do not detract from the usefulness of the book for floristic studies, phytogeographic work, and systematics, and hopefully it will stimulate interest in preparing regional floras such as the one on western Canada currently in preparation by Vitt and
Schofield. I would expect anyone interested in North American bryophytes to find it useful.

Literature Cited

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ENVIRONMENT

The Boreal Ecosystem


This book should be avoided by all naturalists. It is upsetting to see such a poor work be sold in the 1980’s. No advanced knowledge is contained in this text. The knowledge put forth in the 482 pages of text could easily fit on 50 pages without loss of any information. The author uses whole sentences to describe what a word would depict. Whole paragraphs denote only that water flows downhill or that forests contain trees. The author starts discussing a subject and then jumps to a totally unrelated area as though several paragraphs were missing from the page. Words are used several times and then suddenly defined on a subsequent page. Contradictions occur so often that I began to mistrust what the author was saying before page 100. The phrases “examples are many,” without a single example and “nothing is known,” when several references exist, are common. Many references are lacking and those used seldom relate to the topic. Most of the lengthy tables are not related to the subject matter and show very little information. Few maps are shown but hundreds of obscure lakes are named as reference points.

This book is definitely not recommended. It is one of the poorest books I have ever tried to read. Naturalists would be led astray by reading this book. The author may have had experience in the boreal forest but clearly has not conveyed what he may have learned in this book.

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The Canadian Environment: Data Book on Energy and Environmental Problems.

By Madelyn Webb. 1980. Saunders, Toronto. 166 pp., illus. $9.95.

This compilation of environmental data makes an interesting and easily accessible source book for introductory studies at a secondary school or undergraduate university level. The well organized data provide a good background against which site specific data can be compared or from which such studies can progress in more advanced environmental research. The attempt to cover all energy and environmental issues results in a volume of interesting information but also causes the approach to be of an overview nature. Some subjects appear overemphasized (for example, 4 pages on bacterial levels in Lake Superior) while others seem to be glossed over (the air pollution chapter).

The first, and largest chapter is devoted to a status report on Canadian energy supplies. Data tables cover the complete range from solar or tidal power through coal liquefaction to nuclear. The approach in most chapters is an introductory statement followed by tables of data and ending up in an up-to-date source list for more detailed studies. The second chapter, on population, gets straight to the cause of pollution problems and leaves us with the background for prediction of future trends.

The next five chapters treat specific areas of pollution problems: water, metals, pesticides, air, and solid waste. Acid rain is treated as a water pollution problem, with the rest of the chapter emphasizing nutrients, bacteria, and thermal effluents. The metals and air pollution chapters spend much effort on a small number of pollutants but the pesticides treatment provides a better overview approach to help under-
standing of the overall problem. Solid wastes overdoes packaging and omits any of the more hazardous waste products. Even if this approach is energy oriented, a treatment of energy from wastes would have added much to the chapter. The land use chapter gives us a wide overview of agriculture and a little on fisheries and forestry.

The final chapter on locating government documents was somewhat disappointing. It really only explains how the author and title can be found on Census Canada documents. The serious student, wishing to research further one of the areas in this report, would best follow the advice of the final paragraph "If you are still confused ask your librarian for help."

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Ecology and Field Biology


This book is the most complete text available on field ecology. This edition is much like the second. However, additional information on ecosystem and evolutionary ecology and the elimination of information concerning human ecology are notable changes. Instead of heavy treatment of North America, other parts of the world are dealt with more often in this edition. Global paleoecology and zoogeography are also now treated. Although theoretical ecology is outlined the book deals more often with real-world ecology. Especially good discussions occur on aquatic ecology, biogeochemical cycles, C3 vs. C4 plants, ecological succession, energy flow, global climatology and primary production, inversions, laws of tolerance, marine ecology, niche space, phenology, soil orders, and solar radiation spectra. The expanded appendices concerning statistical methods, population sampling, community productivity and structure, and environmental measurements contain methodology that should be helpful to all field biologists. The journal list and the three bibliographies are expanded and updated. A glossary now appears with fairly good coverage. Many new illustrations appear and the index has better coverage of text subjects.

Typographical errors are still abundant. Words and even sentences are missing in many spots. References cited in the text are absent from the bibliographies.

Overall, Smith has done a good job covering information and/or concepts discovered since his previous edition (1974). Since much of this book's material is not found in other ecology texts, reading this book will provide a naturalist with the most up-to-date information available to us on basic ecology.

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A Reference Book of Urban Ecology

By Anne Innis Dagg. 1981. Otter Press, Waterloo, Ontario. 190 pp., illus. $5.00.

Until recently, urban areas were considered to be biologically barren and rather uninteresting systems to study. However, interest in urban ecology has risen dramatically in the last few years with the realization that increasingly large numbers of people are living or working in urban areas and that the adverse environmental conditions in cities may be affecting the health of its inhabitants. This modest-looking book by Canadian biologist Anne Innis Dagg and illustrated by Harry Warr neatly summarizes recent knowledge of urban ecology with examples drawn, where possible, from Canadian cities. This national viewpoint is particularly timely in that three-quarters of Canadians currently live in cities and most of us are probably not particularly well-informed about the many ecological peculiarities of urban areas.

The first section provides considerable basic information on the physical and biotic properties that contribute to making urban areas ecologically unique habitats. Included is an account of the subtle and not-so-subtle differences between urban and rural climates. One of the main accomplishments of this book is its celebration of the wealth of wildlife that can be discovered in urban and suburban areas with a little extra effort. The author notes that urban wildlife are usually quite adaptable species and suggests that the key to attracting them is the type of varied habitat that can be achieved through well-planned city parks and
suburban backyards. Life history sketches are presented for a wide variety of urban wildlife (including 34 taxa of birds and 21 taxa of mammals, reptiles and amphibians), with additional brief descriptions of insects, fish and vegetation types that might be encountered in a Canadian urban setting. I found the content of these sections to be somewhat unbalanced, in that some topics (e.g. orphaned and injured birds) have only a tenuous connection with urban settings. The criteria for recognition as urban wildlife wasn't very objective since the average city-dweller's chance of encountering either a Peregrine Falcon (p. 58) or an Oppossum (p. 84) is still fairly remote. Animal lovers in urban areas will no doubt find the descriptions of the numerous diseases and illnesses that may result from human-wildlife interactions unpleasant. City-dwellers should, and probably will, be particularly distressed by the plethora of deadly pollutants that they produce and encounter more often than their rural counterparts. After this sobering account, the reader is left to ponder, in the author's words, "why humans put up with crowded, sterile, noisy, poisoned environments when our native animals refuse to, leaving the city cores to the pigeons, house sparrows, starlings, rats and mice, all imported species."

As the title suggests, this book is primarily an overview of urban ecology. It effectively avoids chocking on technical jargon. Consequently, it does not provide much scientific data, except in anecdotal form, and offers only a very limited list of other urban ecology references and a brief glossary. Nevertheless, it is reasonably priced by today's standards and I conclude that it can serve to introduce users of Canada's urban areas to the variety of ecological pleasures and pitfalls that await them.

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A Handbook of Fish Habitat Protection on Forest Lands in British Columbia

By D. A. A. Toews and M. J. Brownlee. 1981. Land Use Unit, Department of Fisheries and Oceans, Vancouver. 165 pp., illus.

The forest industry has tremendous impact on fish habitat. Forests regulate snow melt, runoff, reduce soil erosion and siltation, and moderate stream temperatures. Leaf fall provides an important energy resource to stream bacteria, periphyton, invertebrates and fishes.

Harvesting timber and pulpwood may involve removal of soil cover and construction of roads. These in turn increase erosion, block streams with logging wastes, and destroy benthic habitats with bark shed during log drives. Forest operations often require culvert and dam construction which may block fish migrations. Spraying to control the forest insect pests may kill fishes. It is clear that harvesting our forests can damage our fish resources and other wildlife.

Yet there are many modification of traditional logging techniques that will protect the streams, lakes and estuaries. Some cost no more and, in addition, protect the soil needed for regeneration of future forests. Others may increase lumbering costs but be a wise investment in terms of an overall management of natural resources.

To implement forestry management techniques that protect aquatic fauna, better communication is needed between fishery and forest biologists, forest engineers, loggers, construction crews, and others. This handbook was written to discuss the relationship between timber and fish resources and to offer guidelines to the Fisheries and Oceans staff who interface between the two resources. It is so well written and illustrated it should be required reading for anyone in the two industries, in pertinent government departments, and for the concerned naturalist. The principles and practices are applicable outside of British Columbia.

The handbook describes the basic theory and principles of good management. It outlines and illustrates correct and incorrect forestry practices. Photos illustrate for example landslides associated with road construction, effects of badly designed culverts, loss of streamside cover, and bank stability. Humorous cartoons depict environmental problems and human interactions with tongue in cheek. These make the messages clear and positive rather than preachy.

The authors, artists, designers and co-operating individuals in the forestry and fisheries fields are to be congratulated. This is a very readable and informative book, one that should go far towards linking the two solitudes.

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The Stikine River


The motto of The Alaska Geographic Society is "To teach many more to better know and use our natural resources". In view of these stated objectives, the volume entitled The Stikine River should be regarded as a success. The book serves as a comprehensive introduction to one of the most inaccessible, and hence unexplored regions of northern British Columbia and Southeastern Alaska. As one might expect from a 96 page volume with well over one half of the space devoted to photographs, the book merely stimulates the appetite rather than providing any lasting gratification; if you would, an apertif rather than an entree.

The album format (11 by 8½ inches) is a particularly suitable vehicle for the many spectacular photographs which accompany the condensed text. Only three pages are devoted entirely to text while forty-four contain only photographs and captions; the remaining pages have both text and photographs. The order of the chapters generally follows the flow of the 400-mile-long river from its origin high on the Spatsizi Plateau in remote north central British Columbia to tidewater near Wrangell on the Alaska panhandle. This treatment suffers when chapters on present and potential developments, native history, and commercial riverboating are interspersed, seemingly at random, with the downriver progression of the rest of the volume. The overt and impassioned pleas against mining and hydropower developments and highway construction in the first part of the book detracted from my enjoyment of the remainder of the volume. In our view a single chapter near the end would have delivered the message much more effectively.

Chapters of particular interest to us were those dealing with some of the lesser known areas of the Stikine Basin. Two of these are titled "Spatsizi; Land of the Red Goat" and "Edziza: Volcanic Wilderness". The names Spatsizi and Edziza have stirred the imaginations of adventurers and scientists for years, treatment of these awesome regions within the book will also serve to tantalize its readers. A third chapter, "The Grand Canyon of the Stikine", gives an exciting pictorial coverage of portions of this sixty-mile stretch of unconfquered white water. The chapter entitled "107 Years of Stikine Riverboating" provides an interesting account of the history of commercial boating on the river between 1862 and 1969, however, the ten page alphabetical listing of all the boats known to have operated during this period is surely of interest to only the most inveterate of riverboat historians.

Some errors which should be pointed out to users of the book include: on page 44, the coho salmon in the picture are sockeye salmon; on page 82, "land otter" should read river otter and "red oser and dogwood" should read red osier dogwood; on page 81, only three species of Pacific salmon spawn in Canadian tributaries of the Stikine (coho, sockeye, and king or chinook) and the "smelt" referred to in the text are eulachons; on page 84, sedges are not grasses and the Chief Shakes Hot Springs are closer to twenty miles upstream of Wrangell.

In conclusion, we enjoyed the spectacular photography and very readable text employed by the editors of the book and found that the book had attained the level of excellence of other volumes of the Quarterly series of The Alaska Geographic Society. The book could proudly grace any coffee table and should serve to arouse an interest in learning more about this vast, fascinating wilderness.

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North American Forest Lands at Latitudes North of 60 Degrees


This symposium volume presents a series of papers dealing with forest ecology, forest research and management, and socio-economic aspects of high-latitude forestry. The unfortunate choice of Latitude 60° as the southern limit becomes evident from the first five papers when the reader is presented with the wide variety of conditions found around the world north of this latitude. Productive commercial forests of northern Europe and on the floodplains of interior Alaska lie within this region, as well as the open, stunted forest-tundra of Siberia, Alaska, and the Northwest Territories.

When viewed in this context, the volume contains disappointments. It is difficult to appreciate how forest management in central Alberta, Norway, Fin-
land, Yakutia, and northern Minnesota relate to the forests north of 60° in north America. Certain aspects must be similar, but the silvics, silviculture, and harvesting practices may be widely different.

The individual papers, however, are very informative. A series of papers on forest management, harvesting, and silvicultural practices in west-central Alberta, Norway, and Finland serve as useful sources of information for the knowledgeable person who can select those aspects that are applicable to northern North America. A paper on the forest vegetation of Yakutia, stressing revegetation of burned and logged areas is particularly valuable, as it breaks the language barrier between ecologically similar areas.

The meat of the symposium is contained in the section “Forest Research and Management at High Latitude”. One paper describes the forest types, with heavy emphasis on the floodplains of central Alaska. The descriptions are adequate, but they contain a code that may be a mapping symbol, unrelated to the text. Since no map is provided, the reader is poorly oriented with regards to the extent of various types. Only diligent reading reveals that 79% of the forest land in interior Alaska is covered by a single forest type, the non-commercial Black Spruce stands. A second paper describes the forest resources and forest biology of Alaska, Yukon and Northwest Territories. These two papers are excellent sources of information on most aspects of forest biology in northern North America.

In the section on the socio-economic aspects of high-latitude forestry the value of forests in the native Alaskan economy is examined. Forests and forest vegetation were used as raw materials or food, while the forest fauna was a dominant source of food. Several papers explore the possibility of utilizing the forest resources of 22.5 million acres of forest land in interior Alaska. Most of these papers are theoretical, or have a strong promotional flavour, but the harsh realities of climate, distance from markets, and competition with other sources ring through in one paper. Most contributors, however, are optimistic about the future of a forest industry in Alaska, if proper harvesting, silviculture and marketing methods are adopted to the conditions prevailing in Alaska. The volume concludes with a number of hard-hitting conclusions of workshop sessions on forest production and multiple land use.

The specialist interested in the forest resources and forestry practices of the northern boreal forest will find this volume to be of lasting interest.

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**MISCELLANEOUS**

**Adventures of a Zoologist**


Scheffer is one of the last of a group of great naturalists which includes C. Hart Merriam, Elliot Coues, T. H. Scheffer (Victor’s father), Ira Gabrielson, Olaus and Adolph Murie, Leo Couch, and Robert Cushman Murphy. They did much of the pioneering vertebrate zoological research, working in the days before down clothing, freeze-dried food, helicopters, snow machines, remote sensing, and other such modern equipment and techniques.

*Adventures of a Zoologist* is a journey through the 50-year career of a naturalist who has encouraged and inspired many. The book begins with Scheffer’s initial inspiration and encouragement in the field of zoology by one of his professors, entomologist Trevor Kincaid. We then follow Scheffer to graduate school, then to the Aleutian Islands where he assists the Olaus J. Murie in a faunal survey of the island chain. As an employee of the Bureau of Biological Survey, the predecessor to the Fish and Wildlife Service, Scheffer alternately studied the mammals of Washington State, the origin of the Mima Mounds near Olympia, mountain beavers, the rare Columbia White-tailed Deer, a muskrat “eat out”, and marine mammals.

The majority of Victor Scheffer’s professional career has dealt with studies of the northern fur seal on the Pribilof Islands. Since his retirement from civil service, Scheffer has not been idle. He has taught college courses at the University of Washington and College of the Cayman Islands. In addition, he has been instrumental in protection of Washington’s Olympic coast. In 1963, he was a member of a secret team chosen by the U. S. Arms Control and Disarmament Agency to inspect foreign bases on Antarctica for military activities. In May of 1973, President Richard Nixon appointed Victor Scheffer as the first chairman of the newly organized Marine Mammal Commission established under direction of the Marine Mammal Protection Act of 1973.
In addition to his scientific endeavors, Victor Scheffer has been a prolific writer. He is particularly adept at writing scientific materials for the nonscientist. His books include: *Seals, Sea Lions, and Walruses* (1958); *The Year of the Whale* (1969); *The Year of the Seal* (1970); *The Seeing Eye* (1971); *A Voice for Wildlife* (1974); and *A Natural History of Marine Mammals* (1976).

The autobiographical sections in *Adventures of a Zoologist* are presented in an interesting and relaxed manner. The photographs are generally clear and relevant and they add greatly to the book. Historical anecdotes are inserted to place the events in Scheffer’s career into a larger perspective.

However, I was greatly disappointed in the final chapter, entitled “A Moral Ending”. Scheffer writes: “I believe that we are turning toward what zoologists call low-consumptive uses of wildlife — uses that range from bird-and-beast watching and looking at wildlife movies to purely cherishing the thought that animals are out there sometimes sharing the earth with the rest of us.” He takes zoologists, ecologists, wildlife managers, and hunters to task for not being humane and for not appreciating the natural world. I think that Aldo Leopold, Ernest Swift, Jose Ortega Y. Gasset, Gene Hill, Albert Hochbaum, Adolph and Olaus Murie and many others would be greatly insulted by Scheffer’s claim. These men, although professional zoologists and/or hunters, fully appreciated the natural world and were humanists of the highest order. It is unclear from reading *Adventures of a Zoologist* what has precipitated the change in Scheffer from a “blood and mud” zoologist to a “humanist”.

Scheffer hopes to persuade readers that “the life of a zoologist can be exciting as well as difficult; humane as well as adventurous.” I feel that the book actually accomplishes this objective. At the same time it provides meaningful insights to a man who many of us, who have chosen the life of a zoologist, have found an inspiration. I think you will find *Adventures of a Zoologist* quite interesting.

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**Photography: Art and Technique**

By Alfred A. Blaker. 1980. Freeman, San Francisco. (Canadian distributor: Oxford University Press, Toronto). 460 pp., illus., plus 40 pp. synopsis of techniques. $29.95.

This text represents a diversion from the author’s previous photographic endeavor. Blaker is well known for his knowledge of both laboratory (*Photography for scientific publication: a hand book*, Freeman, San Francisco, 1965), and field scientific photographic techniques (see *Canadian Field-Naturalist* 93: 218-219). However, his most recent effort, as the title suggests, is aimed at the more artistic areas of photography. The reader could view this change in direction negatively. Can a photographer skilled at seeing scientifically actually provide a good treatise on the more elusive topics of “artism” on photography? Or will the work be overly complicated with mathematical formulas and filled with static photographs designed only to be representative?

Blaker presents the information in a series of six parts. The discussion moves from a history of photography, to the camera and the photographic process, to darkroom work, and finally to special techniques and composition.

The first section is designed to inform the reader on the historical development of photography. If considered as a brief synopsis to set the stage for subsequent topics, the text is quite good. However, this section cannot stand alone and there are much more complete historical accounts of photography available.

The section on the camera describes all available types of equipment. From this section the reader is able to gain information on what will best suit his/her photographic ambitions. For example, the nature photographer will obviously prefer the lighter, more easily manipulated, 35-mm SLR camera because of its improved capabilities in the field over the more complicated, bulky, view or twin-lens reflex cameras. For the photographer just beginning an interest in photography this section is very useful; however, for the more advanced image maker a trip to his/her local photographic retailer will prove more useful to determine “state of the art” equipment.

Blaker's next section, “the act of photography,” discusses various techniques of creating an image. Topics fundamental to photography (exposure, light characteristics and uses, filters, and dark room procedures) are described from a very technical standpoint. The discussion provides an understandable overview for the incipient photographer or a good review for the more mature image seeker.

The section on special techniques is, in my opinion, the strongest in the text, especially the portion on close-up photography. The author displays an
extraordinary skill for photomacrography. His descriptions of techniques are among the most readable in the literature. This relatively new (to the amateur) photo technique can be technically difficult and very elusive to describe. However, as Blaker states "photomacrography is no more difficult than any other type of photography". By following the authors step-wise instructions, the problems of exposure in photomicrography can be simplified and in fact manipulated to result in a most pleasing macroimage.

This section is very applicable to those making nature photographs. Many nature photographers are continually seeking new and exciting subjects. Field photographers will travel great distances to capture exotic or rare wildlife and plant species on film. However, by using macrophotography, the number of fascinating, novel subjects becomes overwhelming. As Blaker explains "Finding and recording things that others can not easily see is an open ended challenge . . . you can find new images throughout the rest of your life."

Blaker's final chapters are concerned with photographic seeing and composition, or the mental processes behind making the image. This discussion flows in a very logical manner; from the perceiving of an image, to optimal methods of composing this perception, and finally to looking at the end product. The major problem I found with this section was the number of general statements made and the scarcity of specific information on composition. The only knowledge gleaned from Blaker's words on composition is that a photographer must preconceive his image and that composition is correct if it "works". I believe there is much more that can be said on this topic.

It was mentioned at the onset of this review that, with this text, the author has embarked into a new area of photographic endeavor. Unfortunately, he is not entirely successful. The work is quite obviously written with a technical slant and lacks the artistic flare suggested in the title.

Despite this rather negative statement the book on the whole is a very worthwhile accomplishment. I am aware of no other text besides Langford's classic work Basic Photography that contains as much well presented technical photographic information in one volume. Alfred Blaker is certainly among the best photographic craftsmen of our time.

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Kluane: Pinnacle of the Yukon


In this first major book on Kluane National Park, the attempt is made to instill a sense of wonder for this magnificent wilderness area and to give the reader some solid information on its nature. To do this, it presents a stunning display of Kluane scenery through numerous colour and black-and-white photographs. It presents the hard facts through the writings of an impressive array of natural scientists who have all had extensive first hand experience there. All of this is pulled together by an editor who combines an obvious love of this land with an expert knowledge of its resources. The result is a 'picture book' that is far more than a coffee-table decoration; it is an excellent summary of the important scientific and environmental values of Kluane.

The book begins with a Forward by the Honourable Jean Chretien who, as Minister responsible for Parks at that time, was instrumental in its establishment. Although worthy of much praise for his efforts on behalf of Canada's national parks during his tenure, Chretien seems to spend too much energy in the Forward congratulating himself rather than dealing with the issues at hand. I suppose it comes with the (political) territory (?). Happily, only one other contributor shares this problem.

A very wide and interesting spectrum of topics is covered in the 15 chapters of the book. They review the natural and human history of Kluane and include such unusual categories as "Flying in the St. Elias Mountains" and "Climbing in the Kluane Ranges". All are written quite well although, as one might expect with so many 'cooks' stirring this particular 'broth', some chapters are produced with more flair and excitement than others. "The Glaciers: Nature's Sculptors" is one of the finest in this regard. The authors make these seemingly inert lumps of ice come alive and dynamic and this provides fascinating reading. There is lots of 'meat' presented here but with no loss in meaning or knowledge. At the other end of the scale, the chapter on large mammals ("Horns and Hooves"), while competent, is very dull. Surely there are more important things to talk about concerning Kluane's large mammals than their weight, number of young, etc.

It is a credit to the editor — and his contributors — that when a chapter errs in the balance between style and fact, it usually does so on the side of fact. A
number of discussions (those dealing with mammals, birds, flora and bedrock, for example) are rather neutral in their presentation and would have benefited from more interpretation of the particular Kluane situation in a broader context. The individual chapters could have been tied together a bit better too, allowing the reader to appreciate the interrelationships of land, nature and the man in Kluane with greater clarity.

The photography is excellent. The layout and design of illustrative material is superb on the whole and provides the reader with a terrific visual appreciation of the park as well as a very effective description of the features and phenomena discussed in the text. A great deal of thought and care has obviously gone into this aspect of the book.

The text is well laid out on good paper stock and is easy to read. It is interrupted with maps, photographs and (usually effective) line-drawings that pace the reading nicely. The type-setting is sloppy in places, however. This is particularly evident in the later chapters where individual words run on into each other far too frequently. This is, though, a fairly minor problem.

Some factual errors were noted in this review (such as the suggestion that breeding Golden-crowned Sparrows are disjunct from those populations in southern Alberta and British Columbia) but these seem to be few. Appendix A, however, which is intended to include the scientific and common names of all flora (and fauna) listed in the text, is quite incomplete. A causal check easily uncovered a number of omitted species. (A similar though less serious deficiency was noted in the index.) It's unfortunate that the opportunity to include complete floral and faunal checklists was not taken. This would have added a great deal of useful information without greatly increasing the number of pages in the book.

One can also argue that the “Further Reading” section is less than complete. It seems inconsistent, for example, to include Scott and Crossman's *Freshwater Fishes of Canada* but not Godfrey's *Birds of Canada.*

When all is said and done, I highly recommend this stimulating, informative, and visually spectacular book to all those interested in Canada's national parks in general and our northern parks in particular. Theberge, who was a major force in the establishment of Kluane Park in 1972, may feel well pleased with this effort. Through it, he shows those of us not fortunate enough to have experienced this magnificent land just what we’re missing — and that all the time and sacrifice expended by him and others for its establishment as a national park was most worthwhile.

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**Dictionary of Theoretical Concepts in Biology**


Perhaps a better title for this book would be 'Introduction to some really neat ideas'. The editors understand that theories wither and lose much of their interest when constrained as static entities cut off from their intellectual environments. Theories are fully comprehensible (and exciting) only in the context of a system of lively, evolving ideas. Consequently, this is not a dictionary in the conventional sense; do not look here for 'definitions'. This is a natural history of ideas, and not a taxonomy.

For each of the 1166 entries, the reader is referred to one or more papers or books. Usually these include the article that contained the first more or less explicit statement of the idea. Sometimes, as with 'Evolution' and 'Spontaneous Generation' for example, this is not possible, and we are referred instead to articles reviewing the ideas at advanced stages of development (in these cases, to Arber 1907, and Oparin 1924). Further references point to important stages in the development of the concepts, and there is often mention of a recent review article, especially for currently active ideas with long pedigrees.

The editors add short explanatory phrases where there might be confusion as to the sort of biology involved, as with 'Inertia [of ecosystems]' or 'Jamin's Chains [theory of sap ascent]'. The entries are not otherwise annotated. There is, however, extensive cross-referencing, and this, together with the authors and titles of the cited papers, is usually sufficient to give a good idea of the 'flavour' of the concepts, at least in areas one is familiar with.

The entries are impressively thorough in many respects. For example, under 'Niche [ecology]' we have thirteen entries spanning over seventy years, including not only Elton, Hutchinson, and the oft-cited Grinnell 1917, but also a much earlier paper by Grinnell (1904). Furthermore, there are other entries on 'Niche Expansion', 'Niche Hyperspace', 'Niche Overlap Hypothesis', 'Niche Shift', and 'Niche-Variation Hypothesis', with cross-references to 'Competitive Exclusion', 'Broken-Stick Model', 'Habitat Shift', and 'Ludwig's Hypothesis'. Relevant concepts have been borrowed from other disciplines, such
as with 'Catastrophe Theory' from mathematics, and 'Holism' and 'Order' from philosophy. The references extend from the end of the 1970's back as far as Genesis (for the 'Doctrine of Special Creation'), and cover concepts as basic as 'Habitat' and 'Species Concepts'.

There are some flaws. 'The Theory of Island Biogeography' cites MacArthur and Wilson, Preston, and a textbook by Roughgarden, but does not mention David Lack's Island Biology 1976, (Blackwell Scientific, Oxford), which, at least from the historical perspective, seems an oversight. Under 'Balance of Nature' we are given several excellent review articles, but no historical references. The earliest citation is Hairston, Smith, and Slobodkin, 1960, which is not a very good choice for putting this very important idea into context. Quibbles of this sort can be raised at many places throughout the book, but they do not seriously detract from the high quality of what is given. A more serious complaint is that although many ideas current in English are traced through to their roots in other languages, coverage of ideas from outside the Anglo-American tradition is poor. Even so common a concept as 'Biocoenosis' is absent.

Roe and Frederick obviously understand biological theory. They seem also to understand theoreticians, and the twinkle in the eye and the mischievous streak that seem to characterize so many of the good ones. As a consequence, we are given a few very interesting citations, such as Geisel 1955 (better known as Dr. Seuss) for his important contribution to niche theory (about Nutches that use Nitches for huches).

In a rather unsystematic test, the book scored a satisfyingly high rate of success in identifying the theoretical concepts I saw mentioned in several recent ecological journals. It should be a valuable reference for anyone who reads the biological literature, and a splendid desert-island companion for a certain eccentric fringe of theoreticians.

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Systematics and Biogeography, Cladistics and Vicariance


The reader is warned in the Preface that the text is difficult to follow sequentially and that the analytical chapters are apt to prove confusing. He is not disappointed.

Chapters 1 and 2 are, respectively, an introduction and a history of branching diagrams, mostly from 382 B.C. to 1866 A.D. Chapter 3 describes "component analyses," a term coined by the authors for enumeration of the groups of taxa in cladograms. They seem unaware of the prior use of this term in multivariate analysis. The message that one cladogram (a dendrogram of character relatedness) can correspond to many phyletic trees (dendograms of descent) is overwhelmed by the medium: more than 320 branching diagrams in this chapter alone. The discussion is involved, and its intent is seldom clear. The writing would have benefited from further editing. No clear instructions for component analyses are presented. Chapter 4 derives cladograms from existing evolutionary, phenetic and cladistic classifications. All dendrograms are considered to be cladograms, so pheneticists and "evolutionary systematists" are considered closet cladists. In Chapter 5 the threefold parallelism of ontogeny, comparative anatomy, and paleontology as evidence of phylogeny is discussed. Nelson and Platnick conclude that the parallelism seems falsified, because post hoc hypotheses protect comparative anatomy and paleontology from falsification, but evolution may be viewed as an extrapolation of ontogeny alone.

The last three chapters deal with biogeography. Chapter 6 considers the origins of biogeographic diversity, biogeographic regions, distributions and relationships of regions. The approach of Wallace and Darwin, based on determining relationships of geographic areas on relative numbers of shared taxa, is rejected and that of A.-P. de Candolle, who identified geographic regions strictly on the basis of endemism, is praised. Chapter 7 is based chiefly on hypothetical relationships between Asia, Java, Sumatra and Borneo. A cladistic approach to biogeography presupposes that there are areas of endemism that are interrelated among themselves. The areas of endemism are delimited by the more or less coincident distributions of taxa that occur nowhere else, and the interrelationships of these areas are to be made known by cladograms formed by summing repeated components (groups of areas) from the cladograms of the organisms. In Chapter 8 some real, though not cladistic, data are actually analyzed. Single linkage cluster analyses from coefficients of faunal similarity for areas in southeast Asia and Australia based on butterflies, birds, and bats are taken to be cladograms, and are compared by component analysis. Congruencies are
found and are shown in a general area cladogram. An approach which uncovers congruencies is obviously a worthwhile contribution. Non-replicated components are classified as false or ambiguous and are thought by the authors to represent random variability. The authors finish the book with speculation about human evolution.

The Selected Reference list is even shorter than the heading suggests.

About one third of the book deals with history of biogeography, especially the older history. The tone is haughty throughout. The contributions of Candolle, Mitchell and Rosa are considered important, but Darwinists and dispersalists are condemned. Punches are thrown at Wallace although he is usually excused for his errors. Wallace's Line is not mentioned, although almost all of the biogeographic analysis in Chapter 8 deals with the Indo-australian area.

Aside from the further development of "component" analysis (already described in Systematic Zoology 28(1):1-21), the book contains no new data or theory, nor list of biogeographical regions of the world. The historical sections are interesting. The theoretical chapters are, as the authors admit, apt to baffle the reader. The theory of cladistics, vicariance and component analysis is not clearly explained. We do not recommend this volume for students. While the historian and dedicated theoretician will find something of value, in our opinion, the average taxonomist and biogeographer need not read this book, although he ignores cladistics and vicariance at his peril. For a "clear and lucid" summary of the cladistic position in systematics R. R. Sokal (Quarterly Review of Biology 56:173-176) recommends Phylogenetic patterns and the evolutionary process: method and theory in comparative biology by Niles Eldredge and Joel Cracraft, also published by Columbia University Press, but not cited by Nelson and Platnick, or Phylogenetics: The theory and practice of phylogenetic systematics by E. O. Wiley, published by John Wiley in 1981, reviewed favourably by L. E. Watrous and somewhat less than favourably by D. H. Colless (Systematic Zoology 31: 99-104).

DON E. MCALLISTER and FREDERICK W. SCHUELER
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Autobiography of John Macoun, Canadian Explorer and Naturalist, 1831-1920


Originally published in 1922, this new edition of the Macoun autobiography appears at a time of heightened interest and activity in the study of Canadian history, Canadian explorations and the history of Canadian science. In addition to the original introduction by Ernest Thompson Seton the new edition contains a new introduction by Richard Glover, several new photographs of Macoun with family and friends, a biographical essay and extensive editorial notes by William A. Waiser, and maps of Macoun's five major expeditions from 1872-1881.

For those unfamiliar with the life and work of Professor John Macoun this publication provides a fascinating glimpse of the personal and professional development of a young Irishman, born in 1831, who, with his family, moved to Ontario in 1850. His recollections of this early "greenhorn" period are often humorous, but are included with a pedagogical intent "to show that it is only by experience we learn." An early interest in natural history in general and botany in particular led to Macoun's decision at the age of 25 years to exchange a life of farming for that of teaching.

After his initial teaching job in Brighton, Ontario, which lasted two years, Macoun enrolled in the Toronto Normal School in August in 1859. Six months of intensive work enabled him to graduate with an "A 1" certificate and to start teaching, and studying botany, at Castleton in 1860. This year proved to be one of the turning points of his life. He moved to another teaching post in Belleville, Ontario, and "before the winter was over I had discovered I could hold my own with the best of teachers and stood well with the people. I then decided to devote all my spare time to natural history..." He used the best available books on botany, geology and geography, observed nature constantly and collected plants wherever he went. Macoun also established a network of correspondants in the United States and Britain. He joined the Botanical Society of Canada in 1863. Now he had a chance to meet young Canadian botanists who, with their enthusiasm, were not only an inspiration, but also a "spur to keep ahead of them."

Macoun, forever aware of the shortcomings of his early education constantly strived for self-improvement. He had great faith in his ability to learn and think, and emphasized the necessity of thinking to his students and friends. When Albert College in Belleville received a University Charter in 1866 the Chair of Natural History was offered to Macoun. His serious
explorations started in 1869 when he studied the flora of the Lake Superior region. Subsequent summer vacations took him to other parts of Ontario.

The second turning point in his career occurred in 1872 when, on board ship on Lake Superior, Macoun met Sandford Fleming, Chief Engineer of the Canadian Pacific Railway. Fleming invited the "Professor" to accompany his survey party across the prairies to the Pacific Ocean as Botanist to the Survey. This exciting offer, which Macoun accepted without hesitation, led to a future of exploration. He became an expert of the "Great North West" and eventually changed his vocation from that of professor to natural history at Albert College to explorer in the Department of Interior in 1879. In 1881 he became Botanist to the Geological and Natural History Survey of Canada. The accounts of his five journeys in 1872, 1875, 1879, 1880, and 1881 provide a fascinating view of the then largely unknown "North West" seen by Macoun in good years of adequate precipitation. His vivid descriptions of the country and of the difficulties encountered and overcome make for absorbing reading. His vignettes of the personalities encountered, such as British "greenhorns", Hudson's Bay personnel, political figures, Indians, and other explorers, are often humorous and enlightening. Macoun's publications and lectures which followed his western journeys stressed enthusiastically the agriculture potential of the Canadian prairies and were thus diametrically opposed to the findings of Captain John Palliser. Palliser during and after his 1857-59 exploration considered that a large part of the prairies were, in fact, part of the "Great American Desert" and therefore unsuitable for cultivation.

Macoun moved to Ottawa to take up his position as Botanist. This, however, did not mean an end to his surveys and explorations. In fact, until his retirement after a stroke in 1912, at the age of 81, Macoun travelled extensively during the summer months and worked up his collections during the winter periods. In 1884 he accompanied members of the British Association for the Advancement of Science to the West. The numerous friends he made during this journey were instrumental in his being invited to represent Canada at the Colonial Exhibition in England two years later. He was hoping to write a "Natural History of Canada" and to this end, with the aid of several assistants, collected plants, birds, insects and fishes. Among his publications best known to the general public are *Catalogue of Canadian Plants* and *Catalogue of Canadian Birds*.

Late in 1887 Macoun was appointed "Naturalist to the Geological Survey and Assistant Director and Botanist." Even prior to this appointment he lobbied for a new museum building and increased his collecting efforts for the new museum throughout the 1890s. He was 80 years old when the Victoria Memorial Museum eventually opened in 1911. The following years, after having suffered a stroke, the Macouns moved to Vancouver Island. There, in spite of increasing infirmity, he collected and studied the flora of the island till the end of his life.

Our understanding of Macoun's time and life is greatly enhanced by the editorial notes and biographical essays of William A. Waiser. My only criticism for this edition concerns the placing of the five maps, depicting Macoun's western journeys, at the end of the book, instead of with the appropriate chapters.

The Ottawa Field Naturalist Club is to be congratulated on the publication of this fine "Centennial Project." The modest price of the book is an added incentive. Highly recommended.

MARIANNE GOSZTONYI AINLEY

History and Philosophy of Science Program, McGill University, Montreal, Quebec.
NEW TITLES

Zoology


*Caribou and the barren-lands. 1981. By George Calef. Canadian Arctic Resources Committee, Ottawa. 176 pp., illus. $34.95 plus $1.25 shipping.


*A handbook for fish habitat protection on forest lands in British Columbia. 1981. By D. A. A. Toews and M. J. Brownlee. Department of Fisheries and Oceans, Vancouver. 165 pp., illus.


Edited by Olof C. Wallmo. University of Nebraska Press, Lincoln. xviii + 606 pp., illus. U.S. $29.95.


*Wild mammals of western Canada. 1981. By Candace and Arthur Savage. Western Producer Prairie Books, Saskatchewan. 177 pp., illus. $34.95.
Botany


A field guide to Uganda forest trees. 1981. By Alan Hamilton. Botany Department, Makerere University, Kampala. 280 pp., illus. $12.50.


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Their Excellencies the Governor General and Mrs. Edward Schreyer

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Eggshell Thinning and Organochlorine Residues in Rocky Mountain Peregrines, *Falco peregrinus*, and Their Prey

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Eggshell thinning, and organochlorine residues in egg contents and in prey, were determined for Peregrine Falcons (*Falco peregrinus*) in Colorado and northern New Mexico. Eggs from 141 eggs from 16 territories in 1973-79 averaged 16% thinner than eggs collected prior to 1947, 13% thinner than eggs laid by captives from the region in 1978. Similar amounts of thinning have been found in declining peregrine populations in Alaska, California and Britain. DDE averaged (geometric mean) about 20 ppm (wet weight) in the contents of 47 eggs, an amount predicted to correlate with about 18% thinning. PCBs averaged (geometric mean) about 2 ppm (wet weight) in egg contents, an amount below that producing no adverse effect on reproduction in captive Screech Owls (*Otus asio*). Among birds eaten by peregrines or available to them, 19 of 29 species had at least one pooled sample with 0.5 ppm DDE or more (whole body, wet weight), and 11 of these species had 1.0 ppm or more. Previous studies suggested that a diet containing 1.0 ppm DDE or more could be expected to produce the eggshell thinning we found. Migratory insectivorous prey species contained 5.8 ppm DDE (S.E. = 2.98), several times more than any permanent resident species. Because prey species with high DDE levels were found at all peregrine eyries examined in the region, reproductive performance of both wild-produced and captive-released falcons is not expected to improve there until a downward trend in prey contamination occurs.

Key Words: Peregrine Falcon, *Falco peregrinus*, DDT, PCB, eggshell thinning.

Early studies on organochlorine pollutants in Peregrine Falcon eggs in Alaska and north-western Canada revealed DDT and its metabolites in concentrations 15 to 30 times greater than the whole-body levels found in small samples of prey (Cade et al. 1968; Enderson and Berger 1968). Subsequent eyrie surveys indicated vacancy as high as 75% in those regions (Fyfe et al. 1976). Reduction in eggshell thickness dating back to 1947 was first described for North American Peregrines by Hickey and Anderson (1968), and an inverse correlation between DDE residues in egg contents and shell thickness was soon discovered in Alaskan peregrines (Cade et al. 1971), suggesting a mechanism for reproductive failure. In an innovative study, Peakall (1974) was able to show that levels of DDE extracted from the interiors of peregrine eggshell specimens from California had been adequate to cause thinning as early as 1948.

In 1964 a widespread reduction of nesting peregrines was found in the central Rocky Mountains (Enderson 1965). Evidence that these falcons are at least weakly migratory include: 1) the only three recoveries of banded peregrines were in central New Mexico and northern Mexico, 2) a check of several eyries in mid-winter revealed no falcons, and 3) the winter weather at most mountain eyries is extremely severe. By 1973 the species had suffered an estimated nesting decline of at least 50% in the region. High DDE levels were found in a sample of 4 eggs, and 9 eggshells averaged 20% thinner than normal (Enderson and Craig 1974).

In the spring of 1974, two captive-bred downy young were placed in a Colorado eyrie containing one addled egg and one cracked egg, and in 1976 two pairs received captive-bred young (Burnham et al. 1978). This effort was expanded to seven states in the region and in 1980 nearly 60 young were successfully placed in the wild. The information presented here bears directly on the reproduction that can be expected from released and wild-produced peregrines and may be useful in management planning.

In this paper we report on pesticide residues, prim-
arily DDE, in the contents of peregrine eggs, the levels of these materials in a wide variety of principal prey species, and on eggshell condition, as these variables relate to the goal of increasing this drastically reduced population by the release of captively produced young.

Methods

Eggshell thickness measurements were made on 141 eggs from 48 first clutches and 12 second clutches laid in 16 territories in Colorado and northern Mexico in 1973-79. In the years 1973-76 the collection of eggs was not systematic and we obtained only eggs that were added, broken, or abandoned. In 1977-79 we routinely collected and incubated all eggs from eyries that were accessible. Often dummy eggs were substituted to maintain incubation behavior until captive-bred young could be placed in the eyrie, or no dummies were used and second clutches were laid and later replaced by dummies or young.

Thickness was measured optically from fresh chips taken at three places on the equators of the rinsed and desiccated shells and included shell plus shell membranes. In 14 instances where membranes were absent the average membrane thickness of 0.073 mm for 127 eggshells was added to the shell thickness. Optical measurement, accurate to ±0.004 mm, was made with a 60X compound microscope using an ocular scale calibrated from a Bausch and Lomb 0.01 mm stage micrometer. Reproducibility of measurement on each chip, and for chips from the same egg, was greater than that which we obtained with mechanical micrometers, probably because surface irregularities were discounted. We did not calculate clutch mean thickness in instances where more than one egg from a clutch was available because within-clutch variation was often great. We obtained 36 eggs from second clutches and these were grouped with eggs from first clutches because shell thickness and residue values showed no trends between clutches.

Intact added peregrine eggs for organochlorine analysis were either emptied into acetone-washed vials with foil-lined stoppers and frozen or frozen intact prior to analysis. Eggs collected in 1973-75 were analyzed by the Denver Wildlife Research Center, Fish and Wildlife Service, using methods described by Peterson et al. (1976). Eggs collected in 1976-79 were analyzed by the Patuxent Wildlife Research Center, Fish and Wildlife Service, using methods described by Cromartie et al. (1975). In 1973-74 egg contents were analyzed for DDE, dieldrin and polychlorinated biphenyls (PCBs), the latter quantified as Arochlor 1254. The efficiency of recovery was 84-100%. In 1975 only DDE and PCBs (Arochlor 1260) were measured. Eggs collected in 1976-79 were analyzed for p,p'-DDE, p,p'-DDD, p,p'-DDT, dieldrin, heptachlor epoxide, oxychlordane, cis-chlordane, trans-nonachlor, cis-nonachlor, hexachlorobenzene, mirex, β-BHC, and PCBs (Arochlor 1260) and the range of recovery was 83-104%. The lower limit of sensitivity was 0.10 ppm and the reported residue levels are accurate to two significant figures. Identification of residues was confirmed on a combined gas chromatograph mass spectrometer for 8 of the 43 samples collected in 1976-79. Percent moisture was determined from 10g aliquots and residue levels were corrected to approximate fresh egg weight assuming a moisture content of 85%, the highest reported for a nearly fresh egg in our sample collected early in incubation when desiccation was probably slight.

Prey remains were collected at peregrine eyries and identified by comparison with museum skins. In 1977-79 we collected adult birds identified as important or potential peregrine prey. Seven to 10 adults of each species were shot in May or early June within 9 km of active or recent eyries. Some species were collected near more than one eyrie. Freshly shot individuals were wrapped in acetone-washed foil and frozen. Samples were prepared for analysis by removing the feet, beak, feathers, and large intestine of each bird and finely homogenizing the remainder. The individuals of each species from a locality were homogenized separately. Equal weights, usually 10 g, of the 7-10 individual homogenates were then pooled and the mixture wrapped thoroughly in acetone-washed foil and sent frozen to Wisconsin Alumni Research Foundation Institute (later became Raltech Scientific Services) for analysis. A 10 g aliquot of each pool was mixed with sodium sulfate, allowed to dry and subjected to Soxhlet extraction with 50:50 ethyl ether:petroleum ether for 8 hours. The sample was then evaporated just to dryness and brought to 25 ml with 25% toluene in ethyl acetate. A 5 ml aliquot was transferred to a gel permeation apparatus. The eluate was then evaporated just to dryness and brought to 10 ml in hexane for injection on a 1.5% OV-17 plus 1.95% QF-1 on 80/100 G.C.O. gas chromatograph column. The lower limit of detection for chlorinated pesticides was 0.01 ppm and for PCBs (Arochlor 1254) 0.10 ppm, and the range of recovery was 80-90%. Arithmetic means are used throughout unless stated otherwise.

Results

Eggshell Thickness and Chemical Residues

Of the eggs collected, 77 contained large embryos or nearly full-term chicks, 57 showed little or no development, and development could not be determined for 7. We found no difference in the average thickness of shells from eggs showing little development compared to those with large embryos or hatched eggs. Figure 1 shows the eggshell thickness of eggs col-
lected in the period 1973-79 compared to data obtained by Anderson and Hickey (1972) from collections made prior to 1947 in Alberta, Saskatchewan, and Montana. We also measured 16 eggs with no embryonic development laid in 1978 by nine captive females originating in Colorado or adjoining states and fed Coturnix quail and young poultry. The mean shell thickness of the 141 wild-laid eggs was 0.302 mm (S.E. = 0.002), vs. the means for the captive-laid eggs of 0.348 mm (S.E. = 0.005), and of 0.359 mm (S.E. = 0.003) for the pre-1947 eggs. The 95% confidence limits for the captive-laid eggs and the pre-1947 eggs overlapped substantially and the samples were not statistically different. The 95% confidence limits for recent wild-laid eggshells did not overlap with those for the museum specimens or captive-laid eggs, and the former were thinner by 16% and 13% respectively. The wild-laid eggshells, 1973-79, were significantly different in thickness (one-way analysis of variance, F-ratio = 2.44, P < 0.05 between years. Those laid in 1977 were significantly thinner than those laid in 1978 and 1979 (t-tests, P < 0.05).

Forty-seven eggs from 30 clutches were analyzed for organochlorines (Table 1). In six cases eggs from first and second clutches from a female in a given year were analyzed and clutch averages for DDE and total organochlorines were calculated. Second clutches usually had lower levels than first clutches, but the differences were not significant (paired t-tests, P > 0.05) either for DDE or total organochlorines. Prior to 1976 egg contents were not analyzed for materials other than DDE and PCBs. From 1976-79 other residues were included in the total organochlorine column of Table 1 and are shown in order of frequency in single eggs: heptachlor epoxide (97%; range 0.10-1.10 ppm), oxychlordane (79%; 0.08-0.35), DDT (66%; 0.10-2.6 ppm), DDD (47%; 0.08-0.41 ppm), B-BHC (45%; 0.12-0.25 ppm), and HCB (32%; 0.05-0.40 ppm). Three eggs from eyrie PR in 1975 averaged 66.0 ppm DDE and 66.6 ppm PCBs, both
Table 1. Residues of DDE, dieldrin, PCBs and total organochlorines in 47 peregrine eggs from Colorado and New Mexico. Values are arithmetic means (standard errors) where more than one egg was analyzed.

<table>
<thead>
<tr>
<th>Tyrie</th>
<th>Year</th>
<th>Eggs analyzed</th>
<th>Organochlorine residues (ppm, wet wt.)</th>
<th>Total Ocs.</th>
</tr>
</thead>
<tbody>
<tr>
<td>CO</td>
<td>1973</td>
<td>1</td>
<td>21.8</td>
<td>5.0</td>
</tr>
<tr>
<td>RG</td>
<td>1973</td>
<td>1</td>
<td>13.6</td>
<td>3.0</td>
</tr>
<tr>
<td>CE</td>
<td>1973</td>
<td>1</td>
<td>24.8</td>
<td>3.7</td>
</tr>
<tr>
<td>LA</td>
<td>1973</td>
<td>1</td>
<td>32.6</td>
<td>5.0</td>
</tr>
<tr>
<td>CE</td>
<td>1974</td>
<td>1</td>
<td>10.7</td>
<td>1.6</td>
</tr>
<tr>
<td>RG</td>
<td>1974</td>
<td>1</td>
<td>12.3</td>
<td>3.8</td>
</tr>
<tr>
<td>PR</td>
<td>1975</td>
<td>3</td>
<td>65.0(5.0)</td>
<td>66.6(2.3)</td>
</tr>
<tr>
<td>CE</td>
<td>1976</td>
<td>2</td>
<td>24.0(2.4)</td>
<td>1.6(0.4)</td>
</tr>
<tr>
<td>FX</td>
<td>1976</td>
<td>1.2</td>
<td>31.0(4.5)</td>
<td>6.2(0.9)</td>
</tr>
<tr>
<td>HH</td>
<td>1977</td>
<td>3</td>
<td>28.1(1.8)</td>
<td>2.3(0.2)</td>
</tr>
<tr>
<td>FX</td>
<td>1977</td>
<td>2.1</td>
<td>11.4(3.2)</td>
<td>4.0(2.5)</td>
</tr>
<tr>
<td>LV</td>
<td>1977</td>
<td>2</td>
<td>15.3(1.9)</td>
<td>2.8(0.4)</td>
</tr>
<tr>
<td>TU</td>
<td>1977</td>
<td>1</td>
<td>11.3</td>
<td>1.0</td>
</tr>
<tr>
<td>CR</td>
<td>1977</td>
<td>1</td>
<td>31.5</td>
<td>0.9</td>
</tr>
<tr>
<td>LA</td>
<td>1977</td>
<td>2</td>
<td>13.0(0.6)</td>
<td>0.8(0.1)</td>
</tr>
<tr>
<td>SB</td>
<td>1977</td>
<td>1</td>
<td>9.6</td>
<td>ND</td>
</tr>
<tr>
<td>CM</td>
<td>1978</td>
<td>1</td>
<td>8.3</td>
<td>0.19</td>
</tr>
<tr>
<td>CE</td>
<td>1978</td>
<td>3</td>
<td>7.8(0.2)</td>
<td>0.23(0.01)</td>
</tr>
<tr>
<td>CR</td>
<td>1978</td>
<td>1.2</td>
<td>33.3(3.7)</td>
<td>0.15(0.2)</td>
</tr>
<tr>
<td>PX</td>
<td>1978</td>
<td>1.3</td>
<td>18.9(0.7)</td>
<td>0.12(0.0)</td>
</tr>
<tr>
<td>PX</td>
<td>1979</td>
<td>3.2</td>
<td>18.7(0.7)</td>
<td>0.14(0.0)</td>
</tr>
<tr>
<td>HS</td>
<td>1979</td>
<td>2</td>
<td>32.0(0.0)</td>
<td>0.13(0.01)</td>
</tr>
<tr>
<td>CR</td>
<td>1979</td>
<td>1</td>
<td>63.0</td>
<td>2.6</td>
</tr>
<tr>
<td>LV</td>
<td>1979</td>
<td>1.1</td>
<td>21.1(5.0)</td>
<td>1.5(0.4)</td>
</tr>
</tbody>
</table>

Geometric Mean 19.6 0.21 2.0 21.9
Arithmetic Mean 23.3 0.22 5.0 25.5

NA = Not analyzed
ND = Not detected

1Eggs were from first clutches except where number from first and second clutches are shown.
2Residues corrected for desiccation.
3In 1973-74 PCBs were quantified as Arochlor 1254, and in 1975-79 as Arochlor 1260.

unusually large values. This set was found abandoned.

The correlations among eight commonly occurring organochlorines in peregrine eggs are shown in Table 2. DDT and its metabolites DDD and DDE had significant positive correlation coefficients (t-tests; P < 0.01), an expected result. Several other compounds showed significant positive correlations suggesting that many of these lipid-soluble compounds are acquired by peregrines collectively. Only heptachlor epoxide showed weak significant inverse correlation with shell thickness (P < 0.05). No significant negative correlation was found between DDE and shell thickness (r = 0.068). Similarly, a plot of log DDE against shell thickness for the 47 eggs collected since 1973 showed no apparent inverse relationship contrary to expectation. However, only 5 (11%) of the eggs had residues below 10 ppm, and none below 6 ppm DDE. Most eggs contained enough DDE to correlate with shells 20-25% thinner than normal, interpolated from regressions for Brown Pelicans (Pelecanus occidentalis) (Bius et al. 1972), Prairie Falcons (Falco mexicanus) (Enderson and Wrege 1973), and Alaskan peregrines (Cade et al. 1971). The present sample of eggs is probably so uniformly and highly contaminated that the regression cannot be shown. Lacking from the sample are eggs with thicker shells and low DDE levels.

Residue levels in 14 individual eggs collected in 1973-76 were compared with levels in 1977-79 eggs, the latter collected when all clutches found were obtained for artificial incubation. The early group averaged 32.3 ppm DDE (S.E. = 5.2), the later group averaged 20.9 (S.E. = 2.0). These means are significantly different (Mann-Whitney U-test, 0.05 > P > 0.01). However, multiple regression analysis of the DDE values, or their logarithms, vs. years failed to show a significant decrease of DDE from 1973-79.

Organochlorine Residues in Prey

We identified the remains of 107 individuals of
small and medium-sized birds of 31 species at 14 eyries in Colorado and northern New Mexico. Of these, remains of birds of 13 species were found at more than one eyrie. We collected samples of 12 of these species, omitting Black-billed Magpies (*Pica pica*), and analyzed them for organochlorine residues (Table 3). In addition we collected samples of 17 species, some of which were identified as prey at only one eyrie, that were common and sometimes vulnerable to peregrines (Table 4). All these collections, made near 12 eyries,
Table 4. Organochlorine residues in additional prey species available to peregrines

<table>
<thead>
<tr>
<th>Species</th>
<th>Individuals found as prey</th>
<th>Pools analyzed (individuals)</th>
<th>Residues (ppm, wet wt.)¹</th>
<th>Total Organochlorines</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kildeer Charadrius vociferus</td>
<td>1</td>
<td>3(25)</td>
<td>19.5 (6.4)</td>
<td>20.5 (6.9)</td>
</tr>
<tr>
<td>Common Nighthawk Chordeiles minor</td>
<td>1</td>
<td>2(18)</td>
<td>0.35 (0.15)</td>
<td>0.44 (0.15)</td>
</tr>
<tr>
<td>Western Kingbird Tyrannus verticalis</td>
<td>–</td>
<td>2(14)</td>
<td>1.1 (0.68)</td>
<td>1.22 (0.8)</td>
</tr>
<tr>
<td>Say's Phoebe Sayornis saya</td>
<td>–</td>
<td>1(7)</td>
<td>2.0</td>
<td>2.1</td>
</tr>
<tr>
<td>Western Wood Pewee Contopus sordidus</td>
<td>–</td>
<td>1(7)</td>
<td>1.2</td>
<td>1.5</td>
</tr>
<tr>
<td>Violet-green Swallow Tachycineta thalassina</td>
<td>1</td>
<td>6(42)</td>
<td>5.9 (1.2)</td>
<td>7.3 (1.3)</td>
</tr>
<tr>
<td>Tree Swallow Iridoprocne bicolor</td>
<td>–</td>
<td>1(7)</td>
<td>32.8</td>
<td>33.5</td>
</tr>
<tr>
<td>Cliff Swallow Petrochelidon pyrrhonota</td>
<td>–</td>
<td>1(9)</td>
<td>2.0</td>
<td>2.3</td>
</tr>
<tr>
<td>Steller's Jay Cyanocitta stelleri</td>
<td>2</td>
<td>1(7)</td>
<td>0.51</td>
<td>0.52</td>
</tr>
<tr>
<td>Piñon Jay Gymnorhina cyanoccephalus</td>
<td>1</td>
<td>1(7)</td>
<td>0.12 (0.51)</td>
<td>0.63</td>
</tr>
<tr>
<td>Western Bluebird Stilts mexicana</td>
<td>1</td>
<td>1(6)</td>
<td>0.09</td>
<td>0.09</td>
</tr>
<tr>
<td>Townsend's Solitaire Myiastes townsendi</td>
<td>2</td>
<td>2(14)</td>
<td>0.28 (0.02)</td>
<td>0.40 (0.01)</td>
</tr>
<tr>
<td>Solitary Vireo Vireo solitarius</td>
<td>–</td>
<td>1(7)</td>
<td>1.9</td>
<td>2.0</td>
</tr>
<tr>
<td>Yellow-rumped Warbler Dendroica coronata</td>
<td>–</td>
<td>2(13)</td>
<td>0.97 (0.03)</td>
<td>1.1 (0.09)</td>
</tr>
<tr>
<td>Brown-headed Cowbird Molothrus ater</td>
<td>1</td>
<td>2(14)</td>
<td>1.2 (0.41)</td>
<td>1.4 (0.43)</td>
</tr>
<tr>
<td>Black-headed Grosbeak Pheucicus melanocephalus</td>
<td>–</td>
<td>2(14)</td>
<td>0.06 (0.02)</td>
<td>0.11 (0.03)</td>
</tr>
<tr>
<td>Red Crossbill Loxia curvirostra</td>
<td>1</td>
<td>1(7)</td>
<td>0.02 (0.11)</td>
<td>0.13</td>
</tr>
</tbody>
</table>

¹Means (standard errors) (range)
²Detected in only one pool
ND – Not detected

Included species taken while peregrines were resident in the region.

There was wide variation in DDE, PCBs, and total organochlorine levels among the 12 species of prey most often found in peregrine eyries (Table 3). The White-throated Swift, American Robin, Red-winged Blackbird, Western Meadowlark, Brewer's Blackbird, and Starling were represented by sample pools where DDE was about 0.5 ppm or greater; those species clearly represented major sources of DDE to peregrines in the region. In some cases, such as Brewer's Blackbird, wide variation existed between DDE levels in pools from different localities. The White-throated Swift, the most frequently found species, had the highest average for PCBs in this group and one pool contained 0.76 ppm. The Common Flicker and Clark's Nutcracker, although represented by more than one pool, had very low organochlorine levels.
Single pools for the Pine Siskin and the Mountain Bluebird also had low residues.

Other birds in the region available to peregrines but not known to be eaten frequently also bore substantial residues (Table 4). Seven of these species seemed especially vulnerable to peregrines including the Killdeer, Brown-headed Cowbird, Western Kingbird, Common Nighthawk, Cliff Swallow, Tree Swallow, and Violet-green Swallow. The latter was abundant at many peregrine eyries and six pools averaged 5.9 ppm DDE. Although Killdeer were much less numerous, three pools averaged 19.5 ppm DDE. PCBs also were about 0.5 ppm in the Violet-green Swallow, Tree Swallow, and Pinon Jay. The latter, and the Red Crossbill, eat conifer seeds and both bore little DDE but much higher amounts of PCBs. The Violet-green Swallow had the most PCBs; six pools averaged 0.55 ppm.

Of the 29 species of birds analyzed, 17 were represented by more than one sample pool. Where only a single pool was analyzed, care must be taken in interpreting the reported residue values because of occasional wide variation between pools for the same species.

We grouped the DDE data for the 29 species by their predominant food-habits and migratory status to characterize the sources of this compound to peregrines (Table 5). The migratory category included several species that remained in the region in low numbers in winter but that generally winter to the south.

Despite great variation, DDE levels among insectivorous prey were clearly higher than among omnivores and granivores. Similarly, migratory forms appeared to bear more DDE than non-migratory species of equivalent food habits. These patterns also appeared in the geometric means which tend to minimize the effect of extremely high levels found in a few species. The Common Flicker was the only resident insectivore collected, and it had an exceptionally low DDE value.

On average, peregrine eggs were 23 times more contaminated than peregrine prey. In 1977-79 peregrine eggs averaged about 21 ppm DDE. Pools of the 12 species frequently eaten by peregrines in that period (Table 3) averaged about 0.9 ppm. This degree of biomagnification of organochlorine residues is consistent with that reported for peregrines elsewhere (Cade et al. 1968; Enderson and Berger 1968).

Discussion

Peregrine Falcons in Colorado and northern New Mexico are exhibiting low occupancy of historical territories, poor reproduction, and thin-shelled eggs. Their prey contains substantial amounts of organochlorines. The population decline since the advent of DDT was estimated at about 50% by 1973 (Enderson and Craig 1974). This situation apparently has not improved. In 1980, only 5 of 18 eyries that had adult pairs sometime in 1970-77 were occupied by pairs. Two others had lone adults, and two more had pairs including immature birds, suggesting that the recruitment of adults had been inadequate. In 1973 natural reproduction was known to be very poor (0.2 young per adult pair, Enderson and Craig 1974), since 1975 the removal of eggs and substitution by captive-bred young has obscured the natural reproductive rate. Some pairs, however, were still reproducing naturally. From 1975 to 1980 we found six pairs with a total of 13 flying young late in the breeding season. Despite restriction of DDT in North America, peregrines in this region were not recovering and this contrasts with Brown Pelicans (Pelecanus occidentalis) (Anderson et al. 1975) and ospreys (Pandion haliaetus) (Spitzer et al. 1978).

EggsHELLS laid in 1973-79 averaged 16% thinner than pre-1947 museum eggshells, showed high variation in thickness within clutches, and some approached normal thickness (Figure 1). W. Burnham (unpublished data) has hatched all of over 30 wild eggs received intact and incubated artificially in 1979-80, but the shell condition of the majority of those eggs would almost certainly have precluded their hatching under natural incubation. Among wild peregrines egg
breakage is unusual where the thinning is less than 10% (Anderson et al. 1969; Blus 1970; Coulter and Risebrough 1973). Peregrine eggs laid in California in 1947-52 by a declining population were about 12% thinner than those laid before 1947 (Hickey and Anderson 1968) and 17% thinning was associated with lowered reproduction in Alaskan peregrines (Cade et al. 1971). An 18% thinning was associated with the declining British peregrine population (Ratcliffe 1980).

We found about 20 ppm DDE (geometric mean) in egg contents (Table 1). That value corresponds to about 18% thinning from the pre-1947 value, as predicted by a regression of thickness plotted against log DDE in egg contents for Alaskan peregrines (Cade et al. 1971). That amount of thinning is in close agreement to the 16% thinning we found.

DDE and PCBs are closely correlated in our egg samples (Table 2) and the significance of the latter is unknown. In a careful statistical analysis of organochlorine residues in Sparrowhawks, Newton and Bogan (1978) found PCBs showed the strongest relationship of any compound with egg adding, and they concluded from the literature that PCBs have not been linked to eggshell thinning in field or controlled laboratory studies. McLane and Hughes (1980) found no effect on eggshell thickness, young hatched, and young fledged in captive Screech Owls fed Aroclor 1248 where levels reached from 3.9-17.8 ppm in egg contents. In the present study, PCB levels are below these, and since the peregrine eggs incubated artificially hatched successfully there is no evidence PCBs have impaired reproduction in this population.

Prey available to peregrines in the region showed extreme variation in DDE contamination (Tables 3 and 4), and the intake of contaminants by individual peregrines would depend on the prey species taken. At least six species of commonly eaten prey are ubiquitous and are represented by pools of individuals with about 0.5 ppm DDE or more. Among the 29 species of prey we analyzed, 19 had at least one pool with about 0.5 ppm DDE or more and 11 had 1.0 ppm or more. Even if peregrines accumulated DDE in wintering areas, we believe that the major sources were migrant prey available near peregrine eyries in summer.

Because prey selection by peregrines in the region is no doubt subject to many vagaries, and because of the great variation of DDE contamination in prey, it is difficult to correlate the residues we found in prey with the DDE and shell thinning in falcon eggs. In fact, a day-to-day variation in DDE intake by a laying peregrine may have caused the wide variation in eggshell thickness within a clutch. Several laboratory and field studies have found shell thinning in birds fed DDE. Captive Black Ducks (Anas rubripes) and Mallards (Anas platyrhynchos) produced eggs 8 to 22% thinner than controls when fed about 3 ppm DDE (wt weight) for periods up to a year (Heath et al. 1969, Longcore and Samson 1973). Ring Doves (Streptopelia risoria) fed about 3 ppm DDE (wt weight) produced eggs 9.2% thinner than controls (Peakall et al. 1973). Among raptors, Screech Owl (Otus asio) eggs were found to be thinned by 13.3% when the birds were placed on a diet containing 2.8 ppm DDE (McLane and Hall 1972). Liner (1975) fed captive American Kestrels 3 ppm DDE 2-3 months prior to egglaying and recorded a 14% decrease in eggshell thickness compared to controls. Dose-response curves he calculated predicted that 1 ppm of dietary DDE would produce about 7% thinning, and 2 ppm DDE about 11% thinning. He was also able to show that both experimental and wild kestrels showed the same shell-thinning response to DDE. The experimental birds did lay thinner-shelled eggs overall, perhaps due to genetic differences or the effects of captivity.

Alekutin peregrines are apparently reproducing normally. They are non-migratory and suffer only 7.7% shell thinning (White et al. 1973). Analyses of up to three individuals of 12 commonly eaten prey species revealed that only two migrant birds had whole-body DDE levels above 0.37 ppm DDE, and none above 1.88 ppm. These few analyses and a count of many food remains found at eyries indicated that the bulk of Aleutian peregrines prey contained less than 0.5 ppm DDE.

The above studies suggest that peregrines feeding heavily on prey exceeding about 1 ppm DDE in the breeding season could be expected to produce eggs with shells thinned by the amount we found even if they had no important previous exposure to DDE. The presence of several pools among our samples with over 5 ppm DDE does not hold much promise for normal peregrine reproduction.

Since 1974, 128 captive-bred young peregrines have been released in Idaho, Wyoming, Utah, Colorado, South Dakota and New Mexico by placing young in eyries, cross-fostering to prairie falcons, or by "hacking" the young until they became independent. When young were placed in the eyries of wild peregrines, fledging success was as good or better than that expected in a DDE-free population (Burnham et al. 1978), but because of the DDE levels revealed in the present study released birds can be expected to reproduce poorly. Under these conditions, the release of captive-bred birds serves to augment reproduction and hopefully increase the population. In 1980, a banded male that was almost certainly a released bird bred in Colorado. Released birds surely will help to maintain the occupancy of traditional eyries, and
because of the diversity of the captive breeding stock they will enhance the genetic variability of the small wild population.

Moreover, this augmentation should arrest the decline until DDE levels subside in peregrine prey, especially migrant species. A report of such a reduction in migratory songbirds is encouraging (Johnston 1974), but is offset by the finding that, nationwide, DDE in starlings increased significantly from 1974 to 1976 so that they returned to 1970 values (White 1979). The pronounced contamination by DDE in migratory prey suggests acquisition of residues on their wintering grounds. This possibility needs prompt study requiring international cooperation because several of the migrant species winter south of the United States. If the residues in migrants could be reduced to those found in resident prey, the peregrine population in the Rocky Mountain region would very likely become self-sustaining.

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Literature Cited


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Prey Characteristics of Upland-Breeding Red-winged Blackbirds, *Agelaius phoeniceus*

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Neck-collar food samples collected from Red-winged Blackbird (*Agelaius phoeniceus*) nestlings from two agricultural upland sites indicated that Lepidopteran larvae from grasses and legumes predominated during the main nestling period but were later replaced by adult Orthopterans. Sampling of prey abundance indicated that the Red-winged Blackbirds were preying selectively on species characterized as cryptically coloured, slow-moving, diurnal, foliage feeders. Overall, insects from 27 families in 9 orders as well as spiders, isopods, snails and grain were represented.

Key Words: Red-winged Blackbirds *Agelaius phoeniceus*, prey, upland, Quebec.

A number of studies have found pest insects in the stomachs of Red-winged Blackbirds (*Agelaius phoeniceus*) prompting several authors (Hintz and Dyer 1970; Robertson et al. 1978; McNicol et al. 1979) to suggest that Red-winged Blackbirds may be of some economic benefit to agriculture. Since Red-winged Blackbirds are a serious pest owing to the damage they do to ripening corn (Weatherhead and Bider 1979), any benefit derived from them would have implications for their management. Only through food-habits studies can the most important prey items be identified and specific studies be designed to determine the value to agriculture of Red-winged Blackbird predation on a given prey species (McNicol et al. 1979).

Insectivity by Red-winged Blackbirds is most pronounced during the breeding season, the only time during the year that insects exceed plant food in the diet (Hintz and Dyer 1970; Mott et al. 1972; McNicol et al. 1979). During this period nestling food may be sampled using the pipe-cleaner neck-collar technique (Orians 1966). Detailed reports have been published on neck collar samples from nestling Red-winged Blackbirds in marsh habitat (Snelling 1968; Orians and Horn 1969; Orians 1973; Voigts 1973). No data from neck-collar samples of upland nesting Red-Winged Blackbirds have been published, however, despite the fact that most Red-winged Blackbirds breed in upland habitat (Grabber and Graber 1963; Dyer 1970). Our aim in this study was to sample nestling food in upland habitats to identify prey items potentially harmful to agriculture and to determine if the more common prey items shared characteristics such as colouration and mobility. We felt the latter objective to be particularly important if the data were to be applicable to other areas, given the likelihood that although prey species may vary between study sites according to prey availability, the characteristics of the prey should remain more constant.

**Methods**

Samples were taken during the periods 2–21 June 1979 and 23 July to 2 August 1979 from nests located at two sites in southwestern Quebec: one in Beauharnois Co. (45° 15' N, 70° 55' W) (Site 1) and another 3.1 km away in Chateauguay Co. (Site 2). Land at Site 1 was sown to grain, corn, alfalfa and clover, or was used for pasture and hay. There were few trees or shrubs in the area. Site 2 was along a railway embankment bordered by corn and fallow fields.

Neck-collars were made from flesh-coloured pipe cleaners. They were applied only when nestlings were judged to be at least two days old. All nestlings in the same nest were collared at the same time for a period of one hour. At least two days separated successive applications of collars to the same nestlings. Food taken from the mouths and gullets of collared nestlings was preserved in alcohol for later identification. The total food taken from all nestlings in the same nest over one hour was considered one sample. To facilitate species identification specimens of several of the important larval forms recovered in the neck-collars were collected from the field and reared to adults for comparison with specimens in the Lyman Entomological Museum, Macdonald College.

Quadrat sampling was begun when it appeared that many of the larval prey, which were the bulk of the nestling diet, came from grasses, or alfalfa and clover. This kind of sampling allowed an evaluation of the
kinds of prey items available to birds foraging in these habitats, but did not allow an exact determination of their numbers. Samples consisted of ten 0.1–m⁻² quadrats of vegetation, each taken 10 paces apart, starting from a randomly selected point. Four samples were taken in each of a hay field, a pasture, a roadside ditch and a drainage ditch, the principal habitats available to the birds. Two samples were taken across the width of a mixed alfalfa and clover field. Each quadrant of vegetation was carefully examined for larvae, which were preserved in alcohol for later identification. During the second minor nesting period at Site 1 in late July and early August, grasshoppers were the main component of the diet. These were sampled by taking three transects, each consisting of 50 sweeps of a sweep net, beginning at randomly selected points in a hay field, in a mixed alfalfa and clover field, and along a drainage ditch.

All insects collected in the neck-collar samples were identified at least to the family level; the major diet items were identified to species. Identification was done with the aid of Borror et al. (1976) and Chu (1949) for adults and larvae respectively. Some specimens were identified through the assistance of experts of the Biosystematics Research Lab, Agriculture Canada. For analysis, samples were separated by site and sampling period.

Results

Nestling Red-winged Blackbirds were fed a variety of insects from 27 families in 9 orders, as well as spiders, isopods, snails and grain (Tables 1, 2 and 3). However, in every collection of samples, one insect order composed more than 50 percent of the volume. The largest collection of samples (Site 1, June 2–21) was dominated by the family Noctuidae (54 percent by volume), of which larvae of a single species, Amphipoea velata (Walker), made up 31 percent. Samples taken from Sites 1 and 2 during June were both dominated by lepidopteran larvae, although Site 2 had a high proportion of mayflies (Ephemeroptera), presumably because of its proximity to the Chateauguay River. Samples taken at Site 1 from 23 July to 2 August differed markedly from previous samples in that lepidopteran larvae, mayflies and beetles were absent and were replaced in the diet by orthopterans and orb-weaver spiders (Araneidae). This seasonal change in the diet was also noted by Snelling (1968), and likely reflects a change from predominantly lepidopterans to orthopterans in the fauna of large herbivorous insects. As a result, greater similarities exist between samples taken in June from the two different sites than exist between samples from the two breeding periods at Site 1. A significant rank order correlation was found between the numbers of items of each major classification (11 arthropod orders, snails and grain) at Site 1 during June and those at Site 2 (Spearman rank correlation, r = 0.60, P < 0.05). However, no correlation was found between the major classifications (12 arthropod orders, snails and grain) at Site 1 for the two sampling periods.

Several pest species were identified in the nestling diet, including larvae of the Clover Leaf Weevil, Hyptera punctata (Fab.), the European Skipper, Thymelicus lineola (Ochsenheimer), and the Dark-sided Cutworm, Euxoa messoria (Harris). Although the family Noctuidae, which contains many important pest species, was the most important insect family in the diet, the most important noctuid taken by the birds was Amphipoea velata (Walker), a species of no known economic significance. Other groups of insects that contained possible pests but which made up only a small part of the diet, were short-horned grasshoppers (Acrididae), leafhoppers (Cicadellidae), aphids (Aphidae) and click beetles (Elateridae).

Quadrat sampling produced few specimens of the lepidopteran larvae eaten by the birds. In 160 0.1–m⁻² quadrat samples in grass, only one specimen of A. velata and none of the European Skipper or Apamea spp. were recovered although 12 sawfly larvae (Tenthredinidae) were collected.

Sweep-netting between 23 July and 2 August at Site 1 recovered many more short-horned grasshoppers (Acrifidae) than long-horned grasshoppers (Conocephalinae) in all habitats sampled (Table 4). This differential may be underestimated since short-horned grasshoppers are better jumpers and fliers and therefore better able to avoid the sweep net. Many of the short-horned grasshoppers were small, but even in the larger size classes, which were taken by the birds, the short-horned greatly outnumbered the long-horned grasshoppers. This contrasts with the relative abundance of the two grasshopper types in neck-collar samples. Significantly fewer Acrifidae relative to Conocephalinae were taken in neck-collar sampling than by sweep-netting in each habitat (Fisher exact probability tests, P < 0.05).

Discussion

The results of this study indicate that female Red-winged Blackbirds were selective in the prey they fed to their nestlings. Considering first the mobility of the prey species selected, most insects in the nestling diet were passive, slow-moving species with no escape reaction, requiring a high degree of searching but little active pursuit (e.g., lepidopteran larvae). This pattern is particularly apparent in the second nesting period in which the slow moving, green-coloured long-horned grasshoppers were taken over the more abundant and agile short-horned grasshoppers.
Table 1. Contents of 36 neck-collar samples from nesting Red-winged Blackbirds, southern Quebec — Site 1, 2–21 June 1979.

<table>
<thead>
<tr>
<th>Arachnida</th>
<th>No. of items</th>
<th>Proportion of total volume</th>
<th>Frequency of occurrence</th>
<th>Proportion of total volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phalangida</td>
<td>16</td>
<td>0.072</td>
<td>0.25</td>
<td>0.01</td>
</tr>
<tr>
<td>Araneida</td>
<td>12</td>
<td>0.054</td>
<td>0.22</td>
<td>0.01</td>
</tr>
<tr>
<td>Insecta</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ephemeroida</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ephemeridae-A</td>
<td>17</td>
<td>0.076</td>
<td>0.17</td>
<td>0.09</td>
</tr>
<tr>
<td>Odonata</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Libellulidae-I</td>
<td>1</td>
<td>0.005</td>
<td>0.03</td>
<td>0.02</td>
</tr>
<tr>
<td>Orthoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acrididae-I</td>
<td>1</td>
<td>0.005</td>
<td>0.03</td>
<td>0.01</td>
</tr>
<tr>
<td>Tettigoniidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Conocephalinae-I</td>
<td>8</td>
<td>0.036</td>
<td>0.11</td>
<td>0.03</td>
</tr>
<tr>
<td>Total Orthoptera</td>
<td>9</td>
<td>0.041</td>
<td>0.14</td>
<td>0.04</td>
</tr>
<tr>
<td>Hemiptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Miridae-A</td>
<td>1</td>
<td>0.005</td>
<td>0.03</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Nabidae-I</td>
<td>1</td>
<td>0.005</td>
<td>0.03</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Homoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cercopidae-I</td>
<td>7</td>
<td>0.032</td>
<td>0.03</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Cicadellidae-I&amp;A</td>
<td>29</td>
<td>0.131</td>
<td>0.17</td>
<td>0.02</td>
</tr>
<tr>
<td>Coleoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carabidae-A</td>
<td>4</td>
<td>0.018</td>
<td>0.08</td>
<td>0.01</td>
</tr>
<tr>
<td>Dytiscidae-I</td>
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<td>0.005</td>
<td>0.03</td>
<td>0.01</td>
</tr>
<tr>
<td>Scarabaeidae-A</td>
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<td>0.032</td>
<td>0.11</td>
<td>0.04</td>
</tr>
<tr>
<td>Byrrhididae-A</td>
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<td>0.004</td>
<td>0.03</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Elateridae-A</td>
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<td>0.009</td>
<td>0.06</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Cantharidae-A</td>
<td>1</td>
<td>0.005</td>
<td>0.03</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Curculionidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hybera punctata-I</td>
<td>18</td>
<td>0.081</td>
<td>0.14</td>
<td>0.05</td>
</tr>
<tr>
<td>Total Coleoptera</td>
<td>34</td>
<td>0.153</td>
<td>0.47</td>
<td>0.12</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pyralidae-A</td>
<td>1</td>
<td>0.005</td>
<td>0.03</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Thtricicidae-P</td>
<td>5</td>
<td>0.023</td>
<td>0.08</td>
<td>0.02</td>
</tr>
<tr>
<td>-I</td>
<td>5</td>
<td>0.023</td>
<td>0.06</td>
<td>0.02</td>
</tr>
<tr>
<td>Geometridae-I</td>
<td>3</td>
<td>0.014</td>
<td>0.08</td>
<td>0.02</td>
</tr>
<tr>
<td>Noctuidae-A</td>
<td>2</td>
<td>0.009</td>
<td>0.06</td>
<td>0.02</td>
</tr>
<tr>
<td>Amphipoea velata-I</td>
<td>40</td>
<td>0.180</td>
<td>0.39</td>
<td>0.31</td>
</tr>
<tr>
<td>Euxoa messoria-I</td>
<td>3</td>
<td>0.014</td>
<td>0.06</td>
<td>0.02</td>
</tr>
<tr>
<td>Others-I</td>
<td>14</td>
<td>0.063</td>
<td>0.22</td>
<td>0.22</td>
</tr>
<tr>
<td>Hesperiidae-P</td>
<td>1</td>
<td>0.005</td>
<td>0.03</td>
<td>0.01</td>
</tr>
<tr>
<td>Thymelicus lineola-I</td>
<td>2</td>
<td>0.009</td>
<td>0.06</td>
<td>0.01</td>
</tr>
<tr>
<td>Unidentified-I</td>
<td>1</td>
<td>0.005</td>
<td>0.03</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Total Lepidoptera</td>
<td>77</td>
<td>0.346</td>
<td>0.75</td>
<td>0.65</td>
</tr>
<tr>
<td>Diptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Chironomidae-A</td>
<td>1</td>
<td>0.005</td>
<td>0.03</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Tipulidae-A</td>
<td>1</td>
<td>0.005</td>
<td>0.03</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Formicidae-A</td>
<td>7</td>
<td>0.032</td>
<td>0.03</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>4</td>
<td>0.018</td>
<td>0.08</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Shell fragments</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Grain</td>
<td>5</td>
<td>0.023</td>
<td>0.08</td>
<td>0.01</td>
</tr>
<tr>
<td>Total No. of items</td>
<td>222</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: A — Adult
I — Immature
P — Pupa
Table 2. Contents of 10 neck-collar samples from nestling Red-winged Blackbirds, southern Quebec — Site 2, 6–14 June 1979.

<table>
<thead>
<tr>
<th></th>
<th>No. of items</th>
<th>Proportion of items</th>
<th>Frequency of occurrence</th>
<th>Proportion of total volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arachnida</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phalangida</td>
<td>17</td>
<td>0.27</td>
<td>0.10</td>
<td>0.03</td>
</tr>
<tr>
<td>Araneida</td>
<td>2</td>
<td>0.03</td>
<td>0.20</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Insecta</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ephemeroptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ephemerediida-A</td>
<td>16</td>
<td>0.25</td>
<td>0.70</td>
<td>0.36</td>
</tr>
<tr>
<td>Hemiptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Miridae-A</td>
<td>2</td>
<td>0.03</td>
<td>0.10</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Nabidae-I</td>
<td>1</td>
<td>0.02</td>
<td>0.10</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Homoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cercopidae-I</td>
<td>1</td>
<td>0.02</td>
<td>0.10</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Cicadellidae-I</td>
<td>1</td>
<td>0.02</td>
<td>0.10</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Coleoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carabidae-A</td>
<td>2</td>
<td>0.03</td>
<td>0.20</td>
<td>0.03</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tortricidae-P</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>-I</td>
<td>1</td>
<td>0.02</td>
<td>0.10</td>
<td>0.01</td>
</tr>
<tr>
<td>-I</td>
<td>2</td>
<td>0.03</td>
<td>0.20</td>
<td>0.04</td>
</tr>
<tr>
<td>Noctuidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Amphipoea velata-I</td>
<td>4</td>
<td>0.06</td>
<td>0.30</td>
<td>0.09</td>
</tr>
<tr>
<td>Others-I</td>
<td>5</td>
<td>0.08</td>
<td>0.30</td>
<td>0.26</td>
</tr>
<tr>
<td>Hesperiidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Thymelicus lineola-I</td>
<td>6</td>
<td>0.09</td>
<td>0.50</td>
<td>0.12</td>
</tr>
<tr>
<td>Unidentified-I</td>
<td>1</td>
<td>0.02</td>
<td>0.10</td>
<td>0.01</td>
</tr>
<tr>
<td>Total Lepidoptera</td>
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<td>19</td>
<td>0.30</td>
<td>0.53</td>
</tr>
<tr>
<td>Diptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unidentified-A</td>
<td>1</td>
<td>0.02</td>
<td>0.10</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Gastropoda</td>
<td>1</td>
<td>0.02</td>
<td>0.10</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Shell fragments</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total No. of items</td>
<td></td>
<td>63</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: A — Adult
I — Immature
P — Pupa
Table 3. Contents of six neck-collar samples from nestling Red-winged Blackbirds, southern Quebec — Site 1, 23 July-2 August 1979.

<table>
<thead>
<tr>
<th>Item</th>
<th>No. of items</th>
<th>Proportion of items</th>
<th>Frequency of occurrence</th>
<th>Proportion of total volume</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arachnida</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phalangida</td>
<td>2</td>
<td>0.03</td>
<td>0.17</td>
<td>0.04</td>
</tr>
<tr>
<td>Araneida</td>
<td>13</td>
<td>0.18</td>
<td>0.67</td>
<td>0.14</td>
</tr>
<tr>
<td>Insecta</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Orthoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Acridida-I</td>
<td>2</td>
<td>0.03</td>
<td>0.17</td>
<td>0.16</td>
</tr>
<tr>
<td>Tetrigoniidae</td>
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<td>0.09</td>
<td>0.50</td>
<td>0.38</td>
</tr>
<tr>
<td>Cnemidophila-A&amp;I</td>
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<td>0.13</td>
<td>0.50</td>
<td>0.03</td>
</tr>
<tr>
<td>Total Orthoptera</td>
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<td>0.12</td>
<td>0.67</td>
<td>0.54</td>
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<td>Hemiptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Phytophaga-A</td>
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<td>0.09</td>
<td>0.17</td>
<td>0.08</td>
</tr>
<tr>
<td>Homoptera</td>
<td>9</td>
<td>0.13</td>
<td>0.50</td>
<td>0.03</td>
</tr>
<tr>
<td>Cicadellida-A</td>
<td>17</td>
<td>0.25</td>
<td>0.67</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Aphidida-A&amp;I</td>
<td>1</td>
<td>0.02</td>
<td>0.17</td>
<td>0.01</td>
</tr>
<tr>
<td>Lepidoptera</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Hesperidida-P</td>
<td>1</td>
<td>0.02</td>
<td>0.17</td>
<td>0.01</td>
</tr>
<tr>
<td>Diptera</td>
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<td></td>
<td></td>
</tr>
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<td>Syrphidae-A</td>
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<td>0.02</td>
<td>0.17</td>
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</tr>
<tr>
<td>Dolichopodida-A</td>
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<td>0.17</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Unidentified-I</td>
<td>1</td>
<td>0.02</td>
<td>0.17</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Hymenoptera</td>
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<td></td>
</tr>
<tr>
<td>Formicidae-A</td>
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<td>0.33</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>Crustacea</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Isopoda</td>
<td>1</td>
<td>0.02</td>
<td>0.17</td>
<td>0.01</td>
</tr>
<tr>
<td>Grain</td>
<td>6</td>
<td>0.09</td>
<td>0.17</td>
<td>0.08</td>
</tr>
<tr>
<td>Total No. of items</td>
<td>69</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: A — Adult  
I — Immature  
P — Pupa

Table 4. Numbers* of short-horned (Acrididae) and long-horned (Cnemidophila) grasshoppers recovered in neck-collar and sweep net samples, SW Quebec, 1979.

<table>
<thead>
<tr>
<th>Habitat for sweep net sample</th>
<th>Neck-collar</th>
<th>Hayfield</th>
<th>Alfalfa</th>
<th>Drainage ditch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acrididae</td>
<td>2</td>
<td>114</td>
<td>8</td>
<td>9</td>
</tr>
<tr>
<td>Cnemidophila</td>
<td>8</td>
<td>3</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>

*All paired comparisons differ significantly at P < 0.05 (Fisher exact probability). Only specimens longer than 1 cm are included.

Coincident with low mobility amongst insect prey taken by Red-winged Blackbirds was cryptic colouration. Among the principal food items recovered during the main nestling period, the larvae of *Amphipoda velata*, most undetermined noctuids, the European Skipper and Clover Leaf Weevil were all green with one or more longitudinal white stripes, a typical disruptive colour pattern. Most of the larvae taken in quadrat sampling, however, were brown. These were mainly cutworms in alfalfa and clover and sawflies in grasses. Tinbergen (1960) found that sawfly larvae in a European pine wood generally ran a low risk of predation by tits. Prop (1960) showed that this was due to the low palatability of sawfly larvae and that species with a typical green and white disruptive colour pattern were more palatable. The failure of Red-winged Blackbirds to prey on the abundant sawfly larvae may reflect their low palatability. It is also possible however, that because the brown larvae are principally ground-resting they are as cryptic to the birds as green larvae found on plants and the bird's preference for the latter reflects only a preference for foraging in vegetation rather than on the ground. Further research will be required to determine the relative palatability of the various species of green and brown larvae.

As mentioned above, the locations from which prey items were taken also reflect high selectivity. The most important prey species were herbivorous insects taken from grasses or alfalfa and clover whereas insects
from the soil and surface litter were strikingly absent. Dark-sided Cutworms were as common as larvae of the Clover Leaf Weevil in quadrat samples from an alfalfa and clover field although none of the former and many of the latter were recovered from neck-collar samples taken in or near this field. Clover Leaf Weevil larvae pass the day in the crown of alfalfa and clover whereas the Dark-sided Cutworm was found on the soil surface and may in fact pass the day below the soil surface (Cheng 1973). Since no sub-surface sampling was done, Dark-sided Cutworms may have been more abundant than the quadrat sampling indicated.

The same foraging pattern is reflected by the absence of noctuid pupae in the nestling diet in spite of noctuid larvae being very abundant. Most noctuids pupate on or beneath the soil surface whereas the lepidopteran pupae that were recovered in neck-collar samples belonged to families (Hesperiidae and Tortricidae) which often pupate in vegetation.

It has been suggested that Red-winged Blackbirds use a gaping type of foraging (Orians 1973), described by Beecher (1951) as a technique whereby the closed bill is inserted into the substrate and then forced open to expose prey items. Evidence for this is suggested by the manner in which kernels of milk stage corn are evacuated, and by the use of larvae with a leaf rolling habit (Tortricidae). However, most insects fed to nestlings are normally exposed, and the failure to take items that are normally concealed, as do species with a well developed gaping behaviour (Beecher 1951), suggests that gaping is little developed.

The Red-winged Blackbird is thought to have been originally exclusively marsh-dwelling (Graber and Graber 1963), so it may be best adapted for foraging for emergent aquatic insects on the vertical vegetation of marshes. Its short legs make it a better forager in vegetation than other more terrestrial and long-legged blackbirds. In highly productive western marshes, where it compete with the Yellow-headed Blackbird (Xanthocephalus xanthocephalus), it is better able to exploit the denser vegetation of the marsh edge than the open areas of the marsh (Orians and Horn 1969). The same attributes are evident in the Red-winged Blackbird's exploitation of foliage-feeding larvae in upland habitats.

As with previous studies (Hintz and Dyer 1970; Robertson et al. 1978; McNicol et al. 1979) the occurrence of insects harmful to agriculture in neck-collar samples obtained in this study suggests the potential economic importance of Red-winged Blackbird predation on these species. The Clover Leaf Weevil and European Skipper show the most promise for further investigation as the larvae of these two species are typical of the type preferentially preyed on by Red-winged Blackbirds. Some circumstantial evidence that Red-winged Blackbirds may be having an impact on skipper populations is found in the fact that the European Skipper becomes a pest of major importance in areas of marginal agricultural land along the edge of the Laurentians (McNeil et al. 1975), a region where Red-winged Blackbird population densities are low (P. J. Weatherhead, unpublished data). Detailed studies of the species in question are needed to determine the importance of Red-winged Blackbirds as a mortality factor.

A final point concerns the occurrence of grain in the nestling diet. McNicol et al. (1979) have already determined that waste grain is an important dietary component for adult Red-winged Blackbirds in agricultural habitat during the breeding season. The amount of grain found in this study indicates it is unimportant in the nestling diet, but its occurrence at all is unusual. In considering why many granivorous birds are unable to take sufficient advantage of human cereal production to become pests, Dyer and Ward (1977) suggested that the high protein demand of growing nestlings requires a largely insectivorous diet during the breeding season. They went on to suggest that the development of protein-rich cereals could remove this limitation. As Red-winged Blackbirds are already important pests, their ability to supplement nestling diets with waste grain could result in larger populations and thus more severe problems. It would appear worthwhile to undertake further studies in several years' time to determine whether grain is becoming a more important dietary item or is remaining incidental.

Acknowledgments
We are grateful to Robin Stewart for his many helpful insights. Financial support was provided by Agriculture Canada, le Ministere de l'Agriculture du Quebec and by a Natural Sciences and Engineering Research Council operating grant No. U0096 to Patrick Weatherhead.

Literature Cited


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Breeding Bird Populations in Northern Manitoba

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Breeding bird censuses were conducted, using the spot-mapping method, in forest and forest-edge (including one riparian strip) plots at Churchill, Herriot Creek, and Gillam in northern Manitoba, and comparisons are made with avifaunas at four other localities in the subarctic and six localities in the boreal forest. Dominant tree species included Picea glauca, P. mariana, Larix laricina, and Pinus banksiana. Total bird species in the forest plots varied from 19 to 29 and total pairs from 69 to 96 per 40 ha. In the forest-edge plots, number of species varied from 12 to 24 and pairs per 40 ha from 71 to 242. The average number of pairs per species per 40 ha was highest in 2 forest-edge plots, 7.9 and 12.7, and varied from only 3.0 to 3.6 in the other plots. The distribution of pairs per species around the mean was slightly skewed, \( g_J = 1.4 \) to 1.7. Coefficients of species and population similarities were very high between the Churchill and Herriot Creek plots and moderately high between these plots and other areas in the subarctic. Coefficients were significantly lower between the Churchill-Herriot Creek populations and those in the boreal forest to the south, reconfirming the distinctiveness of the subarctic avifauna. The occurrence of highly skewed distribution (\( g_J \geq 2.0 \)) of species populations around the mean at several locations in both the subarctic and boreal forest may indicate ecological immaturity of the biotic community.

Key Words: Bird populations, northern Manitoba, forest-tundra, subarctic, community structure.

The present study is concerned principally with describing and analyzing breeding bird populations in northern Manitoba in the vicinity of Churchill (58° 46' N, 94° 10' W), near the mouth of Herriot Creek 26 km southwest of Churchill (58° 33' N, 94° 19' W) and at Mile 333 on the Hudson Bay railroad near Gillam (56° 21' N, 94° 43' W) about 265 km south of Churchill (Figure 1). Statistical comparisons, using relatively new procedures, are also made with bird populations at other localities in the subarctic and within the boreal forest (Figure 1). The field work was carried out during June, July, and August in 1956, 1957, and 1958.

All three localities lie in the Hudson Bay Lowland, a boggy plain underlain by flat-lying sedimentary rock (Caley and Liberty 1957). Radiocarbon dating of peat samples taken southeast and north of Churchill indicate that the last ice recession occurred near the end of the Thermal Maximum or Xerothermic Period between 5000 and 4000 years ago (Karlstrom 1956, Prest 1957). Marine submergence occurred over the Lowland until about 3000 years ago (Antevs 1931). Some authorities, however, believe that a somewhat longer time has been available for the invasion and establishment of the present biotic communities (Scoggan 1957; Lee 1960). Plant communities of the region have been described by Moir (1954), Ritchie (1956, 1957, 1959), Hustich (1958), and Sjörs (1959).

Recent accounts of birds in the Churchill area are those of Jehl and Smith (1970) and Cooke et al. (1975). Erskine (1977) included the Churchill area in his comprehensive summary of bird counts over all of boreal Canada. An unpublished study by Twomey (1937) included mapping of some nesting territories on a plot that we covered more thoroughly twenty years later. Godfrey (1953) listed birds along the Hudson Bay railroad, including the Gillam region.

Census Plots

Tree composition in the census plots was determined in part by counts on 2500 m² quadrats scattered at random over 5 percent of the area and in part by the point-centered quarter method of Cottam and Curtis (1956). Diameters of a few representative trees were measured at breast height with a steel diameter tape and converted into basal area. The height of these trees was determined with an Abney level and their age with an increment borer (Table I).

One forest plot and two forest-edge plots were established near the village of Churchill. Under and between the trees in the forest plot (Figure 2), there was a discontinuous shrub stratum of Dwarf Birch (Betula glandulosa) and willow (Salix spp.), an irregular stratum of low woody plants consisting of species of Ledum, Empetrum, and Vaccinium, and a thick ground cover of mosses over about 75 percent of the surface. A number of herbaceous species was scattered over the ground; sedges (Carex spp.) were present in depressions and lichens (Cladonia spp.) on higher mounds.

The forest-edge plots at Churchill bordered tundra, contained mostly stunted and densely branched White
Figure 1. Location of census areas. Limits of biotic areas are from Halliday (1937) and J.W. Aldrich (in Kendeigh 1974).

Table 1. Dominant tree species in forest study areas of Manitoba

<table>
<thead>
<tr>
<th>Area</th>
<th>Density trees ha$^{-1}$</th>
<th>Number of trees measured</th>
<th>Basal area m$^{2}$ha$^{-1}$</th>
<th>Average height m</th>
<th>Average age years</th>
</tr>
</thead>
<tbody>
<tr>
<td>Churchill (13 ha)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White Spruce, Picea glauca</td>
<td>672</td>
<td>13</td>
<td>2.38</td>
<td>7.4</td>
<td>131</td>
</tr>
<tr>
<td>Tamarack, Larix laricina</td>
<td>642</td>
<td>8</td>
<td>1.17</td>
<td>7.2</td>
<td>114</td>
</tr>
<tr>
<td>Herriot Creek (10.25 ha)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White Spruce, Picea glauca</td>
<td>571</td>
<td>6</td>
<td>2.14</td>
<td>14.8</td>
<td>111</td>
</tr>
<tr>
<td>Black Spruce, Picea mariana</td>
<td>722</td>
<td>10</td>
<td>1.07</td>
<td>7.9</td>
<td>73</td>
</tr>
<tr>
<td>Tamarack, Larix laricina</td>
<td>432</td>
<td>5</td>
<td>1.08</td>
<td>12.0</td>
<td>118</td>
</tr>
<tr>
<td>Gillam (10.75 ha)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black Spruce, Picea mariana</td>
<td>399</td>
<td>6</td>
<td>2.60</td>
<td>14.8</td>
<td>61</td>
</tr>
<tr>
<td>Jack Pine, Pinus banksiana</td>
<td>319</td>
<td>5</td>
<td>1.51</td>
<td>10.2</td>
<td>35</td>
</tr>
<tr>
<td>Tamarack, Larix laricina</td>
<td>72</td>
<td>3</td>
<td>0.21</td>
<td>8.9</td>
<td>21</td>
</tr>
</tbody>
</table>
and Black spruces (Picea glauca and P. mariana), and were situated on the sheltered side of a rocky ridge. The size of the two areas could only be approximated because of irregular boundaries and spacing of trees but was estimated at about 10 ha. There were about 1236 trees per hectare, 6.4 cm in diameter, and 3 m high (n = 17). Aside from a few scattered clumps of willows, the shrub layer contained species of Ledum, Rhododendron, Vaccinium, and Andromeda. The ground was covered with moss.

Black Spruce invaded the forest plot at Herriot Creek about 40 years after the other two species had become well established (Table 1). There was an irregular, widely spaced stratum of willows, Dwarf Birch, and Alder (Alnus crispa), commonly 1-1.5 m high, and a lower woody stratum of one or more species of Ledum, Rhododendron, Shepherdia, and Vaccinium. The forest floor consisted of small peat hummocks and depressions covered with a moss carpet of many species, including Sphagnum. Mats of Dryas integrifolia were common in the better drained areas. Treeless areas, interspersed over about one-third of the area, consisted of small bogs containing water and bog meadows of grasses and sedges with Dwarf Birch and willows around the margins. Some of the bog meadows contained tree stumps, indicating that the openings were of recent development.

The forest-edge plot at Herriot Creek, at its junction with Churchill River, was a riparian strip that extended about 1.9 km, averaged 52.6 m wide, and covered about 10 ha. It differed importantly from the forest-edge plots at Churchill in having a very dense stand of shrubs (Alnus, Betula, and Salix), with the tallest willows attaining 2.3 m in height. On the river side, the tall shrubs were bordered by grasses, sedges, and a low shrub (Myrica gale); on the forest side occurred a mixed stand of spruce and Tamarack (Larix laricina).

The Jack Pine (Pinus banksiana) in the relatively young Gillam forest plot (Table 1) was confined to a sand and gravel ridge covered with a thin layer of humus. Black Spruce was intermingled among the Jack Pine but formed denser stands in lower and wetter areas. A few small bogs were present. Isolated groups of Balsam Poplar (Populus balsamifera), Quaking Aspen (P. tremuloides), and Paper Birch (Betula papyrifera) occurred on the ridge in areas disturbed by a small Indian settlement some 30 years previously. Alder and willow shrubs occurred irregularly and often widely spaced, and a lower layer containing species of Ledum and Vaccinium was conspicuous throughout the forest. Sphagnum and other mosses and Cladonia and other lichens made a ground covering.

A few observations were made in a 12 ha Black Spruce scrub area (forest edge) at Gillam (Figure 3). Spruce and a few Tamarack formed an open stand with most of the trees 1.8 to 2.7 m high. The discontinuous shrub layer consisted of Salix, Alnus, Ledum, Empetrum, and Vaccinium. Rubus chamaemorus was common throughout. The ground was irregular with peat mounds covered by mosses and lichens and depressions often containing water and supporting a thick growth of grasses and sedges. The area was
subject to recurrent fires. For further details and lists of plant species collected on the various plots, see Gillespie (1960).

Methods
Our censuses were taken with the spot-mapping method (Kendeigh 1944). The plots were gridded at 50- m intervals, and the locations of singing males were mapped while we traversed back and forth along parallel lines. At least five counts were taken on each area during morning hours. Some nests were located. The population of each species was based on number of whole territories and sum of partial territories on the plot. Species with less than one-half a territory are marked in the table with a "+"; species seen only once were considered visitors only and not recorded. Weather conditions were near normal.

Species composition and bird populations in the various plots were compared in different ways. Coefficients of species similarity (Ss) were determined using the Sørensen equation:

\[ Ss = \frac{2C}{A+B} \]

where \( C \) is the number of species occurring in both plots, and \( A \) and \( B \) the total number of species in each. Coefficients of population similarity (Sp) were obtained by the equation (Odum 1950):

\[ Sp = 1.0 - \frac{\sum (pa - pb)}{Pa + Pb} \]

where \( p \) is the population size of an individual species in plot \( a \) or \( b \) and \( P \) is the combined population of all species in each plot. Plus marks in the table are included in calculating \( Ss \) and as zero population for calculating \( Sp \). Both coefficients are expressed as percentages.

Skewness or asymmetry (\( s_f \)) in distribution of pairs per species around the mean was calculated with the equation:

\[ s_f = \frac{\sum (X_i - \bar{X})^3}{(n-1)(n-2)s^3/n} \]

where \( s \) is the standard deviation of \( X_i \) from \( \bar{X} \) and \( n \) is the number of species. Plus marks in the table are considered as species present but with zero (< 0.5) pairs. Critical values for significance are given in Table D.25 of Zar (1974). These statistics have been found useful in analyzing populations in other localities (Kendeigh and Fawver 1981, Kendeigh 1982).

Results
Several species of shorebirds nested in the forest areas (Table 2) but did at least part of their feeding elsewhere. A grebe and two species of ducks also frequented the bogs at Herriot Creek. Several other non-passerine species were recorded but population data were obtained only on passerines. Nine species of Fringillidae, seven species of Parulidae, and four spe-
Table 2. Breeding bird populations in Manitoba (pairs/40 ha)

<table>
<thead>
<tr>
<th>Species</th>
<th>Forest plots</th>
<th>Forest-edge plots</th>
<th>Riparian Strip</th>
</tr>
</thead>
<tbody>
<tr>
<td>Horned Grebe, <em>Podiceps auritus</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Northern Pintail, <em>Anas acuta</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>American Wigeon, <em>Anas americana</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Rough-legged Hawk, <em>Buteo lagopus</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Merlin, <em>Falco columbarius</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Spruce Grouse, <em>Canachites canadensis</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Common Snipe, <em>Capella gallinago</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Spotted Sandpiper, <em>Actitis macularia</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Solitary Sandpiper, <em>Tringa solitaria</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Greater Yellowlegs, <em>Tringa melanoleuca</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Lesser Yellowlegs, <em>Tringa flavipes</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Short-billed Dowitcher, <em>Limnodromus griseus</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Northern Phalarope, <em>Lobipes lobatus</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Hawk Owl, <em>Surnia ulula</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Common Nighthawk, <em>Chordeiles minor</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Common Flicker, <em>Colaptes auratus</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Northern Three-toed Woodpecker, <em>Picoides tridactylus</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Yellow-bellied Flycatcher, <em>Empidonax flaviventris</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Alder Flycatcher, <em>Empidonax alnorum</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Olive-sided Flycatcher, <em>Nuttallornis borealis</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Tree Swallow, <em>Iridoprocne bicolor</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Bank Swallow, <em>Riparia riparia</em></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>Gray Jay, <em>Perisoreus canadensis</em></td>
<td>3</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Common Crow, <em>Corvus brachyrhynchos</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Boreal Chickadee, <em>Parus hudsonicus</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>American Robin, <em>Turdus migratorius</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Hermit Thrush, <em>Catharus guttatus</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Swainson's Thrush, <em>Catharus ustulatus</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Gray-cheeked Thrush, <em>Catharus minimus</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Ruby-crowned Kinglet, <em>Regulus calendula</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Solitary Vireo, <em>Vireo solitarius</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Tennessee Warbler, <em>Vermivora peregrina</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Orange-crowned Warbler, <em>Vermivora celata</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Yellow Warbler, <em>Dendroica petechia</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Magnolia Warbler, <em>Dendroica magnolia</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Yellow-rumped Warbler, <em>Dendroica coronata</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Blackpoll Warbler, <em>Dendroica striata</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Palm Warbler, <em>Dendroica palmarum</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Northern Waterthrush, <em>Seiurus noveboracensis</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Wilson's Warbler, <em>Wilsonia pusilla</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Rusty Blackbird, <em>Euphagus carolinensis</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Pine Grosbeak, <em>Pinicola enucleator</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Redpoll, <em>Carduelis flammea or C. hornemanni</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Savannah Sparrow, <em>Passerculus sandwichensis</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Dark-eyed Junco, <em>Junco hyemalis</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Tree Sparrow, <em>Spizella arborea</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Chipping Sparrow, <em>Spizella passerina</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>Harris' Sparrow, <em>Zonotrichia querula</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>White-crowned Sparrow, <em>Zonotrichia leucophrys</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td>White-throated Sparrow, <em>Zonotrichia albicollis</em></td>
<td>4</td>
<td>3</td>
<td>3</td>
</tr>
</tbody>
</table>
Table 2. Breeding bird populations in Manitoba (pairs/40 ha) (concluded)

<table>
<thead>
<tr>
<th>Species</th>
<th>Forest plots</th>
<th>Forest-edge plots</th>
<th>Riparian Strip</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fox Sparrow, <em>Passerella iliaca</em></td>
<td>9</td>
<td>+</td>
<td>3</td>
</tr>
<tr>
<td>Song Sparrow, <em>Melospiza melodia</em></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total Species</td>
<td>19</td>
<td>29</td>
<td>23</td>
</tr>
<tr>
<td>Total Pairs</td>
<td>69+</td>
<td>96+</td>
<td>80+</td>
</tr>
<tr>
<td>Pairs/Species/40 ha</td>
<td>3.6(4.3)²</td>
<td>3.3(4.6)</td>
<td>3.3(3.6)</td>
</tr>
<tr>
<td>Skewness (g₁)</td>
<td>1.5</td>
<td>1.6</td>
<td>1.4</td>
</tr>
</tbody>
</table>

¹ Species represented by less than 0.5 territory. Species recorded only once on a plot are not listed.
² Numbers in parentheses exclude waterbirds.

cies of Turdidae were predominant. These same groups were most numerous in the forest-edge and riparian plots.

There was a greater similarity between species composition and populations between Churchill and Herriot Creek than between either area and Gillam (Table 3). The same was true for forest-edge and riparian bird communities. Faunas and populations were less similar between areas of forest edge than of forest except for the Herriot Creek and Gillam faunas. Churchill and Herriot Creek are along the northernmost edge of the ecotone between boreal forest and tundra (tree line) while Gillam is well within the ecotone (Figure 1).

The Churchill area had the fewest species in both forest and forest-edge areas, and the Herriot Creek area had the largest total populations (Table 2). Excluding water birds, one species was found exclusively at Churchill, six at Herriot Creek, and 11 at Gillam. Since forest species may occur on the forest edge and forest-edge species penetrate to varying extents into the forest interior, especially in open forests, there was considerable similarity between

Table 3. Coefficients of species similarity (Ss) and population similarity (Sp)

<table>
<thead>
<tr>
<th>Localities (Manitoba)</th>
<th>Ss (%)</th>
<th>Sp (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Forest</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Churchill and Herriot Creek</td>
<td>75(81)</td>
<td>62</td>
</tr>
<tr>
<td>Churchill and Gillam</td>
<td>48(47)</td>
<td>42</td>
</tr>
<tr>
<td>Herriot Creek and Gillam</td>
<td>42(47)</td>
<td>31</td>
</tr>
<tr>
<td><strong>Forest-edge and riparian strip</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Churchill and Herriot Creek</td>
<td>58(60)</td>
<td>30</td>
</tr>
<tr>
<td>Churchill and Gillam</td>
<td>28(30)</td>
<td>19</td>
</tr>
<tr>
<td>Herriot Creek and Gillam</td>
<td>47(51)</td>
<td>12</td>
</tr>
<tr>
<td>Forest and forest-edge</td>
<td>65(71)</td>
<td>36</td>
</tr>
<tr>
<td>(including riparian strip)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

¹Percentages within parentheses exclude waterbirds.

total faunas and average populations found in each (Table 3). Eight of 34 species were exclusive to the forest, 11 of 31 species were exclusive to the forest edge.

Only a brief study was made of the relation of forest to tundra avifaunas. An area of forest and forest edge (10 ha) was marked at 50-m intervals and adjacent tundra (20 ha) at 100-m intervals at a location 40 km above the mouth of Herriot Creek. Circumstances permitted only a one-day count of the bird populations. The contrast in species distribution was well defined (Figure 4), with seven species restricted to the tundra, 11 to the forest edge, and only three occurring in both (Ss = 25%). Foster (1954) recorded six additional species of water birds in another tundra area near Churchill. The species composition of our plot was similar (Ss = 63%) to that on three tundra plots at tree line censused near Parsons Lake in the Mackenzie Delta (Owens, R.A. 1974, unpublished report by F. F. Slaney and Co. Ltd., for Canadian Arctic Gas Study Ltd.). Excluding shorebirds, all species in the Mackenzie Delta were recorded in this plot except the Yellow Warbler, and this species was abundant in the riparian strip at the mouth of Herriot Creek.

Discussion

The distinctiveness of biota in the subarctic has long been recognized although referred to in different terms: "Hudsonian fauna" (Allen 1892), "Hudsonian life zone" (Merriam et al. 1910), "northern transition" (Halliday 1937), "forest-tundra ecotone" (Marr 1948), "taiga" (Hustich 1949), "open boreal woodland" (Hare 1950), "zone subarctique" (Rousseau 1952), and "forest-tundra faciation" of the boreal forest (Kendeigh 1974). Do our data support recognition of this biota? To facilitate statistical comparisons, counts of species in forest areas at Churchill and Herriot Creek were averaged ("Churchill"). This is justi-
TUNDRA

FOREST EDGE

Figure 4. Distribution of birds on forest edge and tundra along Herriot Creek on 26 June 1957. Broken lines represent boundaries of ponds and arrows show directions of bird flights.

- BW — Blackpoll Warbler
- CG — Canada Goose, Branta canadensis
- F — Common Flicker
- FS — Fox Sparrow
- GT — Gray-cheeked Thrush
- HS — Harris’ Sparrow
- LL — Lapland Longspur, Calcarius lapponicus
- LY — Lesser Yellowlegs
- NP — Northern Phalarope
- NW — Northern Waterthrush
- R — American Robin

- RA — Common Raven
- RB — Rusty Blackbird
- RP — Redpoll
- SL — Smith’s Longspur, Calcarius pictus
- SP — Semipalmated Plover, Calidris semipalmatus
- SPS — Semipalmated Sandpiper, Calidris pusilla
- SS — Savannah Sparrow
- TS — Tree Sparrow
- W — Whimbrel, Numenius phaeopus
- WS — White-crowned Sparrow

fied since high Ss and Sp (Table 3) indicated that these bird faunas were more similar than they were different. Waterbirds and visitors were excluded at all localities.

Forest-tundra faciation (Subarctic)

Census data were compared for five other areas in the forest-tundra faciation. Areas to the northwest included a mature lichen woodland of Black Spruce, White Spruce, Jack Pine, and Paper Birch east of Great Slave Lake (Harris et al. 1974); three plots in Black Spruce, White Birch, and Tamarack west of Great Slave Lake (Carbyn 1971); and a variety of communities containing Black Spruce, Tamarack, White Birch, and several species of scrub trees and shrubs west of Great Bear Lake (Ebel et al. 1975). The Gillam area, censused by us, lies to the south and three Black Spruce plots at Big Trout Lake, Ontario (Lee and Speirs 1977), are to the southeast.

There was a decline in richness of fauna to the northwest and an increase to the southeast (Table 4). Population levels (pairs per 40 ha) were lowest in the extreme northwest and highest in the extreme southeast. Similarity values (Ss, Sp) were higher between
the “Churchill” and Harris et al.’s areas than between the “Churchill” and other areas. Because occurrences of less common species on relatively small census plots and population levels fluctuate from year to year, we suspect similarity values would be higher, with $S$s exceeding 50 percent, were comparisons based on averages for several years rather than one or two years. Only four of the species in Harris et al.’s area and three in Ebel et al.’s area were not recorded at “Churchill”. However 9 of 17 species in Carbyn’s areas were different. Lee and Speirs recorded 13 of the 22 species found at “Churchill” and 21 additional species. Only three species were recorded in all five areas: Yellow-rumped Warbler, Blackpoll Warbler, and Dark-eyed Junco; four species were missing from only one area: Gray Jay, Boreal Chickadee, Ruby-crowned Kinglet, and Gray-cheeked Thrush.

**Boreal forest**

Six areas in the boreal forest were selected for comparison with the avifauna at “Churchill” (Table 4). Black Spruce was the predominant tree species in all areas except in one of the two areas censused by Erskine (1974) where White Spruce was predominant and in Sanders’ areas where Balsam Fir (*Abies balsamea*), Paper Birch, and Quaking Aspen were most important. Spruce budworm infestation was at low level or absent in all areas. All avifaunas in the boreal forest had significantly low values of $S$s and $Sp$ compared with “Churchill”. Our statistical treatment therefore confirms the distinctiveness of the subarctic forest-tundra faciation.

**Community Structure**

Aside from the number of species present, the structure of bird communities reflects the manner in which breeding pairs are distributed among the species. The mean number of pairs per species per 40 ha ($p/s$) gives the general level of species abundance, perhaps more useful than median or mode. However, distribution of $p/s$ around the mean is seldom symmetrical, so that a measure of skewness ($g_1$) is helpful.

Pairs per species were high in the forest-edge plots at Churchill, in the riparian strip at Herriot Creek, and in Koonz’s forest area; low in Ebel et al.’s areas, but varied only between three and six $p/s$ in all other areas (Tables 2, 4).

There was a significant skewness in the distribution of pairs per species around the mean at all localities. As noted elsewhere (Kendeigh and Fawver 1981), $g_1$ values over 2.0 commonly contain one or more species conspicuously more numerous than others. Thus in Carbyn’s areas, the Dark-eyed Junco and in Harris et al.’s area, the Yellow-rumped Warbler each had populations 5 times the average. In the “Churchill” areas with $g_1$ of 1.5, the most abundant species, Northern Waterthrush, was only 3 times the average. Nearly symmetrical distribution of populations around the mean have been found in some old mature and stable stands of deciduous forest (Kendeigh 1982). An ecologically mature community would be expected to have evolved a high diversity of niches and species occupancy. This would stimulate interspecies competition and a better balance between species populations. Whether or not the extent of skewness varies

---

**Table 4.** Comparison of forest bird faunas and populations with “Churchill” area

<table>
<thead>
<tr>
<th>Locality and author</th>
<th>$S$s</th>
<th>$Sp$</th>
<th>$g_1$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Forest-tundra faciation</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ebel et al. 1975, Northwest Territories</td>
<td>9</td>
<td>22</td>
<td>2.4</td>
</tr>
<tr>
<td>Carbyn 1971 (3 areas), NW Territories</td>
<td>17</td>
<td>100</td>
<td>5.9</td>
</tr>
<tr>
<td>Harris et al. 1974, NW Territories</td>
<td>21</td>
<td>84</td>
<td>4.0</td>
</tr>
<tr>
<td>“Churchill” (2 areas), Manitoba</td>
<td>22</td>
<td>86</td>
<td>3.9</td>
</tr>
<tr>
<td>Gillam, Manitoba</td>
<td>22</td>
<td>80</td>
<td>3.6</td>
</tr>
<tr>
<td>Lee &amp; Speirs 1977 (3 areas), Ontario</td>
<td>34</td>
<td>134</td>
<td>3.9</td>
</tr>
<tr>
<td><strong>Boreal forest</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Erskine 1974 (2 areas), British Columbia</td>
<td>14</td>
<td>47</td>
<td>3.4</td>
</tr>
<tr>
<td>Erskine 1973, Saskatchewan</td>
<td>19</td>
<td>86</td>
<td>4.5</td>
</tr>
<tr>
<td>Koonz 1974, Manitoba</td>
<td>10</td>
<td>92</td>
<td>9.2</td>
</tr>
<tr>
<td>Erskine 1972, Manitoba</td>
<td>16</td>
<td>70</td>
<td>4.4</td>
</tr>
<tr>
<td>Sanders 1970 (2 areas), Ontario</td>
<td>45</td>
<td>122</td>
<td>2.7</td>
</tr>
<tr>
<td>Erskine 1971, Ontario</td>
<td>15</td>
<td>91</td>
<td>6.1</td>
</tr>
</tbody>
</table>

1An 8.1 ha plot at Sisipuk Lake in western Manitoba; an unpublished report of W.H. Koonz of the Manitoba Department of Renewable Resources and Transportation Services.
inversely with maturity must await determination from analysis of many more studies in a variety of biotopes.

Acknowledgments
The field work in northern Manitoba was done while the senior author was a graduate student at the University of Illinois. George C. West and J. Bristol Foster provided valuable assistance. A. Penny and A.E. Cooney, Officers-in-Charge of the Defence Research Northern Laboratory at Fort Churchill, Manitoba, and their staff supplied laboratory and other facilities. Lt. Col. John T. Lorenz, Commander of American military personnel at Fort Churchill, furnished air transportation. D.M. Robertson, Regional Meteorologist, supplied weather information for Churchill and Gillam. J. Robertson and W.R. Burns, Manitoba Game Branch of the Department of Mines and Natural Resources, provided useful information about the study areas. Anna R. Gillespie accompanied the senior author during part of the summers of 1957 and 1958 and contributed invaluable aid in the field. Angus F. MacIver of Churchill, William Graham and Len Gordon of Gillam graciously extended many courtesies. J.C. Ritchie and Richard D. Brewer contributed greatly to the progress of this study through their discussions of the problems involved. The final manuscript benefited from comments of D.A. Welsh and two anonymous referees. The field studies were financed by a grant from the U.S. National Science Foundation to the junior author, S.C. Kendeigh.

Literature Cited
United States Department of Agriculture, Washington, D.C.


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Summer Feeding Ecology of the Blacknose Dace, *Rhinichthys atratulus*, in a tributary of Lake Ontario

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The summer feeding ecology of Blacknose Dace, *Rhinichthys atratulus*, was studied in Orwell Brook, a New York tributary of Lake Ontario. Chironomid larvae were the major prey of the 360 Blacknose Dace examined although their contribution to diet generally decreased from June to September. Chironomid larvae were also the principal prey consumed during each 4-h sampling interval for 24 h during July. Blacknose Dace fed heaviest during crepuscular periods with peak feeding occurring from 1600-2000 h and another minor peak from 0400-0800 h.

Key Words: feeding ecology, food organisms, diel variation, periodicity, summer, Blacknose Dace, *Rhinichthys atratulus*, New York, Lake Ontario tributary.

The Blacknose Dace, *Rhinichthys atratulus*, is one of the most common minnows found in fast-flowing streams in northeastern North America (Scott and Crossman 1973). In New York, Blacknose Dace occur in all watersheds of the state except Long Island (Werner 1980). This minnow is considered an important bait species, and may provide forage for trout in streams (Scott and Crossman 1973). Johnson (1981 and unpublished data) found that Blacknose Dace compose 11% of the diet of Brown Trout, *Salmo trutta*, (250-350 mm) and 22% of the diet of Fallfish, *Semotilus corporalis*, (≥150 mm) in the Salmon River system in New York. Although Blacknose Dace are unquestionably an important non-game species only limited information is available on their food habits. Considerable data exists on the diurnal food habits of the species, but little is known of feeding periodicity and diel variation in diet composition. The purpose of this investigation was to attempt to quantify the summer food habits of Blacknose Dace in a New York tributary of Lake Ontario.

Methods and Materials

Blacknose Dace were collected monthly from June through September 1979 in Orwell Brook, Oswego County, New York. The stream, located on the Tug Hill Plateau, flows 14.5 km through predominantly pasture land before discharging into the Salmon River approximately 17 km from Lake Ontario. Summer discharges in the study section, approximately 4 km from the Salmon River, range from 0.20-0.40 m³ and water temperatures seldom exceed 22°C. The substrate throughout most of the stream consists mainly of gravel and cobbles. Besides Blacknose Dace, the dominant fish species found in Orwell Brook are juvenile Steelhead Trout (ages 0 and 1), *Salmo gairdneri*, Brown Trout, *Brook Trout*, *Salvelinus fontinalis*, subyearling Coho Salmon, *Oncorhyncus kisutch*, Cutlips Minnow, *Exoglossum maxilllings*, and Northern Hog Sucker, *Hypsenticulum nigricans*. During the summer of 1978, naturally produced subyearling Chinook Salmon, *O. tshawytscha*, were also abundant in the stream (Johnson 1980).

Fish were collected each month with a 3-m seine generally from 1200-1430 h. However, during July collections were made at continuous 4-h intervals for one 24-h period in order to determine both diel trends in diet composition and food consumption. Upon collection, specimens were slit and placed in 10% formalin for preservation.

In the laboratory, Blacknose Dace were weighed (wet weight in grams) and measured (total length in millimeters) prior to examination of their stomach contents. Contents of the anterior one-third of the digestive tract were used in determining diet composition and feeding periodicity. In general, aquatic invertebrates were identified to family and terrestrial invertebrates to order. Dry-weight estimates were derived for each prey taxa to quantify their percent contribution to the total diet. Estimates were obtained by drying individuals of each prey taxon for 24 h at 105°C (Johnson 1981).

Diel feeding periodicity was examined by plotting the mean dry weight of the stomach contents (mg) per mean dry weight of fish (mg) (x 10⁻⁵) for each 4-h interval. Dry weight estimates for Blacknose Dace were determined using a dry weight to wet weight conversion which was derived from 30 observations.

Results

Stomachs of 360 Blacknose Dace were examined during the course of this investigation. Of these fish,
### Table 1. Percentage dry weight composition of the diurnal diet of Blacknose Dace, June through September, 1979, in Orwell Brook, N.Y.

<table>
<thead>
<tr>
<th>Month</th>
<th>June</th>
<th>July</th>
<th>August</th>
<th>September</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Fish</td>
<td>60</td>
<td>60</td>
<td>60</td>
<td>60</td>
</tr>
<tr>
<td>Mean total length (mm)</td>
<td>54</td>
<td>58</td>
<td>54</td>
<td>56</td>
</tr>
<tr>
<td>Size range (mm)</td>
<td>37-74</td>
<td>41-77</td>
<td>43-74</td>
<td>43-72</td>
</tr>
<tr>
<td><strong>Aquatic Taxon</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Oligochaeta</td>
<td>—</td>
<td>—</td>
<td>10.36</td>
<td>—</td>
</tr>
<tr>
<td>Cladocera</td>
<td>0.01</td>
<td>—</td>
<td>0.03</td>
<td>—</td>
</tr>
<tr>
<td>Hydracarina</td>
<td>0.39</td>
<td>0.86</td>
<td>0.44</td>
<td>—</td>
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<tr>
<td>Plecoptera</td>
<td></td>
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<td>2.81</td>
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<td><em>Oligochaeta</em></td>
<td></td>
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<tr>
<td>Baetidae</td>
<td>0.44</td>
<td>1.54</td>
<td>1.09</td>
<td>1.59</td>
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<td><em>Ephemeroptera</em></td>
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<tr>
<td>Ephemereellidae</td>
<td>0.54</td>
<td>1.21</td>
<td>—</td>
<td>0.56</td>
</tr>
<tr>
<td>Ephemeroidea</td>
<td>0.62</td>
<td>—</td>
<td>4.37</td>
<td>—</td>
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<tr>
<td>Heptageniidae</td>
<td>0.50</td>
<td>1.87</td>
<td>1.64</td>
<td>1.97</td>
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<tr>
<td>Leptophlebiidae</td>
<td>0.59</td>
<td>2.63</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Unidentified</td>
<td>1.18</td>
<td>2.03</td>
<td>2.08</td>
<td>3.18</td>
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<tr>
<td><em>Trichoptera</em></td>
<td></td>
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<tr>
<td>Glossosomatidae</td>
<td>0.12</td>
<td>5.93</td>
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<td>Helicopsychidae</td>
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<td>—</td>
<td>—</td>
<td>—</td>
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<tr>
<td>Hydropsychidae</td>
<td>2.22</td>
<td>2.74</td>
<td>7.32</td>
<td>10.20</td>
</tr>
<tr>
<td>Odontoceridae</td>
<td>3.85</td>
<td>—</td>
<td>2.08</td>
<td>—</td>
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<tr>
<td><em>Philopotamidae</em></td>
<td>1.11</td>
<td>—</td>
<td>1.31</td>
<td>—</td>
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<tr>
<td>Unidentified</td>
<td>0.26</td>
<td>—</td>
<td>1.09</td>
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<tr>
<td><em>Megaloptera</em></td>
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<tr>
<td><em>Sialidae</em></td>
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<td></td>
<td>4.68</td>
<td>—</td>
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<tr>
<td><em>Coleoptera</em></td>
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<td></td>
</tr>
<tr>
<td><em>Elmidae</em></td>
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<td>1.37</td>
<td>1.80</td>
<td>2.53</td>
</tr>
<tr>
<td><em>Psephnidae</em></td>
<td>1.25</td>
<td>3.57</td>
<td>2.57</td>
<td>4.26</td>
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<td><em>Diptera</em></td>
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<td></td>
</tr>
<tr>
<td>Ceratopogonidae</td>
<td>0.12</td>
<td>0.74</td>
<td>2.40</td>
<td>17.17</td>
</tr>
<tr>
<td>Chironomidae larvae</td>
<td>55.31</td>
<td>42.52</td>
<td>27.92</td>
<td>10.61</td>
</tr>
<tr>
<td>Chironomidae pupa</td>
<td>1.07</td>
<td>—</td>
<td>—</td>
<td>3.65</td>
</tr>
<tr>
<td>Simuliidae</td>
<td>0.06</td>
<td>1.21</td>
<td>0.60</td>
<td>—</td>
</tr>
<tr>
<td>Tipulidae</td>
<td>0.83</td>
<td>1.88</td>
<td>11.14</td>
<td>5.80</td>
</tr>
<tr>
<td>Total Aquatic Invertebrates</td>
<td>70.71</td>
<td>71.19</td>
<td>78.90</td>
<td>72.75</td>
</tr>
<tr>
<td>Plant material</td>
<td>0.39</td>
<td>3.02</td>
<td>6.99</td>
<td>12.68</td>
</tr>
<tr>
<td><em>Etheostoma flabellare</em></td>
<td></td>
<td>13.70</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Total Aquatic</td>
<td>71.10</td>
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<td>85.89</td>
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180 (60 per month) were examined from June, August, and September 1979 for determination of diurnal diet composition. An additional 180 specimens were collected during July as part of the diel portion of the study. In assessing diel food habits 30 Blacknose Dace were examined at each 4-h interval for a period of 24 h. The sixty fish collected at 1200 h and 1600 h in July were combined giving an estimate of the diurnal diet composition comparable to the other three months (Table 1).

Chironomid larvae (10.6-55.3%) were generally the major prey of Blacknose Dace throughout the summer, however, the contribution of chironomid larvae to the diet decreased steadily from June to September (Table 1). Conversely, the contribution of such food items as plant material, hydropsychid larvae, and ceratopogonid larvae steadily increased in the diet from June to September. Terrestrial invertebrates were mainly consumed in June (25.4%) and, thereafter, did not contribute substantially to the diet (Table 1).

In July the contribution to the diet of virtually every prey taxa fluctuated during the 24-h period. Chironomid larvae comprised only 29.0% of the diet at 0800 h and as much as 66.0% at 2000 h (Table 2). For the entire 24-h period chironomid larvae were the principal prey of Blacknose Dace comprising 41.4% of the diet. Trichopteran larvae (primarily hydropsychids: 9.5%, and glossosmatids: 4.9%) were generally the second ranking food item contributing 19.1% to the diel diet. The contribution of trichopteran larvae to the diet peaked at 0400 h (36.2%) and the lowest consumption occurred at 2000 h (12.8%). Ephemeroptera nymphs (mainly baetids: 5.6%) were the third most important prey contributing 13.4% of the diel diet with peak utilization at 2400 (23.6%) and lowest utilization at 2000 h (3.2%). Terrestrial invertebrates contributed only 4.8% to the diel diet of Blacknose Dace and were absent from the diet at night (i.e. 2400 and 0400 h). Fish were an unexpected prey taxon encountered during the diel portion of this study composing 3.3% of the diet. Young-of-year Blacknose Dace (6.6% at 0400 h) and yearling Fantail Darter Etheostoma flabellare (20.7% at 1200 h) contributed substantially to the diet during some 4 h intervals.

Peak feeding of Blacknose Dace occurred from 1600-2000 h (Figure 1). For the 24-h period, feeding intensity decreased sharply during the early morning.

![Figure 1](image-url)

**Figure 1.** Diel feeding periodicity (plus 95% confidence limits) of Blacknose Dace in Orwell Brook, Oswego Co., N.Y. during July. Numbers at each 4-hr interval represent empty stomachs (per 30 fish).
(2400-0400 h), increased during mid-morning (0400-0800 h), decreased to its lowest levels throughout the day (0800-1600 h) and substantially increased to its highest levels during early evening (1600-2000 h) (Figure 1).

**Discussion**

The diurnal food habits of Blacknose Dace are well described (Breder and Crawford 1922; Traver 1929; Moore et al. 1934; Gibbons and Gee 1972; Rollwagen and Stainken 1980). In environments where they are available, chironomid and trichopteran (primarily hydropsychids) larvae and ephemeropteran nymphs are the principal food of Blacknose Dace, whereas terrestrial invertebrates are not readily consumed. The low contribution of terrestrial invertebrates in the diurnal diet of Blacknose Dace is suggestive of benthic rather than drift foraging since terrestrial invertebrates are generally more predominant in the diurnal drift (Hinckley and Kennedy 1976; Johnson and Ringer 1980). The occurrence of juvenile fish in the July diet of Blacknose Dace is the second documentation of piscivory in this species, Rollwagen and Stainken (1980) found fish fins in the stomachs of 2.8% of the fish they examined.

Prior to this study no information was available on either diel feeding periodicity or diel variation in diet composition of Blacknose Dace. Ideally, to assess these parameters for any species one should first know the rates of gastric evacuation of each prey species from laboratory studies at existing environmental temperatures. Although admittedly crude, the method I used should give a rough estimate of diel food intake especially for species such as Blacknose Dace which lack a true stomach.

The 24 h study in July indicated that diel feeding studies are necessary to quantify the food habits of Blacknose Dace. Similar variation composition has been shown for subyearling Coho Salmon and Steelhead Trout (Johnson and Johnson 1981). Such variation may be related to the increased activity, hence susceptibility to capture, of aquatic invertebrates at night.

Patterns of food intake of Blacknose Dace in July appear similar to those reported for another cyprinid, the Spotfin Shiner, *Notropis spilopterus*, (White and Wallace 1973). In Orwell Brook, the feeding pattern of Blacknose Dace during summer approximates that of another predominantly diurnal benthic feeder, subyearling Steelhead Trout (Johnson and Johnson 1981). However because they occupy different habitats (i.e. dace primarily occurring in runs and trout in riffles) the potential for competition between the two species is probably low.

**Acknowledgments**

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**Literature Cited**


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Rodent and Lagomorph Damage to Pine Stem Rusts, with Special Mention of Studies in Alberta

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Rodent and lagomorph feeding have been reported on five pine stem rusts that occur in Canada: White Pine Blister Rust (Cronartium ribicola), Stalactiform Blister Rust (Cronartium coleosporioides), Comandra Blister Rust (Cronartium comandrae), Western Gall Rust (Endocronartium harknessii), and Sweetfern Blister Rust (Cronartium comptoniae). The literature reporting the incidence and form of rodent damage on pine stem rusts in North America is reviewed, and the results of several studies in Alberta and the Northwest Territories are reported. A study of rodent damage on cankers of Comandra Blister Rust on Lodgepole Pine (Pinus contorta var. latifolia) in southwestern Alberta found that 23.5–52% of the cankers were damaged annually. Other studies examined rodent damage on cankers of Stalactiform Blister Rust, Comandra Blister Rust, Western Gall Rust, and Sweetfern Blister Rust on Lodgepole Pine and Jack Pine (Pinus banksiana). Rodents prefer to chew the spermogonial and aecial zones of active cankers, thereby preventing or reducing annual sporulation of the rust. It is estimated that 25–40% of the spore-producing bark tissue is removed annually from the rusts, which indicates the important roles of rodents and lagomorphs in controlling pine stem rust populations.

Key Words: Rodents, squirrels, porcupines, chipmunks, mice, lagomorphs, cottontails, hares, pika, pine stem rusts, Cronartium coleosporioides, Cronartium coleosporioides f. album, Cronartium comandrae, Cronartium comptoniae, Cronartium ribicola, Endocronartium harknessii, damage, feeding, Pinus banksiana, Pinus contorta var. latifolia, Pinus monticola, Pinus ponderosa, Pinus strobus, Pinus taeda. North America, Canada, Alberta, Northwest Territories.

A brief report (Salt and Roth 1980) of Red Squirrels (Tamiasciurus hudsonicus) eating the bark of pine galls caused by the Western Gall Rust (Endocronartium harknessii) has prompted this report on the association of rodents (including lagomorphs) and pine stem rust galls and cankers. (Whenever the term rodent is used, it may also include lagomorphs). The role of rodents feeding on rust cankers has been referred to briefly in the book Pine Stem Rusts of Canada (Hiratsuka and Powell 1976) and in a paper by Powell (1974). Both publications include photographs of annual rodent gnawing activity associated with various species of pine stem rusts but not the Western Gall Rust, although rodent chewing on bark infected by this rust is common. Recently, Hunt (1978) reported some observations of slugs also feeding on pine stem rusts.

Salt and Roth (1980) were apparently aware of only one reference on the association of rodents with pine stem rusts. The following report reviews the main literature on rodent gnawing or damage on pine stem rusts that occur in Canada, with special attention to those reports that give quantitative information on the damage. Also discussed are studies of rodent damage on Comandra Blister Rust (Cronartium comandrae) on Lodgepole Pine (Pinus contorta var. latifolia) in Alberta and other rodent-pine stem rust studies in Alberta and the Northwest Territories. Some of this material was included in an unpublished thesis (Powell 1969), although some preliminary data on rodent gnawing on Comandra Blister Rust have been mentioned in the reports by Powell (1974) and Hiratsuka and Powell (1976).

Literature Review

White Pine Blister Rust

Most early literature on rodents and pine stem rusts relates to the White Pine Blister Rust (Cronartium ribicola). Mielke (1935) reviewed in detail over 25 reports of rodents feeding on White Pine Blister Rust-infected bark on Eastern White Pine (Pinus strobus) in eastern North America and Western White Pine (Pinus monticola) in western North America, including many reports from British Columbia. A number of different species of rodents are known or thought to eat the rust-infected living bark. They have not all been observed, since many rodents are largely nocturnal. Squirrels (Sciurus spp., Tamiasciurus spp., and Glaucmys sp.) are regarded as the most important removers of infected bark, but Mielke also mentions damage by porcupines (Erethizon dorsatum), mice (Peromyscus spp., including Arvicola glareola in Europe), chipmunks (Eutamias spp.), cottontails (Sylvilagus sp.), and possibly a pika (Ochotona sp.). Mielke concluded that rodent feeding on cankers generally occurred during winter and early spring,
although in some years the rodents were fairly active in the fall in the west.

Feeding was usually restricted to the living infected canker tissues that had become swollen, often to several times the normal thickness. Severance of twigs and small branches infected by the rust was noted fairly commonly. At Garibaldi, British Columbia, Mielke observed a squirrel gnawing off small canker-infected branches, dropping them to the ground, and later removing the cankers and carrying them to a cache. He suggested that the twigs were gnawed off because they were not stiff enough to support the weight of the animal while it ate the diseased bark. Most feeding, however, occurred on cankers on the larger branches or on stems of the tree, where rodents preferred the aecial and spermogonial (pycnial) zones of the canker but often also ate the bark containing the advancing mycelium of the rust. The central portion of old cankers was usually not touched, since the bark was dead after having produced aecia in earlier years. Cankers often showed evidence of annual rodent visitation in that the active zones of the canker were gnawed off. Mielke (1935) also noted that cankers parasitized by secondary fungi were seldom fed upon.

Mielke included a report from New York State that 41% of 11 100 cankers had been gnawed by rodents and other reports that the entire crop of rust spermatia was consumed in some locations. He mentioned estimates that in 1928 the spore fruiting area of cankers was reduced by 95% at Pembroke, Massachusetts, and that in 1924 at Chee Kye, British Columbia, 45.2% of 1297 cankers were gnawed to some degree, with higher percentages on the more mature cankers and 25% of the aecia-bearing bark removed. Stillinger (1944) reported that the Richardson Red Squirrel (Tamiasciurus hudsonicus richardsi) chewed 28% of 1575 and 38% of 10 360 White Pine Blister Rust cankers observed at two locations in Idaho.

**Stalactiform Blister Rust**

Mielke (1956) found that, out of many thousands of Stalactiform Blister Rust (Cronartium coleosporioides) cankers, only a few small ones on young Lodgepole Pine had not had zones of infected bark removed by rodents. He reported that the margins of the gnawed wounds dry out, leaving a ridge of hardened bark on the cankers that is not usually fed upon. Anderson et al. (1967) reported incidences in Minnesota in which 37-50% of the Stalactiform Blister Rust cankers on Jack Pine (Pinus banksiana) had signs of rodent feeding, which occurred largely on the spermogonial masses in the fall. In many instances the feeding appeared to have prevented further development of the sporulating cankers. Molnar (1952) and Ziller (1974) also reported rodent gnawing on this rust in western Canada.

**Comandra Blister Rust**

Mielke (1957) first reported rodent damage on Comandra Blister Rust cankers on Lodgepole Pine in the western United States. Krebill (1965), Powell (1969, 1974), and Johnson (1979) also refer to rodent damage on this rust on Lodgepole Pine. Krebill (1965) found that over 90% of the sampled Comandra Blister Rust cankers in 12 national forests in the Rocky Mountain states area had been scarred by rodent chewing. Childs (1968) noted gnawed areas on Comandra Blister Rust infections on Ponderosa Pine (Pinus ponderosa). Cordell et al. (1967) found that over 75% of the fruiting Comandra Blister Rust cankers in a Lobolly Pine (Pinus taeda) plantation in eastern Tennessee had been chewed or gnawed off. Bergdahl and French (1976) found that rodent damage, believed to be largely the responsibility of the Red Squirrel (Tamiasciurus hudsonicus minnesota), on Comandra Blister Rust cankers on Jack Pine in Minnesota was closely associated with periods of spore production — particularly spermia production — after about 1 September each year. Marked cankers indicated that rodent gnawing rarely occurred during the winter months and recurrent when aciospores were produced about mid-May each year. Rodent damage was heaviest (62.5% of infections) when 95.9% of the infections produced spermatia in that year, and damage was lightest (5.4%) when only 24% of the infections produced spermatia. Peterson and Krebill (1967) mentioned that the disease caused by Comandra Blister Rust is frequently mistaken for porcupine gnawing or squirrel damage, while Mielke (1961) had earlier noted that “rodent activity is reason to strongly suspect the presence of the disease”.

**Western Gall Rust**

Hedgecock and Hunt (1920) first reported that rodents, especially squirrels and porcupines, fed upon the cambial layers of galls of the Western Gall Rust because of the sweet taste of this layer when either aecia or spermata were present or being formed. They reported repeated feeding of rodents on galls on Lodgepole Pine near Fox Park, Wyoming. Peterson (1960) reported gnawing of Western Gall Rust galls and cankers, especially by squirrels, chipmunks, and porcupines. He reported that piles of small branch galls, which had been stripped to the wood by these animals, are common in some Lodgepole Pine stands.

**Sweetfern Blister Rust**

Recently, Little (1979) reported that rodents, possibly chipmunks, gnawed Sweetfern Blister Rust cankers on Lobolly Pine in New Jersey. He reported that rodent gnawing was confined to cankered stems and that 15.7% of the surviving Lobolly Pines in the plantations had been gnawed.
Rodent Damage on Comandra Blister Rust Cankers in Southwestern Alberta

Methods and Materials
During studies of the biological factors affecting aeciospore production of Comandra Blister Rust cankers on Lodgepole Pine, observations were made on the frequency and damage of fresh and old rodent chewing. Other biological factors affecting aeciospore production have already been reported (Powell 1971a, b, c; 1974). Observations were made from 1966 to 1972 at 24 locations between latitudes 49°45' and 52°10' north (Figure 1). A total of 448 tagged cankers were followed for rodent feeding; 347 were tagged in 1966 or earlier, and 101 were tagged in 1967. The number at any one location varied from 1 to 48. The trees varied in age from 3 to 125 years at time of tagging. By 1972 only 183 trees that had borne cankers in 1966 or 1967 were still alive, most having been killed by the rust.

Ninety-five percent of the cankers were located on the main stem, with an average aboveground height of 35 cm to the center of the canker. The few branch cankers were also generally close to the ground. The average length of the stem cankers was 47 cm, making them accessible to feeding by lagomorphs and ground rodents, especially since many cankers reached ground level.

During most years the percentage of new chewing was recorded and its possible effect on future aecial production was noted. Some observations in 1968 and all in 1971 recorded the total percentage of cankered bark removed by rodents. To obtain this percentage, scaled drawings were made of each canker and the area of bark removed by the rodents. A few locations were visited weekly or more frequently through the sporulation period (early May to September); others were visited once or twice a year.

Results and Discussion
Rodent feeding on rust cankers was widespread at most locations. The Richardson Red Squirrel, Columbian Red Squirrel (Tamiasciurus hudsonicus columbiensis), Snowshoe Hare (Lepus americanus), and Dusky Porcupine (Erethizon dorsatum) were all observed chewing on the sperm西亚- or aecia-bearing bark at one time or another. Judging from teeth marks, chipmunks and mice were also responsible for removing some bark. Rodents generally removed all the bark down to the sapwood but, except for porcupines, usually restricted their activity to the infected bark. Although they showed a preference for the spermogonial and aecial zones, they often ate the infected bark outside the spermogonial zone. The gnawing rarely extended into noninfected healthy bark. In many cases the rodents failed to eat the entire diseased area, which enabled the rust to produce aecia in limited bark areas or to continue to grow beyond the chewed area so that spermogonial and aecial sporulation would again take place in future years. In some cases the rodents hastened the death of the tree by completely girdling the stem or by removing the one remaining live infected strip of bark. On other trees the rodent chewing helped to suppress or destroy the canker, since callus tissue developed around the edge of the chewed areas. In several 20- to 30-year-old stands a small proportion of the trees showed chewed areas, where it appeared that an active rust canker had been inactivated by rodent chewing. In these cases the whole canker area was chewed out, and presumably no infected bark remained from which the rust could continue to infect the tree and produce aecia.

One of the most striking cases of rodent damage found during the study of pine stem rusts in Alberta occurred in a 1924 plantation of Scots Pine (Pinus sylvestris) near Beaver Mines, Alberta. After considerable searching, one strip of active canker with Comandra aeciospores was found at the edge of a recently chewed area. Of 150 trees tallied, all had extensive rodent damage, which suggests that the rust infection was once widespread throughout the plantation.

Rodent damage was characteristic of infected trees, since in infected stands only the rust-infected trees...
showed evidence of damage. The one exception to this was an area where porcupines had been less selective, although they still showed a preference for rust-infected trees. Rodents appeared to attack only trees that had actively producing spermogonial and aecial zones, and they preferred the spermogonial zone. Most of the gnawing probably occurred during the winter or early spring, but some gnawing was recorded sporadically throughout the summer and early fall. In many cases cankers showed evidence of annual rodent visits. Each year the rodents removed the succulent spermogonial zone near the limits of the canker, often leaving a thin strip of callus tissue adjacent to the previous year's chewed area (Powell 1974). Often the rodents removed all of the spermogonial zone and some of the aecial zone, completely ringing the canker, but left untouched the center of the canker composed of dead bark tissues. At locations near Marmot Creek and on the lower slopes of The Wedge, south of Evans-Thomas Creek, where some of the cankers were protected by insect cages (Elliott and Powell 1966), it was not uncommon to discover in the spring that the rodents had chewed the newly infected bark beyond the top and bottom of the cage. There were also a few cases in which the rodents damaged the insect cage and were able to chew the canker inside.

Of 448 cankers observed, 349 (77.9%) received some rodent damage during one or all of the years between 1966 and 1972. In 1968 and 1970 about half of the cankers were chewed, but in 1969 and 1972 only about a quarter were chewed (Table 1). During the seven years of recording, an average of 38.7% of the cankers received some new rodent damage each year. By the seventh year only 6% of the live active or inactive cankers (183) were free of rodent gnawing (Table 1).

At two locations very little rodent damage was recorded in any of the years. These were areas of young, open-grown, infected trees. Generally the greatest incidence of damage occurred in the older stands or in fairly dense stands of 20 to 30 years of age, where damage by squirrels was predominant. At some locations the rodent population remained high, but at others considerable fluctuation occurred. The attractiveness of the cankers to rodents for eating varied depending on year and stand. At some locations the cankers were classified largely as inactive because no spores were produced and there was no evidence of other fungi such as the Purple Mould (Tuberculina maxima) (Powell 1971c). Rodent chewing was absent or very low at these locations. The annual incidence of fresh canker chewing at a number of selected locations is shown in Table 2. At Mist Creek the stand was very open, which may have accounted for the lower incidence. After 1967, fewer cankers were active, which perhaps reduced their natural attractiveness to the rodents. This factor may also have been responsible for the lower incidence of rodent damage at Honey- moon and Ribbon creeks in 1968 and 1969, since much of the active portion of cankers had been removed in the two previous years. The three Saskatchewan River Crossing locations, which were about 1 km apart, had very low incidences of gnawing in 1972, although Saskatchewan River Crossing 2 was an older stand and probably permanent squirrel territory. In the older stands it was not uncommon to find squirrel nests in rust-infected trees. At a plot near Barrier Lake, a nest occurred at the level of a canker, but aecia were never observed during the five years, although fresh chewing occurred each year.

The main result of the rodent feeding was removal of the spermogonial zones and the future aecial zone, which caused an enormous reduction in the volume of potential aeciospores for the following season. Through the rodent activity the cankers often were prevented from producing any aecia for a number of years. A secondary result was that the death of a diseased tree was often hastened. Associated with the rodent damage was a generally copious resin flow, which often contaminated the aecial zone and prevented aeciospore dispersal. At four locations during the winter-spring season of 1966-67, an average of 25% (range for individual locations was 10-34%) of the active canker bark had been removed on those

Table 1. New and total rodent damage on Cronartium comandrae cankers on Lodgepole Pine at various locations in southwestern Alberta, 1966-72

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of locations</th>
<th>Total no. of cankers observed</th>
<th>Cankers with new rodent damage</th>
<th>% of cankers with rodent damage</th>
</tr>
</thead>
<tbody>
<tr>
<td>1966</td>
<td>21</td>
<td>335</td>
<td>133</td>
<td>39.7</td>
</tr>
<tr>
<td>1967</td>
<td>23</td>
<td>401</td>
<td>159</td>
<td>39.7</td>
</tr>
<tr>
<td>1968</td>
<td>23</td>
<td>311</td>
<td>151</td>
<td>48.6</td>
</tr>
<tr>
<td>1969</td>
<td>22</td>
<td>288</td>
<td>77</td>
<td>26.7</td>
</tr>
<tr>
<td>1970</td>
<td>22</td>
<td>250</td>
<td>130</td>
<td>52.0</td>
</tr>
<tr>
<td>1971</td>
<td>22</td>
<td>230</td>
<td>93</td>
<td>40.4</td>
</tr>
<tr>
<td>1972</td>
<td>21</td>
<td>183</td>
<td>43</td>
<td>23.5</td>
</tr>
</tbody>
</table>
cankers that showed rodent damage; in many cases the bark that remained was no longer productive. Similarly, for the 1967-68 winter-season, cankers chewed at 17 locations showed 30% (range for individual locations was 7-73%) of the active canker bark removed, mostly from the potential acacia-bearing zone of the canker. In numerous cases 70-100% of the potential acacia-bearing bark on an individual canker was removed. It was common to find evidence of rodent gnawing around a branch stub that had served as the rust's point of entry into the main stem. The total amount of bark removed from all cankers (230) in 1971 was 37% of the cankered area; the range for individual locations was 8-70%. These results are in line with earlier analyses estimating that rodents reduced the potential acacia-producing bark tissues by 30% in any one year and were responsible for 17% of the cankers being inactivated for at least one year (Powell 1971c, 1974).

Other Rodent-Pine Stem Rust Studies in Alberta and the Adjacent Northwest Territories.

In the Comandra Blister Rust study area in southwestern Alberta — especially near The Wedge (south of Evans-Thomas Creek), at Ribbon Creek, and at Altrude Creek (Banff National Park) — large numbers of Stalactiform Blister Rust cankers were extensively gnawed by rodents each year. Lighter damage also was observed on Western Gall Rust cankers at a number of locations in southwestern Alberta.

In a study of the occurrence of a white-spored Sta-
lactiform Blister Rust (Cronartium coleosporioides f. album) on Lodgepole Pine at Altrude Creek (Figure 2), the incidence of rodent damage was noted over a 7-year period (Powell 1966, 1975). Some new rodent damage to both the white-spored and the normal orange-spored rust cankers occurred each year. The incidence of rodent damage on rust cankers each year ranged from 6% to 75%, with an average of 23.5%. A tally in 1971 indicated that rodents had removed 17.3% of the cankered bark on a total of 40 surveyed cankers, with no percentage difference between the two colored spore forms. Out of a total of 27 white-
spored cankers there were 15 (largely young infections) that showed no evidence of rodent chewing.

In a study of seven natural Lodgepole Pine regenerations plots near Robb (Figure 2), Baranyay and Stevenson (1964) reported on mortality caused by various agents. They mentioned that squirrel activity was mainly associated with infections of Comandra Blister Rust and Stalactiform Blister Rust. Hare gnawing activity, in contrast, was confined to apparently healthy trees. They further noted that the increase in rodent damage from 1959 to 1962 was
information on rodent damage (Y. Hiratsuka, J.M. Powell, and G.A. Van Sickle, unpublished data, 1977). This study involved Lodgepole Pine stands at five locations and one Jack Pine stand that were selected on the basis of infection by three rusts: Comandra Blister Rust, Stalactiform Blister Rust, and Western Gall Rust (Figure 2). The Jack Pine stand, near Fort Rae, NWT, also had 40 cankers of the Sweetfern Blister Rust (*Cronartium comptoniae*), so it too was studied. Table 3 summarizes rodent damage to the rust cankers after 12 years. Rodent damage was greatest on Stalactiform Blister Rust (55.4%), followed by Sweetfern Blister Rust (22.5%), Comandra Blister Rust (9.5%), and Western Gall Rust (9.2%). The incidence of rodent damage on the rusts varied considerably between locations. At Brewster Creek the incidence was 69.6%, but at Fort Rae it was 8.9%, and at Cypress Hills it was only 1.4%; at the other three locations it varied from 24.7% to 26.3%. The majority of the rodent damage occurred on stem cankers; there was very little gnawing on branch cankers. Of the branch cankers, only 3.5% of the Stalactiform Blister Rust, 2.4% of the Comandra Blister Rust, and none of the Western Gall Rust received any rodent gnawing. The Sweetfern Blister Rust cankers were all on the main stem. The annual incidence of rodent damage on stem cankers was 4.4-59.5% on Stalactiform Blister Rust, 2.9-20.2% on Comandra Blister Rust, 0-14.8% on Sweetfern Blister Rust, and 0-8.8% on Western Gall Rust. The incidence of rodent damage on Comandra Blister Rust in this study was considerably lower than in the study in southwestern Alberta, which covered a larger number of locations.

**Conclusion**

The gnawing activity of rodents on pine stem rusts has been noted by a number of authors, often just as an observation with no information on incidence or estimate of damage. Mielke (1935) brought together and reported on the information concerning rodents and White Pine Blister Rust at a time when much activity was centered on controlling the spread of this disease in both eastern and western North America. After his report there was little further reporting of rodent activity on this introduced rust; however, some attention has been given to reporting rodent damage on native pine stem rusts.

Rodents (squirrels, chipmunks, porcupines, and mice) and lagomorphs (cottontails, hares, and pikas) have all been observed or suspected of gnawing on the pine stem rusts. These animals show a preference for chewing on the spermogonial and aecial zones of active cankers, thereby removing the bark and preventing or reducing the annual sporulation of the rust.
<table>
<thead>
<tr>
<th>Location</th>
<th>Rust species</th>
<th>No. of cankers</th>
<th>% damaged by rodents</th>
<th>No. of dead trees with cankers</th>
<th>% of dead trees with cankers damaged by rodents</th>
</tr>
</thead>
<tbody>
<tr>
<td>Alberta</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>David Thompson</td>
<td>Comandra²</td>
<td>43</td>
<td>27.9</td>
<td>15</td>
<td>46.7</td>
</tr>
<tr>
<td>Trail (Banff National Park)</td>
<td>Stalactiform</td>
<td>14</td>
<td>21.4</td>
<td>3</td>
<td>100.0</td>
</tr>
<tr>
<td>Saskatchewan River</td>
<td>Stalactiform²</td>
<td>91</td>
<td>23.1</td>
<td>16</td>
<td>25.0</td>
</tr>
<tr>
<td>Crossing (Banff National Park)</td>
<td>Comandra</td>
<td>19</td>
<td>31.6</td>
<td>4</td>
<td>50.0</td>
</tr>
<tr>
<td>Clear Hills</td>
<td>Western Gall²</td>
<td>74</td>
<td>23.0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Comandra</td>
<td>2</td>
<td>50.0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Stalactiform</td>
<td>1</td>
<td>100.0</td>
<td>1</td>
<td>100.0</td>
<td>100.0</td>
</tr>
<tr>
<td>Cypress Hills</td>
<td>Western Gall²</td>
<td>142</td>
<td>1.4</td>
<td>19</td>
<td>0</td>
</tr>
<tr>
<td>Brewster Creek</td>
<td>Stalactiform²</td>
<td>227</td>
<td>70.5</td>
<td>113</td>
<td>71.7</td>
</tr>
<tr>
<td>(Banff National Park)</td>
<td>Comandra</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Park</td>
<td>Western Gall</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Northwest Territories</td>
<td>Comandra²</td>
<td>1088</td>
<td>8.2</td>
<td>166</td>
<td>31.9</td>
</tr>
<tr>
<td>Fort Rae</td>
<td>Sweetfern</td>
<td>40</td>
<td>22.5</td>
<td>21</td>
<td>28.6</td>
</tr>
<tr>
<td></td>
<td>Stalactiform</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
</tbody>
</table>

¹Only an 11-year period of data from this location.  
²The location was selected for information on this species.

In some cases the rust cankers are inactivated by the gnawing if the total mycelium of the rust is destroyed; in other cases the death of the tree is hastened by a year or so as a result of girdling of the tree by gnawing. Rodent damage occurred much more frequently on stem cankers than on branch cankers. The incidence of gnawing was generally greater on Comandra Blister Rust, Stalactiform Blister Rust, Sweetfern Blister Rust, and White Pine Blister Rust than on Western Gall Rust. The amount of gnawing varies immensely from one location to another and from year to year, but several estimates indicate that 25-40% of the potential rust spore-producing bark tissue is removed annually from the canker-forming rusts.

Characteristically, Comandra Blister Rust and Sweetfern Blister Rust cankers occur close to the ground and could therefore be gnawed either by lagomorphs or by ground and arboreal rodents. Cankers of Stalactiform Blister Rust and Western Gall Rust may occur at slightly higher levels on a tree and consequently suffer most damage from arboreal rodents, though many of these cankers are also found close to the ground.

Rodents and lagomorphs therefore play very important roles in reducing the reproduction of pine stem rust populations; without them there would be far greater stem rust disease problems in forest management.

**Acknowledgments**

I wish to thank Dr. Y. Hiratsuka of the Northern Forest Research Centre, Edmonton, and Dr. G.A. Van Sickle of the Pacific Forest Research Centre, Victoria, for giving me permission to use their unpublished data on rodents and pine stem rusts. I also wish to thank L.S. Skaley, formerly of the Northern Forest Research Centre, for assistance in collecting much of the data on rodent damage of Comandra Blister Rust cankers.

**Literature Cited**


Childs, T. W. 1968. Comandra rust damage to Ponderosa Pine in Oregon and Washington. United States Depart-


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Social Courtship and Pairbonding of Common Goldeneyes, *Bucephala clangula*, Wintering in Minnesota

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We studied courtship behavior and displays of Common Goldeneyes (*Bucephala clangula*) wintering on the Mississippi River in Minneapolis, Minnesota. Age, pair status, and spatial position in the display group affected relative frequencies of certain displays performed by males. *Display Flights* were not observed before late January and did not become frequent until late February. This aerial display apparently functions to encourage the female to follow the displaying male away from the display group. Wintering Goldeneyes began courtship and pairing in December, long before possible reproduction. Some adult males were unwilling or unable to complete courtship sequences to the point of copulation even when approached by a soliciting female and undisturbed by other males. We believe that early pairbond formation entails costs and benefits which vary for the sexes, and in some instances females may be ready to pair before males, a situation indicative of sexual conflict in maximizing their reproductive interests.

**Key Words:** Common Goldeneye, *Bucephala clangula*; courtship behavior, displays, pairbonding.

Courtship behavior and displays of Common Goldeneyes (*Bucephala clangula*) have been the subject of numerous descriptive studies (see Cramp and Simmons 1977), but relatively little is known of probable communicative functions of various displays in pairbonding. Functions of displays can often be inferred through observation of situations in which the display occurs, characteristics of the display, and effects that the display appears to have on other individuals present (McKinney 1975).

We describe here the courtship behavior of Common Goldeneyes wintering on the Mississippi River in Minnesota. Relative frequencies of displays are examined in relation to sex, age, pair status, and spatial position of the performer in the display group. Context and seasonal occurrence of *Display Flights* are reported, and probable functions of this and other displays are discussed.

**Study Area and Methods**

We studied an unmarked population of Common Goldeneyes at a night roost site on the Mississippi River, 0.2 km north of the Broadway Avenue bridge in Minneapolis, Minnesota (see Sayler and Afton 1981). We made observations from 11 December 1972 to 26 February 1973 and from 18 January to 2 March 1975. Ducks were observed with a 20–45X telescope from a car. Observations were dictated into a portable tape recorder and transcribed later.

We attempted to randomly choose individuals for observation by directing the telescope toward an isolated display group; the first individual observed upon focusing was then studied. Because of their lesser abundance in the population, subadult males and paired individuals frequently had to be chosen after systematic search of the roost site. We observed individuals of each sex, age, and pair status during each daily observation period (unless not present on the roost site) to control bias due to possible chronological changes in display frequencies in statistical comparisons between these groups. Displays of a single individual were recorded for as long as possible (R = 5–130 min).

Ducks were observed for varying periods of time (minimum = 5 min) prior to data collection in order to determine their pair status. Individuals were identified as paired by their behavior, such as female inciting, mate defense by males, mutual display, synchrony of behavior, and close positioning of pair members. Subadult males (in their first winter) were distinguished by plumage (Dane and van der Klook 1964). Display data of unpaired adult males were subdivided into three categories based on the male’s spatial position in the display group at the time he performed the display: (1) “leading male” who displayed in front of the female and was followed by her in a moving courtship party; (2) “following male” who displayed beside or directly behind the female; and (3) “peripheral male” who displayed on the edge of the display group, usually 2–4 m away from the other birds. Display names are from Dane and van der Klook (1964).
Results

Display Group Composition
Composition of 111 display groups averaged 4.4 males (SE = 0.2, R = 2–10) and 1.2 females (SE = 0.1, R = 1–5). Number of females per display group declined during winter (r = −0.286, P < 0.01, n = 111), but total group size, number of males, number of adult males, and number of subadult males per group were not significantly correlated with date.

Courtship Displays
Relative frequencies of displays performed by adult paired and unpaired males were significantly different (Table 1). Paired males performed Nodding and Head-forward more frequently than did unpaired males, but performed Fast Head-throw-kicks, Head-throw-bowsprits, Masthead, and Ticking less frequently.

Relative frequencies of displays performed by adult unpaired males differed significantly between the three categorized spatial positions in the display group (Table 1). Following males gave Simple Head-throws at about twice the frequency as did leading and peripheral males. Peripheral males performed Fast Head-throw-kicks about four times as often as the other two classes of males. Leading males gave Bowsprits less than half as often as males in other positions, but gave Head-throw-bowsprits nearly twice as often. Ticking, the most frequently displayed of all, was performed relatively infrequently by following and peripheral males.

Subadult males displayed in 9% of the display groups observed in 1973 (n = 70) and 24% in 1975 (n = 41). Subadult males participated in a similar proportion to their mean abundance in the 1973 winter population (see Sayler and Afton 1981), but in a significantly greater proportion in 1975 (chi-square test, P < 0.001). Subadult males were never observed to be paired. Relative frequencies of displays performed by subadult males differed significantly from those of adult unpaired males (Table 1). Subadult males performed Slow Head-throw-kicks and Nodding more frequently than did adult unpaired males, but performed Bowsprits, Head-throw-bowsprits, and Ticking less frequently. Although we collected no quantitative data, subadult males appeared to display most often in following and peripheral positions, but rarely as leading males.

Our small sample indicated that paired females tended to perform Head-forward more frequently than Head-up less frequently than did unpaired females; however, overall relative frequencies were not statistically different between the two groups (Table 2).
Table 2. Relative frequencies (% of total displays) of displays performed by female Common Goldeneyes

<table>
<thead>
<tr>
<th>Female status</th>
<th>Head-up</th>
<th>Head-forward</th>
<th>Dip</th>
<th>Head-flick</th>
<th>Total displays</th>
<th>No. of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>All females</td>
<td>46.2</td>
<td>30.8</td>
<td>23.1</td>
<td>0</td>
<td>117</td>
<td>28</td>
</tr>
<tr>
<td>Paired females</td>
<td>39.6</td>
<td>37.7</td>
<td>22.6</td>
<td>0</td>
<td>53</td>
<td>12</td>
</tr>
<tr>
<td>Unpaired females</td>
<td>51.6</td>
<td>25.0</td>
<td>23.4</td>
<td>0</td>
<td>64</td>
<td>16</td>
</tr>
</tbody>
</table>

Overall frequencies of paired and unpaired females are not significantly different (chi-square test, $P > 0.05$).

Display Flights

We observed 44 Display Flights in detail during the study (10 in 1973 and 34 in 1975). Our observations of the male's postures and movements agree with descriptions of Dane et al. (1959). Males flew an average of 30 m ($n = 6$, SE = 4.3, $R = 20-45$ m), always away from the group, and landed in an area devoid of other ducks. Wing noise was produced in at least 5 of 44 flights. We do not know whether wing noise always occurs because displays were often performed at a considerable distance (> 350 m) from us and on other occasions many birds were flying concurrently.

Display Flights were not observed before late January and did not become frequent until late February in both years (Figure 1). Two of 44 Display Flights were performed by males that we had classified as paired; the remainder were by unpaired males. In all instances in which the unpaired male's position in the display group was known prior to flight, the display was performed by leading males.

There were four outcomes of Display Flights: (1) if the performing male was not followed, he gave a Fast or Slow Head-throw-kick and returned to the group by swimming or diving (52% of 44 flights); (2) if not followed, the displaying male swam to and joined another display group (14%); (3) the female and other males followed, and courtship display resumed (11%); and (4) only the female followed the performing male (23%). In 2 of 9 flights by unpaired males in which only the female followed, the female immediately assumed the prone position. Successful copulation followed in one instance and the two ducks remained together, seemingly paired, for the remainder of the observation period. In the second case the male mounted the female but apparently failed to achieve intromission, as judging and postcoital display did not occur. The female then flew away from him and joined another active display group.

Copulatory Behavior

Seven copulation sequences were observed in detail between 25 January and 2 March 1975. Five sequences resulted in successful copulation; males apparently failed to achieve intromission in two instances although other males did not intervene. Four copulation sequences involved birds that we had classified as paired, while three sequences involved unpaired birds. Two sequences involving unpaired males followed Display Flights (see above), while the third sequence occurred after the male successfully led the female away from a display group while performing Tickling. We believe that these three males were correctly classi-
fed as unpaired because we had observed each male for more than 30 min and each male had displayed in two or more display groups prior to the copulation sequence.

Females remained prone for minima of 3–15 min \( (X = 7.4, \text{SE} = 1.5, n = 7) \) prior to mounting by the male. Our small sample indicated that females spent similar amounts of time prone in successful and unsuccessful attempts (Mann-Whitney test, \( P > 0.05 \)). Relative frequencies of the five principal male precopulatory displays that we observed and those reported in the literature differed significantly (Table 3).

**Pair Behavior**

We observed a few pairs during initial reconnais-sances of the roost site each year in early December. In general, the percentage of paired females increased during winter as reported by Nilsson (1969), but we could not collect accurate quantitative data on this aspect because of the large number of birds involved (200–600), the relatively short time during daylight each day that birds were at the roost site, and the considerable time needed to accurately determine pair status of an individual.

Paired males persistently defended their mates by threatening and attacking other males that attempted to court them. Threatening with *Head-forward* was the most common defense; indeed, this was the second most common display performed by paired males (Table 1). Attacks on intruding males were of three types: (1) swimming at the intruder while in *Head-forward* (65% of 26 attacks); (2) diving at the intruder (27%); and (3) wild chases or fighting (8%). Pair members occasionally mutually threatened intruding males with *Head-forward* and paired females assisted in driving away intruders, although attacks by females were less frequent (30% of 37 total attacks). Attacks by paired females were of two types: (1) swimming in *Head-forward* (6 of 11 attacks); and (2) diving attacks (5 of 11 attacks).

**Discussion**

Mean composition of display groups in Minnesota was similar to those of other wintering areas, but the maximum size group was smaller. Nilsson (1969) found that the mean groups at two locations in Sweden consisted of 5.2 males and 2.2 females, and 3.2 males and 1.9 females. Maximum size groups have been reported as 30 males and 8 females (Dane et al. 1959) and 20 males and 5 females (Nilsson 1969).

In contrast to our results, Dane et al. (1959) reported that display group size increased from the latter part of December through the end of January. The negative correlation that we found between number of females per group and date may reflect the decreasing proportion of available unpaired females during the winter.

Because our study utilized unmarked birds, certain results of our display frequency analysis should be interpreted with caution. We believe that all males and females classified as paired were correctly identified, but some paired males may have been incorrectly classified as unpaired because H. Dow (personal communication) observed paired males temporarily leaving their mates to join display groups. However, we did not observe this during our observations of paired males. We believe that such errors were rare and should not influence comparisons of those displays whose frequencies differ markedly in relation to pair status.

Overall male and female display frequencies that we observed differed significantly (chi-square tests, \( P < 0.001 \)) from those recorded on movie film by Dane and van der Kloot (1964). These differences may have resulted from: (1) our difficulty in visually recording brief displays (i.e., *Head-flicks*); (2) chronological changes in display frequencies; (3) varying proportions of paired and unpaired birds in the samples; and (4) inclusion of display data from a breeding area by Dane and van der Kloot (1964).

Different display frequencies by males of different pair status and position in display groups probably reflect their needs to signal different types of information. Dane and van der Kloot (1964) noted that *Nodding* and *Head-forward* increased markedly in fre-

---

**Table 3.** Relative frequencies (% of total displays) of the principal precopulatory displays performed by male Common Goldeneyes

<table>
<thead>
<tr>
<th>Study</th>
<th>Bill-shake</th>
<th>Display Drink</th>
<th>Head-flick</th>
<th>Wing-stretch</th>
<th>Head-rub</th>
<th>Total displays</th>
<th>No. of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lind (1959)</td>
<td>8.9</td>
<td>47.9</td>
<td>10.3</td>
<td>25.3</td>
<td>7.5</td>
<td>213</td>
<td>22</td>
</tr>
<tr>
<td>Dane and van der Kloot (1964)</td>
<td>29.7</td>
<td>26.4</td>
<td>19.1</td>
<td>12.5</td>
<td>12.4</td>
<td>2291</td>
<td>180</td>
</tr>
<tr>
<td>Nilsson (1969)</td>
<td>18.2</td>
<td>33.2</td>
<td>8.3</td>
<td>30.0</td>
<td>10.3</td>
<td>253</td>
<td>—</td>
</tr>
<tr>
<td>This study</td>
<td>28.8</td>
<td>34.6</td>
<td>3.8</td>
<td>25.0</td>
<td>7.7</td>
<td>52</td>
<td>7</td>
</tr>
</tbody>
</table>

1Overall frequencies of studies are different (chi-square test, \( P < 0.001 \)).
frequency on the breeding grounds, apparently because they were associated with fighting. Johnsgard (1965) also stated that Head-forward (Laying-the-neck-on-the-water) was a highly aggressive male posture. Comparisons of display frequencies of paired and unpaired males (Table 1) support suggestions that these two displays have aggressive or threatening functions, as these displays were frequently performed by paired males during encounters with other males attempting to court their mates. Head-forward was obviously used to signify threat by paired males and females during swimming attacks.

Attention-getting displays are usually characterized by sudden, striking performances involving movements of the head, wings, or whole body, often coinciding with loud brief calls (McKinney 1975). Plumeage features frequently reinforce optical effects of the display. Characteristics of Masthead and Fast and Slow Head-throw-kicks, and their high frequencies of performance by males in peripheral positions in the display group, suggest an attention-getting function. Relatively loud calls are associated with Fast and Slow Head-throw-kicks (Lind 1959), and the orange-colored legs are conspicuous during the kick (Townsend 1910). Masthead has been suggested to be an aggressive display apparently because this display begins and ends in a posture similar to Head-forward (Lind 1959; Johnsgard 1965). Although the two postures look similar, there are differences in orientation. Head-forward is almost always assumed when the displaying male is facing another individual (Dane et al. 1959; Lind 1959), while Masthead is usually performed lateral to the female (Lind 1959; this study). We suggest that Masthead may function both as an attention-getting display to females and as an aggressive display to other competing males.

Ticking was the most frequent display given by leading males. This display appears to function in leading the female away from a display group as evidenced in one instance that preceded a copulation.

Our results support McKinney’s (1975) suggestion that Display Flights function to encourage the female to follow the displaying male away from the group. Males have been reported to make such flights both toward and away from the female in a display group (Dane et al. 1959; Palmer 1976). Johnsgard (1965) indicated that Display Flights (Short Flights) were always performed towards the female. We observed males fly to a display group and then begin displaying, but their flight postures then appeared similar to normal flight. All ritualized Display Flights that we observed were directed away from the female and group; thus we believe that the above authors may have mistakenly identified flights of males joining display groups as ritualized flight displays. Further photographic studies of the male’s postures in both situations are required to positively reconcile these conflicting observations.

Dane and van der Kloot (1964) characterized displays of subadult males as “odd”, not stereotyped, sometimes so different from those of adult males that they were difficult to identify, but of normal duration. Palmer (1976) stated, without supporting evidence, that the display repertoire of subadult males contained most of the displays of adult males, but that subadult males performed their displays at different relative frequencies. Our data support Palmer’s (1976) contentions, since subadult males performed at least 9 of the 12 displays of unpaired adult males and the overall display frequencies were significantly different (Table 1). Displays of some subadult males appeared awkward, but we had little difficulty distinguishing which display was being performed. Although subadult males were never observed to be paired, it was not because they did not participate in display groups. Our data indicated that subadult males participated in equal or greater proportions than that predicted based on their mean abundance in the winter population.

Wintering Goldeneyes began courtship activities long before possible reproduction, with some birds pairing by early December each year. Spurr and Milne (1976) suggested that male Common Eiders (Somateria mollissima) were subject to strong selection pressures to pair as early in winter as possible, due to the general shortage of females. While we believe that this selection pressure is widely operative among ducks, evidence suggests that other ecological factors also influence optimal pairing chronology. Specifically, we propose that early pairbond formation entails costs and benefits which vary for the sexes (and for species; e.g., Paulus 1980), and in some instances females may be ready to pair before males.

Successful courtship ultimately leads to copulation, yet some wintering adult males are unwilling or unable to complete pairbonding sequences to this point. The percentage of unsuccessful copulations observed among Goldeneyes on wintering and breeding areas ranges from 27-74% (Lind 1959; Dane and van der Kloot 1964; Nilsson 1969; this study). This high failure rate is striking, since few unsuccessful copulations failed because of interference from other males. McKinney (1975) suggested that copulation efficiency might be one of several indirect methods used by females to evaluate a male’s potential as a breeding partner. This seems likely for Goldeneyes, since females are soliciting copulations during the nonbreeding season when fitness losses from poor mate selection are minimal. Thus, females may solicit copulation to evaluate male physiological condition and readiness to pair, or as an inducement to maintain
a pairbond. Females may receive at least two benefits from early pair formation: (1) an improved foraging efficiency due to pair males defending against frequent interactions with other courting males (Ashcroft 1976; this study); and (2) an increase in social dominance at feeding sites (Paulus 1980).

Males pairing in early winter could ultimately be at a disadvantage later in the breeding season. Winter is a potentially severe period for Goldeneyes, a time when cold temperatures and food shortages lead to differential migration and habitat use by the sex and age classes (see Sayler and Afton 1981). Under these adverse environmental conditions, it is important for the male to have adequate endogenous reserves for strenuous courtship to acquire a mate, and also to be prepared for migration and the need to defend the female during the breeding season to protect his reproductive investment. Depending on timing, an early pairing male whose pairbond was usurped later in spring by a male in superior physical condition would likely have a low probability of re-pairing. The costs of a mate change for a female, however, may be negligible. In this context, the incongruity of females soliciting copulations during temporary, nonbreeding season associations, and the apparent inability of some males to achieve intromission may be a matter of sexual conflict in maximizing their reproductive interests (cf., Trivers 1972).

Acknowledgments

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Literature Cited


A Morphological and Ecological Variant of the Tuberous Water Lily, *Nymphaea tuberosa* Paine, from the Jock River, Ottawa, Ontario

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A variant form of the Tuberous Water Lily, *Nymphaea tuberosa* Paine, was discovered among normal clones of the species growing along the Jock River, Ottawa, Ontario. The variant differed morphologically in that it lacked the characteristic red stripe on the petiole. All measurements of leaf and petiole showed significantly different means between normal and variant. Leaf area, thickness, sinuus length and petiole length were all smaller in the variant; the sinuus width of the variant was wider than in the normal form. Accumulation of ions in blade, petiole and rhizome (sodium, potassium, magnesium, calcium phosphorus and nitrogen) were all significantly different between the two forms. Concentrations of accumulated ions were not proportional to soil ion concentrations. Habitat preference also differed significantly in three aspects: oxygen content (normal 5.9 ppm, variant 7.7 ppm), water depth (normal 34 cm, variant 27 cm), conductivity (normal 360 mmho, variant 347 mmho).

Key Words: *Nymphaea tuberosa*, aquatic macrophyte, ecotype, Ottawa, sulphur, potassium.

The Tuberous Water Lily, *Nymphaea tuberosa* Paine, is a rooted, rhizomatous aquatic macrophyte, with floating leaves and small odorless flowers. It grows to the exclusion of other *Nymphaea* species, in profusion along the margins of the Jock River, a small tributary of the Rideau River at Ottawa, Ontario.

In the summer of 1979, the authors proposed to undertake a study of the environmental requirements and accumulative characteristics of the species, using the Jock River populations as experimental material. As soon as the collecting of samples began, it became apparent that there were two forms of *N. tuberosa*, superficially very similar except that one form lacked the characteristic red striping of the petiole.

Although the original study plan using the normal form would have in itself provided useful wetland information, a comparison of the normal and variant forms appeared even more valuable. Thus the study was redesigned to provide environmental and accumulation comparisons between the two forms.

Materials and Methods

Study Area

The study area was a 10 km stretch of the Jock River, a small river 12 km southwest of Ottawa, Canada. The area was selected because the stands of *Nymphaea* were exclusively *N. tuberosa*, with no admixtures of the more common *N. odorata*. The study included 35 separate sites, including 6 unvegetated sites for use in soil comparison with vegetated sites (Figure 1).

The sites of the normal stands were 1, 2, 5, 11, 15, 16, 22, 24, 27, 28, 29. The variant form occupied sites 4, 12, 13, 17, 18, 21, 23, 30. Mixed sites were 3, 6, 7, 8, 9, 10, 14, 19, 20, 25, 26. The remainder of the sites were sampled as examples of unvegetated sites, and used for comparisons of soil and water with the occupied sites.

Collection of the plant material was restricted to the last ten consecutive days in August. The compression of the sampling time was done to eliminate so far as possible the already known seasonal variability of nutrient accumulation and uptake (Boyd 1970, 1971, Bayly and Freeman 1977).

*Nymphaea tuberosa* Paine

*N. tuberosa* is a rooted perennial macrophyte of shallow water systems. The extensive rhizome exhibits numerous knotty tubers. The petiole is usually red-striped, with the broad floating blade 1-3 dm wide and usually green on the lower surface. Petals are white, spatulate to oblanceolate and rounded at the apex. The unscented flowers are smaller than those of the Fragrant Water Lily, *Nymphaea odorata*, generally less than 7 cm across, and the flowers are open for three-four days during the period June to September (Fernald 1950, Gleason 1968).

Sampling and Analysis

Field measurements included air and water temperatures, water pH, oxygen content, conductivity and water depth. A one litre water sample was taken at each site for later analysis. Three soil samples were cored at each site using a split-core soil corer, which delivered an undisturbed core. From each site 10 leaves, plus a section of rhizome was collected. The criterion for leaf section was (a) leaves must be floating, and unblemished, (b) smallest and largest were selected, then second smallest and second largest, etc.
Figure 1. Map of study area
Six non-vegetated sites were selected for control comparisons. All samples were sealed in plastic bags, stored in a freezer chest and immediately transported to the laboratory.

At the laboratory, leaf measurements were made of blade length, blade width, sinus length and width, petiole length, surface area (by planimeter) and blade thickness (by caliper). Figure 2 indicates points of measurement. Moisture content of plant and soil samples was measured using fresh weight and oven-dry (80°C for 48 hours) weight of each sample. After drying, plant samples were ground in a Wiley mill, soil samples with mortar and pestle, both preparatory to extraction procedures. Ground plant material was dry-ashed at 500°C for 6 hours in a muffle furnace, total cations of the ash were then extracted with 6N HCl (Jackson 1965). Available soil cations were extracted by the centrifuge method using 1N ammonium acetate (Jackson 1965). Sodium, magnesium, and calcium were then determined by atomic absorption mode and potassium by flame emission mode using a Jarrel-Ash flame spectrophotometer model 82-270. Soil and plant phosphorus was determined using the method described in McKeague (1976) a modification of that described by Olson and Dean (1965). Soil and plant nitrogen were determined by the micro-Kjeldahl method (Jackson 1965).

Statistical analysis of the data used the SPSS program offered by the Carleton University Honeywell CP-V computer. t-Tests were done to determine whether there were any significant differences existing in the means of the various parameters. Correlation coefficients (r) were calculated using the Pearson Correlation mode of the same program. The significance(s) is presented as a 3-digit figure between 0 and 1. These figures represent the probability that the result (i.e., the correlation coefficient or t value) is due to chance. Therefore, the closer these figures are to 0 the more significant is the result. For this study probabilities less than 0.05 were considered significant.

**Results**

**Water**

Along the Jock River, water quality is highly variable. Rate of flow varies from spring flood to nearly stagnant in the back waters at the time of sampling. Nonetheless the water does move and thus changes on each site as time elapses. At time of sampling pH was circumneutral showing a range of 6.95-7.7, with a pH of 7.1 the most common reading. Oxygen content of water measured 1.9-10.4 ppm, while the water depth range was 15-30 cm, including the unvegetated sites. A measureable flow was found on only three sites and even there flow was so minimal as to be considered still water. The range of cations for the four site categories is shown in Table 1. The water of the unstriped ecotypes showed less Na, K, Mg and more Ca than water of the striped clones, but variation is great and similar variability is present in the unvegetated sites. Phosphorus is present in trace amounts only.

<table>
<thead>
<tr>
<th>Table 1. Ranges in ppm of water cations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site</td>
</tr>
<tr>
<td>Stripped Clones</td>
</tr>
<tr>
<td>Unstriped Clones</td>
</tr>
<tr>
<td>Mixed Clones</td>
</tr>
<tr>
<td>Unvegetated</td>
</tr>
</tbody>
</table>

**Figure 2. Diagrams to illustrate points of measurement in leaves**
Comparison of water samples associated with the two clonal types shows a highly significant difference in oxygen content (striped 5.9, non-striped 7.7) and water depth (34 cm for striped clones, 27 cm for non-striped clones). Water conductivity also shows a significant difference (360 mmho in striped clones, 347 in non-striped clones).

Soils
All soils in the study would be classified as Gleysolic (CSSC 1978) the majority qualifying as Rego Humic Gleysols with an organic A horizon and a C horizon of clay-sized particles. Table 2 shows the comparison of site analyses of soils for available ions and pH. The soils are relatively rich for aquatic substrates. There were significant differences in Na, K, Ca, N and pH between the vegetated and adjacent non-vegetated soils. Differences however are not uniform. There was no significant correlation between water and soil measurements. t-test comparisons of the vegetated sites alone showed a highly significant difference in Na and significant differences in K and Mg.

Vegetation
Ion accumulation and moisture contents are shown in Table 3. General accumulation results for the species shows a significantly higher accumulation of Na, K and Mg in the petioles than in blade or rhizome, while significantly higher accumulations of Ca and N occur in the blade. Lowest ion accumulation is found in the rhizome.

Comparison of striped and non-striped clones shows that ionic accumulation in the plant parts has many significant differences. Difference in sodium occurring in the blades is highly significant and in K, Mg and P is significant. Accumulation differences in petioles is highly significant for Na, K and Ca, and significant for N. In the rhizome, Na, Mg and Ca accumulation is highly significant, while K and P accumulation is significant. Accumulation is not proportional to soil content.

Comparisons of blade characteristics and petiole length are given in Table 4. All differences are highly significant. Comparisons of clonal size was not shown to be statistically significant, although mean area for striped clones was 46 m² and for non-striped clones 35 m².

**Discussion**
The most obvious difference between the two groups of plants remains the red stripe on the petiole of the typical clones, with the stripe lacking in the atypical clones. Evidence of sympatry rests on the presence of the two types within the same general stand, although most sites contain only one type. Although size of stand was not statistically different, nor was the importance of the location, depth measurements indicate that the normal clones are found at greater water depths than the variant, with a range sufficiently great to allow some depth overlap and thus some mixed stands.

Aside from the difference in stripe, the striped clones have leaves with greater surface area and thickness, longer sinuses and petioles. Sinus width of the striped clone leaves is less, since larger leaves have more convergent lobes.

<table>
<thead>
<tr>
<th>Table 2. Soil Analyses</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Vegetation Type</strong></td>
</tr>
<tr>
<td>Measurement</td>
</tr>
<tr>
<td>Na ppm</td>
</tr>
<tr>
<td>K ppm</td>
</tr>
<tr>
<td>Mg ppt</td>
</tr>
<tr>
<td>Ca ppt</td>
</tr>
<tr>
<td>P ppm</td>
</tr>
<tr>
<td>N ppm</td>
</tr>
<tr>
<td>pH</td>
</tr>
</tbody>
</table>

*significant at 0.05 level  
**significant at 0.01 level

<table>
<thead>
<tr>
<th>Table 3. Vegetation Analyses</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Striped Clones</strong></td>
</tr>
<tr>
<td>Measurement</td>
</tr>
<tr>
<td>Na mg/g</td>
</tr>
<tr>
<td>K</td>
</tr>
<tr>
<td>Mg</td>
</tr>
<tr>
<td>Ca</td>
</tr>
<tr>
<td>P</td>
</tr>
<tr>
<td>N %</td>
</tr>
<tr>
<td>Moisture %</td>
</tr>
</tbody>
</table>
TABLE 4. Morphological Comparison of Blade

<table>
<thead>
<tr>
<th>Measurement</th>
<th>Striped Clones</th>
<th>Non-striped Clones</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area (cm²)</td>
<td>352</td>
<td>267</td>
</tr>
<tr>
<td>Thickness (μ)</td>
<td>408.0</td>
<td>373.4</td>
</tr>
<tr>
<td>Sinus length (cm)</td>
<td>9.2</td>
<td>8.5</td>
</tr>
<tr>
<td>Sinus width (cm)</td>
<td>2.2</td>
<td>2.7</td>
</tr>
<tr>
<td>Petiole length cm</td>
<td>63</td>
<td>52</td>
</tr>
</tbody>
</table>

There are few data in the literature concerning ion accumulation in *N. tuberosa*. One belongs to Riemer and Loth (1979) who examined five species of Nymphaeaceae including *N. tuberosa*. Our data generally agree with these authors. Accumulation in the species is much greater in the petiole than the blade, so that the petiole assumes an important function in the process of plant metabolism. However our results show that both calcium and nitrogen are most heavily accumulated in the blade. Riemer and Loth found this for nitrogen only. Some differences of this type may well be due to the time of sampling, but unfortunately Riemer and Loth do not supply the time of sampling in their paper.

Content of sodium is higher in the soils of the normal form and is also higher in the plant material. Correspondingly there is a marked lowering of potassium in the normal form. This set of differences may well be the result of a sodium-potassium interaction in the normal form which is not present in the variant (MacLeod and Snell 1950, Nichols 1963).

Relationships between phosphorus and potassium contents and dry weight/moisture content in many species are quite complex.

Schwabe (1951) found that in *Pteridium aquilinum* "phosphorus deficiency depressed the total dry weight under a high potassium nutrition and the effects of increasing potassium were observed at increasingly high levels of this element with increasing phosphorus supply" (Hewitt 1963). This apparently accounts for negative correlations between dry weight and K-content (r = -0.2140, s = 0.032) and between dry weight and P-content (r = -0.3438, s = 0.001) of striped blades found in the study. These correlations are not found in the non-striped blades since potassium is low in the non-striped soils. Schabe also found that low phosphorus levels decrease moisture content in *P. aquilinum*. This at least partially accounts for the positive correlation between P- and moisture contents of rhizomes of both types (striped: r = 0.4805, s = 0.001; non-striped: r = 0.2368, s = 0.39).

Effects of potassium on moisture content are more complex. Hewitt states "water contents were increased by increasing potassium in the calcium type nutrients, at low or high phosphorus levels". Our study shows positive correlations between moisture and K-contents or rhizomes of both types (striped: r = 0.4369, s = 0.001; non-striped: r = 0.5113, s = 0.001).

Gregory and Richards (1929) and Richards (1932) find that potassium deficiency produces a low net assimilation rate in accordance with the low photosynthetic rates recorded by Briggs (1922) and high respiration rates (Hewitt 1963). If this can be taken a step further, i.e., that high K-content produces high assimilation rates and consequently higher photosynthetic rates; then this may account for the higher oxygen content at non-striped sites in which the plants have a higher K-content than the striped plants. Although the soils are poorer in potassium than the striped soils, the non-striped plants have the ability to accumulate more potassium and thus increase their photosynthetic rates.

Data accumulated points to the distinct possibility that the unstriped variant is a morphological and ecological form of *Nymphaea tuberosa*. At present, the extent of its distribution aside from its presence along the Jock River, remains unknown.

**Literature Cited**


Received 27 July 1981
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Life-history Notes on the Heather Vole, 
*Phenacomys intermedius levii*, in the Canadian Rocky Mountains

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Heather Voles, *Phenacomys intermedius*, were live- and snap-trapped at two different elevations in the front range of the Canadian Rocky Mountains. Most animals were caught at 2240 m in a glacial cirque dominated by spruce (*Picea* spp.), sub-alpine Fir (*Abies lasiocarpa*) and Larch (*Larix lyallii*). The mean litter size was 4.2 and females produced a maximum of three litters per season. Young-of-the-year matured in the summer of their birth. Unlike other microtines, *P. intermedius* are characterized by low trappability, a sex ratio heavily skewed towards females in traps, and high live-trap mortality.

Key Words: Heather Vole, *Phenacomys intermedius levii*, microtine, demography, reproduction.

General knowledge of voles of the genus *Phenacomys* is limited. Soper (1964) attributed this to their low densities, patchy distribution and their possible misidentification as the Meadow Vole, *Microtus pennsylvanicus*. There is also uncertainty about the number of species which occur in North America. Hall (1981) recognized three species; the White-footed Vole, *P. albipes*; the Heather Vole, *P. intermedius* and the Reddish Tree Vole, *P. longicaudus*. Banfield (1974), Burt and Grossenheimer (1964) and Edwards (1955) considered the Arctic or Eastern Heather Vole, *P. ungava* to be a subspecies of *P. intermedius* while Foster (1961), Harper (1956), Saunders (1927) and Soper (1964) considered it to be a distinct species. Other *Phenacomys* (the Olympic vole, *P. olympicus*; the Idaho Mountain Vole, *P. orophilus*; the Preble's Mountain Vole, *P. preblei* and the Dusky Tree Vole, *P. silvicola*) have also been identified (Shaw 1924; Taylor 1915; Walker 1930; Warren 1942). Johnson (1973) provides an evaluation of the subgenus *Arborimus*.

Although *Phenacomys* appear to be rare, they have been found from sea level to 3354 m. *Phenacomys intermedius* and *P. ungava* are terrestrial and found in wide variety of habitats (Foster 1961), although Bearberry (*Arctostaphylos uva-ursi*) leaves and berries can form a large portion of the diet during part of the year (Cowan and Guiguet 1956; Racey 1936). *Phenacomys longicaudus* are primarily arboreal in Douglas and Grand Fir trees (*Pseudotsuga, taxifolia, Abies grandis*; respectively) and feed mainly on their needles (Benson and Borrell 1931; Hamilton 1962). *Phenacomys silvicola* is also arboreal with its preferred foods being Hemlock twigs, spruce and fir needles (Walker 1930, Wight 1925).

The life-history traits of *Phenacomys* are not well known. The mean litter sizes of *P. intermedius* (4.7-5.0; Crowe 1943; Hall and Kelson 1959; Racey 1936; Vaughan 1969) and *P. ungava* (4.8-6.0; Foster 1961; Harper 1956; Soper 1964) are similar and twice that of *P. longicaudus* (2.3-2.6; Benson and Borrell 1931; Hamilton 1962; Taylor 1915). These litter sizes are correlated with the number of mammae: *P. intermedius* and *P. ungava* have eight (this study; Harper 1956; respectively); whereas *P. longicaudus* has four (Hamilton 1962; Taylor 1915). The gestation times of *P. ungava* and *P. longicaudus* are 22 (Foster 1961) and 27 (Hamilton 1962) days, respectively, but gestation is extended in *P. longicaudus* when coincident with lactation. Adult and neonate weights of *P. ungava* (27 g, 2.2 g, respectively, Foster 1961) and *P. longicaudus* (23 g, 2.2 g, respectively, Hamilton 1962) are similar. *Phenacomys longicaudus* young grow more slowly and are weaned much later than *P. ungava* young (Foster 1961; Hamilton 1962).

This study examined the demography and life-history traits of *P. intermedius levii* (Howard) in the front range of the Canadian Rocky Mountains. These data were collected incidental to other studies of small mammals at different elevations.

Methods

The study was conducted in the Kananaskis region, 80 km west of Calgary, Alberta, from May to October, 1979 and 1980. Trapping was carried out in the Kananaskis Valley (1450 m; between Flat and Porcupine Creeks) and in a glacial cirque and adjacent areas (2240 m; part of the Marmot Basin Experimental Watershed). A description of the general area can be found in Carroll (1978).

Mark-recapture grids (with Longworth traps) were used to assess population densities, trappability, survival rates and the number of litters produced per...
season. One trap was placed at each station and each grid was trapped for one night every four to six days. Carrots, whole oats and cotton mattress stuffing provided bait and insulation in all traps. Four grids were operated in 1979. At 1450 m one grid (15 m spacing; 2 × 20) was located on a highway right-of-way and the other (20 m spacing; 5 × 10) in a mixed deciduous-coniferous forest. In the glacial cirque, one grid (20 m spacing; 3 × 16) was located in the meadow and the other (20 m spacing; 10 × 10) on the forested south-facing slope. In 1980, an additional four grids (two at each elevation) were operated. At 1450 m one grid (20 m spacing; 2 × 20) was located on another section of the right-of-way and the other (20 m spacing; 10 × 10) in a stand of Lodgepole Pine. At 2340 m one grid (20 m spacing; 10 × 2) was placed along a stream and the other (20 m spacing; 5 × 10) on a forested south-facing slope outside the cirque.

In 1979, additional live-traps (checked each day and operated for three nights) at both elevations were used to capture animals for a laboratory colony maintained at the Kananaskis Centre for Environmental Research. The postpartum weight, litter size and litter weight were recorded within 24 hours of parturition. Each nestling was weighed every second day from birth to 28 days of age. In 1980, P. intermedius caught on the live-trap lines were killed and autopsied. In both years, at both elevations, snap-trapped P. intermedius were obtained from lines of museum special traps (each operated for three nights) that were baited with peanut butter and rolled oats.

Means are given ± 1 standard error (S.E.) throughout the text.

**Results**

**Habitat and Abundance**

At 1450 m, most P. intermedius were caught in mixed stands of Aspen (Populus tremuloides), Lodgepole Pine (Pinus contorta) and spruce (Picea spp.), although a few were caught in pure Lodgepole Pine stands and on talus slopes. No animals were caught along the grassy right-of-ways. At 2240 m, most P. intermedius were caught within the glacial cirque in dense stands of spruce, Sub-alpine Fir (Abies lasiocarpa) and Larch (Larix lyallii). A few were trapped in meadows, along streams and rocky areas. At both elevations, P. intermedius were trapped in habitats also occupied by Gapper’s Red-backed Voles, Clethrionomys gapperi, Long-tailed Voles, Microtus longicaudus, and Deer Mice, Peromyscus maniculatus. Ninety-four and 123 P. intermedius were caught in 1979 and 1980, respectively. Only 27 of these were caught at the lower elevation (6 in 1979 and 21 in 1980). The numbers caught per 100 trap nights were usually much less at 1450 m than at 2240 m both live-and snap-trap lines (Table 1). Densities, based on the minimum number known alive per month varied considerably from year to year and grid to grid. Only two grids (and one grid for two years) had more than two marked individuals during the trapping season. Maximum numbers on these grids occurred in July (Table 2).

**Trapping Characteristics**

_Phenacomys intermedius_ were not only scarce in some habitats, but had 1) a high mortality in live-traps, 2) a low trappability and 3) a very uneven sex ratio compared with other species trapped in the area. Mortality of _P. intermedius_ on live-trap lines averaged 35% over the two years. Although most animals that died in the traps had eaten the bait, many

**Table 1. Number of _Phenacomys intermedius_ per 100 trap nights.**

<table>
<thead>
<tr>
<th>Location</th>
<th>Trap type</th>
<th>Number of trap nights</th>
<th>Number per 100 trap nights</th>
</tr>
</thead>
<tbody>
<tr>
<td>1450 m</td>
<td>Live-traps</td>
<td>7225</td>
<td>0.07</td>
</tr>
<tr>
<td>1450 m</td>
<td>Snap-traps</td>
<td>4130</td>
<td>0.02</td>
</tr>
<tr>
<td>2240 m</td>
<td>Live-traps</td>
<td>3795</td>
<td>1.13</td>
</tr>
<tr>
<td>2240 m</td>
<td>Snap-traps</td>
<td>741</td>
<td>1.22</td>
</tr>
<tr>
<td>1980</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1450 m</td>
<td>Live-traps</td>
<td>4179</td>
<td>0.05</td>
</tr>
<tr>
<td>1450 m</td>
<td>Snap-traps</td>
<td>3496</td>
<td>0.32</td>
</tr>
<tr>
<td>2240 m</td>
<td>Live-traps</td>
<td>1175</td>
<td>3.32</td>
</tr>
<tr>
<td>2240 m</td>
<td>Snap-traps</td>
<td>1782</td>
<td>0.90</td>
</tr>
</tbody>
</table>

**Table 2. Monthly densities of _Phenacomys intermedius_ on two mark-recapture grids.**

<table>
<thead>
<tr>
<th>Month</th>
<th>Minimum number known alive per hectare</th>
</tr>
</thead>
<tbody>
<tr>
<td>1450 m — small forest grid (2 ha) — 1980</td>
<td>1.5</td>
</tr>
<tr>
<td>June</td>
<td>3</td>
</tr>
<tr>
<td>July</td>
<td>6</td>
</tr>
<tr>
<td>August</td>
<td>4</td>
</tr>
<tr>
<td>September</td>
<td>0.5</td>
</tr>
<tr>
<td>1450 m — large forest grid (4 ha) — 1979</td>
<td>2.3</td>
</tr>
<tr>
<td>August</td>
<td>4.3</td>
</tr>
<tr>
<td>2240 m — large forest grid (4 ha) — 1980</td>
<td>3.8</td>
</tr>
<tr>
<td>August</td>
<td>2.0</td>
</tr>
<tr>
<td>September</td>
<td>2.0</td>
</tr>
<tr>
<td>2240 m — large forest grid (4 ha) — 1980</td>
<td>1.5</td>
</tr>
<tr>
<td>June</td>
<td>6</td>
</tr>
<tr>
<td>July</td>
<td>16</td>
</tr>
<tr>
<td>August</td>
<td>9</td>
</tr>
<tr>
<td>September</td>
<td>2.3</td>
</tr>
</tbody>
</table>
appeared not to have used the nesting material, indicating that they may have died of hypothermy.  
The minimum unweighted trappability (individuals caught at least three times (Boonstra and Krebs 1978) was 42% for 10 adult females in 1979 and 26% for adult females (n = 5) in 1980. Trappability of young females in 1980 was 24% (n = 3). Trappability of all males, in both years, and young females in 1979 could not be calculated because none were caught more than twice.

The number of males and females trapped was independent of both year and elevation (G = 8.37, p > 0.05), so the data were pooled (Table 3). Using all three trapping methods, the sex ratio was significantly biased in favour of females (1 male: 3.1 females; X² = 78.18, p < 0.001). Adult females were the most likely to be caught while adult males were the least trappable. The sex ratio of ten litters born in captivity (with no mortality) was not significantly different from 1:1 (17 males: 20 females; X² = 1.22, p > 0.05).

**Reproduction and Survival**

The mean litter size was 4.24 ± 0.12 (n = 59; mode = 4; range = 2-7; Table 4) for both years and elevations. There were no differences between years (t = 0.11, p > 0.05) or among months (F = 1.23, p > 0.05). The mean litter sizes of primiparous and multiparous females were not significantly different (4.15 ± 0.27, n = 27; 4.31 ± 1.1, n = 32 respectively; t = 0.66, p > 0.05), but overwintered females had significantly larger litters than young-of-the-year females (4.41 ± 0.13 n = 46; 3.62 ± 0.24, n = 13, respectively; t = 2.82, p < 0.01).

Unlike other microtines (C. gapperi, M. longicaudus and M. pennsylvanicus) kept in the laboratory, P. intermedius would not eat laboratory chow. Carrots were also supplied ad libitum but mortality was still high for laboratory reared litters.

The mean non-breeding weight of P. intermedius females caught early in the trapping season averaged 22.8 ± 0.19, n = 16. Eighteen wild-bred females gave birth in the laboratory. Minimum gestation, based on the maximum time between capture and birth of a litter was 19 days. Pregnant females averaged 35.6 ± 1.05 g one or two days before parturition and 28.8 ± 0.95 g the day of parturition. The mean litter weight and the mean neonate weight was 7.99 ± 0.42 g and 1.89 ± 0.07 g, respectively. The growth of young from birth to 28 days of age (from four litters of four with no mortality) was described by:

\[ Y = 0.79 + 0.43X \]

where \( Y = \) weight (g) and \( X = \) age (days) (r = 0.97; p < 0.001; n = 240). All young opened their eyes by 15.5 ± 0.58 days (n = 11 litters). An attempt to determine the age at weaning using the method of King et al. (1963) was unsuccessful because of a low sample size. However, most young were seen eating solid food by 18 days of age.

Both males and females matured in the year of their birth. Males with scrotal testes weighed as little as 15.0 g. In 1980, a female with four embryos (crown-rump length = 3 mm) weighed only 14.5 g.

The length of the breeding season (L.B.S.) at the upper elevation was calculated from the first and last dates of birth using all trapping methods. In 1979, the first birth was recorded on 13 June in the laboratory. The last birth was approximately 28 August based on weight changes and evidence of lactation of a grid animal (L.B.S. = 77 days). In 1980, the first birth was in late May, based on a young-of-the-year caught 16 June and breeding continued until 6 September when a female was caught with three embryos (crown-rump length = 22 mm) (L.B.S. = 101 days).

Seasonal production of litters by females on mark-recapture grids was difficult to estimate because of

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**Table 3. Sex ratios of Phenacomys intermedius.** Age was determined by weight and reproductive condition.

<table>
<thead>
<tr>
<th>Trapping method</th>
<th>Females</th>
<th></th>
<th>Males</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Adult</td>
<td>Young</td>
<td>Adult</td>
<td>Young</td>
</tr>
<tr>
<td>Mark-recapture grids</td>
<td>36</td>
<td>23</td>
<td>4</td>
<td>15</td>
</tr>
<tr>
<td>Live-trap lines</td>
<td>51</td>
<td>22</td>
<td>14</td>
<td>9</td>
</tr>
<tr>
<td>Snap-trap lines</td>
<td>22</td>
<td>10</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td>Subtotal</td>
<td>109</td>
<td>55</td>
<td>22</td>
<td>31</td>
</tr>
<tr>
<td>Total</td>
<td>164</td>
<td>53</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Table 4. Litter sizes of Phenacomys intermedius.**

<table>
<thead>
<tr>
<th>Month</th>
<th>N</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>Mean</th>
<th>S.E.</th>
</tr>
</thead>
<tbody>
<tr>
<td>May</td>
<td>3</td>
<td></td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td>4.00</td>
<td>0.58</td>
</tr>
<tr>
<td>June</td>
<td>26</td>
<td>1</td>
<td>1</td>
<td>12</td>
<td>10</td>
<td>1</td>
<td>1</td>
<td>4.50</td>
<td>0.17</td>
</tr>
<tr>
<td>July</td>
<td>19</td>
<td>1</td>
<td>5</td>
<td>5</td>
<td>7</td>
<td>1</td>
<td>1</td>
<td>4.10</td>
<td>0.24</td>
</tr>
<tr>
<td>August</td>
<td>10</td>
<td></td>
<td>3</td>
<td>5</td>
<td>1</td>
<td>1</td>
<td></td>
<td>4.00</td>
<td>0.30</td>
</tr>
<tr>
<td>September</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.00</td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td>59</td>
<td>2</td>
<td>11</td>
<td>23</td>
<td>19</td>
<td>3</td>
<td>1</td>
<td>4.24</td>
<td>0.12</td>
</tr>
</tbody>
</table>
their low trappability. For this reason, only ten 1979 females were considered. Of these, four had three litters, five had two and one had one (mean = 2.3 ± 0.23). A female surviving the entire breeding season (77 days) and undergoing repeated post-partum conceptions could produce a maximum of four litters. However, no female remained on a grid long enough to produce four litters.

Minimum survival rate was calculated as the number known to be alive at time \( t + 2 \) weeks \( \div \) number caught at time \( t \). A minimum of three captures was required for an animal to be considered in these calculations. In 1979, the minimum survival rate of adult females on the upper forest grid was 0.89/2 weeks (n = 10 animals). In 1980, at both elevations, the minimum survival rates were 0.77 and 0.97/2 weeks for adult (n = 5) and young (n = 3) females, respectively. Residency status was not attained by males in either year, or by young females in 1979. Of the 32 \( P. \) intermedius marked and released in the glacial cirque in 1979, only two females (6.3%) were retrapped in 1980.

Discussion

General conclusions regarding \( Phenacomys \) are difficult to make because of the lack of extensive studies. In part, this may be the result of species being erratically distributed over their range. As shown in this study, \( P. \) intermedius within a given area can be found in moderate numbers in some habitats, but be almost non-existent in others. Since many environmental variables differ between the two elevations, it is not clear why \( P. \) intermedius was less abundant on the valley floor than in the glacial cirque. At both elevations, they were usually trapped in dry habitats, which is generally the case for \( P. \) intermedius and \( P. \) ungava (Foster 1961). Also, some \( Phenacomys \), like other microtines, can undergo extreme population fluctuations. Foster (1961) found that \( P. \) ungava changed in numbers from a low one year of 0/100 trap nights to a high of 2.96/100 trap nights another year. Another problem with collecting \( P. \) intermedius is their low trappability. Boonstra and Krebs (1978) found the minimum unweighted trappability of Townsend's Vole, \( M. \) townsendii to be generally above 70%. This is much higher than the maximum (42%) trappability of \( P. \) intermedius.

The reproductive traits of \( P. \) intermedius are similar to those of \( P. \) ungava. The mean litter size was lower than those previously reported for \( P. \) intermedius and \( P. \) ungava, although not as low as reported for \( P. \) longicaudus. However, such comparisons may not be realistic because some means are based on very low sample sizes (Innes 1978; Pelikán 1979; Zejda 1966). This study and Foster (1961) found old \( Phenacomys \) females to have larger litters than young females. If this is generally the case in all \( Phenacomys \), large sample sizes will be needed to compare mean litter sizes because they will change with the proportions of old and young females collected. \( P. \) intermedius were lighter at birth, grew less rapidly and opened their eyes a day later than \( P. \) ungava. These slight differences may be attributed to the artificial diet fed to \( P. \) intermedius. Like \( P. \) intermedius, \( P. \) ungava will not eat laboratory chow (Foster 1961). The length of the breeding season of \( P. \) ungava was approximately 86 days at Ft. Churchill, Manitoba (Foster 1961). This is within the range reported here and gives enough time for young \( P. \) intermedius and \( P. \) ungava (at least females) to breed in the year of their birth.

One of the most interesting finds of this study is the large difference between the number of males and females caught. Two other \( Phenacomys \) studies have reported catching more females than males. Saunders (1927) caught only \( P. \) ungava females and Taylor (1915) found the sex ratio of \( P. \) longicaudus to be one male for every two females. Saunders (1927) suggested that males and females occupy different habitats. Taylor (1915), on the other hand, suggested that the sex ratio usually favored females or that his collecting method (the destruction of nests) was biased. Saunders' explanation for this bias is unlikely because both male and female \( P. \) intermedius were trapped in all habitats. A more likely explanation is that males avoid traps more than females. This is likely because the overall trappability of this species is very low and males marked and released were rarely caught again whereas females would eventually re-enter a trap. This suggests that \( P. \) intermedius may avoid the confined spaces presented by live-traps or they may avoid traps because of the odor left by other species including man. Adult females, perhaps because of their greater energy demands for reproduction, are more attracted to baited traps than males and young.

In some respects \( P. \) intermedius can be considered an unusual microtine because of its (1) low trappability, (2) heavily biased sex ratio in traps, (3) high mortality in live-traps and (4) poor survival on artificial diets. For these reasons, a complete understanding of their biology may be difficult to obtain.

Acknowledgments

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Literature Cited
Recurrence, Mortality, and Dispersal of Prairie Striped Skunks, *Mephitis mephitis*, and Implications to Rabies Epizootiology

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Detailed study of radio-equipped individuals of the Striped Skunk (*Mephitis mephitis*) in a North Dakota population provided insight into possible mechanisms for spread of rabies during spring and summer. Annual recurrence rates of 138 skunks marked on a study area averaged 11% for adult males, 43% for adult females and 9% for kits. Population changes were from mortality (including rabies) and dispersal. Five instances of adult dispersal (four by males) were recorded; maximum straight-line distance was 119 km. Some males initiated dispersal in spring. Communal denning by adults occurred rarely after whelping began but resulted in intraspecific conflict. Evidence of intraspecific and interspecific strife leading to kit mortality and some adult mortality was found at dens of 9 of 40 litters studied.

Key Words: Striped Skunk, *Mephitis mephitis*; communal denning, mortality, dispersal, rabies.

The Striped Skunk (*Mephitis mephitis*) is the principal vector of rabies in midcontinent North America (Verts 1967; Parker 1975). The disease is believed to be transmitted mainly by biting (Charlton and Casey 1979). Winter is considered an important period in spread of rabies among skunks because of heightened communal denning and antagonistic behavior during breeding (Houseknecht 1969; Parker 1975), but the reported incidence of rabies in midcontinent skunks is highest during April, May, and June (Verts 1967; Webster et al. 1974).

During April, May, June, and July 1976 to 1979, we studied a population of Striped Skunks in eastern North Dakota to understand skunk relationships to nesting ducks. Rabies was present in the study population. This paper summarizes observations of skunk population characteristics and instances of intraspecific and interspecific strife that were documented during the study and have implications to rabies epizootiology.

**Study Area and Methods**

Field work was conducted in southern Griggs County, North Dakota, during April through July 1976, 1977, and 1978, and during April and May 1979 (Figure 1). The area is gently rolling and intensively farmed for small grain and has limited livestock production (Fritzell 1978).

Skunks were live trapped on a 21 km\(^2\) study area in 1976 and on an expanded 33 km\(^2\) study area plus some adjacent lands in 1977, 1978, and 1979. Each year we attempted to capture all adult and a sample of kit skunks using the study area. Trapping began in early April and, except for 1979, continued intermittently through mid-July. In 1979 trapping ceased in early May. Capture effort was most intense during April and early May when traps were set in every \(\frac{1}{4}\) square mile (0.65 km\(^2\)). Some skunks were caught in handheld nets when sighted during routine field activities; most captured kits were dug from dens.

In 1976, 1977, and 1978 skunks were anesthetized with ketamine hydrochloride (Beck 1976) and tagged in each ear; nearly all adults were equipped with radio collars. In 1977 and 1978 fluorescent tape was attached to the collars to enhance visual recognition at night. During 1977 and 1978 we removed the radio collars from nearly all resident skunks immediately after termination of field work. Skunks caught in 1979 were removed from the study area.

All radio-equipped skunks using the study area were kept under surveillance from mid-April to mid-July each year. Their resting sites were located daily and fresh scats found at those sites were examined to determine food habits. Dusk to dawn radio-tracking of all skunks was conducted at approximately 3-day intervals. A record was kept of all skunks sighted during field activities and whether or not they were radio-equipped.

**Results**

We captured 138 adult and 38 kit Striped Skunks; 53% of each group were males. Eighty-five percent of the adults and 87% of the kits were caught on the study area. Most adults were first captured during early spring; only three new females and six new males were caught on the study area after mid-May.

Observations of marked skunks indicated nearly all resident adults had been captured. The ratio of col-
lared to uncollared adults sighted incidentally from mid-May to mid-July was 22.5, 55.4, and 31.0 for 1976, 1977, and 1978, respectively. Some 1976 sightings were likely of an adult female that had lost her radio collar.

Recurrence Rates
Average annual recurrence rates (percentage of marked population alive on study area at close of one field season that was recaptured on the study area the next field season) of skunks on the study area differed among age-sex classes (P = 0.01) and averaged 11% for adult males, 43% for adult females, and 9% for kits (Table 1). All recaptured kits were females. Eight adult females were caught on the study area in three successive years. No skunk was recaptured after an absence of a year.

Adult Mortality
Adult mortality was divided into that occurring during and that occurring between field seasons. Six male and seven female radio-equipped adults died from causes unrelated to investigator activities during the field seasons. Causes of death were 5 shot, 3 probable and 1 positive disease (rabies), 1 probable and 1 positive road kill, 1 killed by farm machinery, and 1 probable instance of Badger (Taxidea taxus) predation. This represented an average annual April-July mortality rate of 8% for males and 11% for females.

Nine adult skunks were reported to have died between field seasons. Causes of death were 3 by fur trappers, 2 shot, 1 positive and 1 probable road kill, 1 by farm machinery, and 1 accidental entrapment in a building. This resulted in an average annual August-March reported mortality rate of 8% for males and 6% for females; no mortality of tagged kits was reported. Much additional mortality likely occurred between field seasons.

Kit Mortality
Nine of 40 (23%) litters studied experienced kit mortality before weaning from intraspecific and interspecific strife. The mortality occurred during June and July each year and was documented from

---

**Figure 1.** Location of study area in North Dakota and adult skunk dispersal distances and directions.
Table 1. Annual recurrence of Striped Skunks captured on a study area in eastern North Dakota.

<table>
<thead>
<tr>
<th>Year marked</th>
<th>Population</th>
<th>Recaptured next year</th>
<th>Recurrence rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1976</td>
<td>7</td>
<td>2</td>
<td>29</td>
</tr>
<tr>
<td>1977</td>
<td>22</td>
<td>3</td>
<td>14</td>
</tr>
<tr>
<td>1978</td>
<td>18</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Total</td>
<td>47</td>
<td>5</td>
<td>11</td>
</tr>
<tr>
<td>Adult females</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1976</td>
<td>7</td>
<td>3</td>
<td>43</td>
</tr>
<tr>
<td>1977</td>
<td>24</td>
<td>12</td>
<td>50</td>
</tr>
<tr>
<td>1978</td>
<td>20</td>
<td>7</td>
<td>35</td>
</tr>
<tr>
<td>Total</td>
<td>51</td>
<td>22</td>
<td>43</td>
</tr>
<tr>
<td>Kits</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1976</td>
<td>0</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>1977</td>
<td>8</td>
<td>1</td>
<td>13</td>
</tr>
<tr>
<td>1978</td>
<td>26</td>
<td>2</td>
<td>8</td>
</tr>
<tr>
<td>Total</td>
<td>34</td>
<td>3</td>
<td>9</td>
</tr>
</tbody>
</table>

1 Number of individuals marked during April, May, June, and July that were known or presumed to be alive in July when study activities terminated for the year.

Evidence found at rearing dens (i.e. remains of dead kits, scats with skunk remains) and from changes in female behavior. Causes of mortality were known for six litters.

In two litters kit mortality was apparently caused by Badger(s). In one instance a Badger dug into a rearing den; subsequent movements by the female skunk showed she had lost or abandoned her litter. In the second instance a female skunk with kits was killed, mutilated, and pulled into a burrow away from her rearing den, apparently by a Badger. Her litter died. Both litter losses occurred in 1978 within 0.5 km of each other.

In three litters kit mortality appeared related to intraspecific strife during visits to female rearing dens by apparently healthy adult male skunks on the fringes of their home ranges. On two occasions a male was found in a rearing den with a female (different males were involved). At one den two tiny kits were at the entrance. One kit was bitten on the back of the neck and was dead; the other appeared uninjured. A fresh skunk scat composed primarily of skunk remains was found at the den the next day. At the other den there was pungent skunk odor (uncommon at dens); remains of a skunk kit were found the next day. Live kits were subsequently seen at dens of both females. On a third occasion we found a decomposing kit and a fresh skunk scat composed almost entirely of skunk remains at a rearing den shortly after one of the above males spent several hours near or at the den during two visits. That female lost her litter.

In one litter kit mortality apparently involved a rabid male skunk. On 23 June 1978, a nonaggressive (unusual) adult male skunk with healed facial cuts was caught less than 1 km from a female’s rearing den and was radio-equipped. The male was near that den during the night of 24–25 June and traveled in the area for several days. On 25 June pungent skunk odor and a dead kit were found at the female’s rearing den. Two days later a decomposing kit and a fresh skunk scat composed almost entirely of skunk remains were found at a nearby den also used by that female. Subsequent movements by the female showed she had lost her entire litter. On 29 June the male was found nearly dead. He had been in recent contact with another skunk as evidenced by pungent skunk odor and yellowish stain (color of skunk musk) on his neck and radio collar. Laboratory analysis revealed he was rabid. The female was found dead in a rock pile on 20 July.

The kit mortality associated with communal denning occurred during two of only three instances of communal denning recorded during about 4100 visits to skunk daytime resting sites after whelping began in early May. The dens containing skunk remains represent 10 to 13 scats with significant (10% or more) skunk remains from a total of about 1250 scats collected.

Dispersal

Five instances of dispersal, all by adult skunks, were documented (Figure 1). In spring 1976 a male that had been radio-tracked from 12 April to 2 June disappeared. He was relocated alive on 25 June, 10 km southwest of his capture site. Contact was not maintained after that time. In November 1976, two radio-equipped adult skunks, reported to be a male and a female, were recovered by a fur trapper 51 km and 54 km northwest of the study area; individual identities were unknown. The male was trapped and the female was found dead on a road. In 1978 an adult male under radio surveillance from 10 April disappeared on 3 June, as did fresh sign at his regularly used dens. He was killed by a gravedigger at 76 km east of the study area on 6 August 1978. An adult male trapped on the study area on 30 April 1978 disappeared by the next day. He was found dead in a farm building on 22 March 1979, 119 km northwest of the study area. That was the only dispersing skunk for which age was ascertained; canine annuit examination showed he was three years old when he died.

Discussion

Results from the present study expand knowledge of Striped Skunk biology and provide insight into
possible mechanisms for spread of rabies among skunks and other carnivores during spring and early summer. We found a high annual recurrence rate for adult female skunks (43%) and low annual recurrence rates for adult males (11%) and juveniles (9%). Few comparative data are available. In Alberta recurrence rates were 33% for adult females and 24% for adult males, and 33% for juvenile females and 9% for juvenile males (Bjorge 1977). No dispersal by adults was reported in that study but five instances of summer-fall dispersal by juvenile females and seven instances by juvenile males were documented. Our findings combined with scattered reports of skunk movements (Verts 1967; Upham 1967; Bjorge et al. 1981) indicate that adult females remain in the same area for extended periods, and that long distance dispersal by adult males is not uncommon. Dispersal by juveniles apparently is common (Bjorge et al. 1981), but more females than males remain near their place of birth.

In the present study dispersal, and both intra- and interspecific strife created circumstances favorable for spread of rabies. One confirmed and several probable cases of rabies occurred. In the confirmed case, an infected male contacted another skunk shortly before his death and appeared responsible for mortality of at least one litter. He may have transmitted rabies to the female of that litter; she died about 25 days after suspected contact with the male. Skunks can die within 22 days after inoculation of rabies virus of salivary origin (Parker and Wilsnack 1966). The apparent involvement of at least one Badger in skunk mortality would have been conducive for interspecific transfer of the disease.

Few instances of long-distance movements have been reported for Striped Skunks. The maximum straight-line movement reported for adults is 10 km by a male in a 3-year period (Verts 1967) and for juveniles 22 km by a female (Bjorge et al. 1981). The adult dispersal recorded in the present study is especially important to rabies epizootiology. With the incubation period for rabies known to range from 14 to 172 days and the period of discernible clinical illness ranging up to 18 days (Parker and Wilsnack 1966), dispersing adult skunks provide a convenient avenue for rapid long-distance transmissions of the disease. It is significant that at least some dispersal by adult males takes place during spring when incidence of rabies is high (Verts 1967; Webster et al. 1974), and intrasexual fighting occurs at some dens. Through contact with other animals an infected dispersing skunk could transmit rabies to widely separated locations.

Intraspecific behavior of skunks at dens is a likely avenue for rabies transmission (Parker 1975). Most Striped Skunks occupy communal dens during winter but communal denning is rare during spring (House-knecht 1969). Spring and summer communal denning by adults was rare in the present study also, but resulted in intraspecific strife conducive to spread of rabies.

All intraspecific strife we recorded involved adult male visits to rearing dens. After estrus, females are increasingly intolerant of males (Wight 1931; Smith 1974). Seton (1953) reported an instance in which a male skunk killed kits. Our study also shows that visits by males to rearing dens elicits aggressive behavior, including fighting, killing, and eating of kits. The potential for transfer of rabies resulting from such encounters is high (Charlton and Casey 1979).

Acknowledgments

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Literature Cited


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Avian Cholera in Waterfowl in Western Canada, 1978-1981

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Avian cholera (Pasteurella multocida infection) occurred each spring between 1978 and 1981 among waterfowl in west-central Saskatchewan. Lesser Snow Geese (Anser caerulescens) and Ross’ Geese (Anser rossii) were affected most commonly. The disease was rapidly fatal for individual birds. Probably several hundred birds died in the area each spring. An outbreak of avian cholera was detected among waterfowl on the west coast of Hudson Bay during August 1979. Lesser Snow Geese were the species affected most commonly and several thousand birds may have died. Juvenile birds died approximately one month later than adults, and P. multocida was not isolated from specimens of juveniles examined. Avian cholera also occurred on a wetland in southern Manitoba in October 1979. More than 100 birds died, mostly lesser Snow Geese of which one had been banded during August near the outbreak site on Hudson Bay. The same serotypes of P. multocida were present in birds from the two outbreaks. Pasteurella anatipestifer, a bacterium that causes disease in domestic ducklings, was identified as the cause of death of two juvenile geese. Avian cholera was not detected there the following spring.

Key Words: Lesser Snow Goose, Anser caerulescens, Ross’ Goose, Anser rossii, avian cholera, Pasteurella multocida, Pasteurella anatipestifer, mortality, Saskatchewan, Manitoba, Hudson Bay.

Avian cholera (Pasteurella multocida infection) is probably the most important infectious disease of North American waterfowl. Its known geographic range has increased greatly during the last decade and major die-offs have occurred in all flyways (Wobeser 1981). Avian cholera has been reported in Canada among Common Eiders (Somateria mollissima) nesting in Quebec (Reed and Cousineau 1967) and in migrating geese in Saskatchewan in 1977 (Wobeser et al. 1979). This paper reports observations of the disease in western Canada in 1978 to 1981.

Materials and Methods

This report is based upon specimens submitted to the Western College of Veterinary Medicine by personnel of various resource agencies, and on specimens and observations collected during field studies in the Kindersley area of Saskatchewan and near Manitou, Manitoba. These areas are used by migrating geese in spring and autumn. Lesser Snow Geese (Anser C. caerulescens) (SG) that migrate through Manitoba breed around Hudson Bay; whereas SG and Ross’ Geese (Anser rossii) (RG) that migrate through Saskatchewan breed along the coast of the western and central arctic mainland and islands.

During field studies the shoreline of wetlands frequented by geese was searched, using binoculars or telescope, an all-terrain vehicle, and a retrieving dog to find and collect dead and sick birds. These were identified to species, sex and age, and a necropsy was performed. Liver from intact carcasses or bone marrow of the ulna from carcasses that had been scavenged was used for bacterial isolation. Isolants were identified as P. multocida on the basis of standard biochemical reactions.

In 1979 and 1980, low level surveys from a fixed-wing aircraft (pilot and two or three observers) were conducted over the Saskatchewan study area to determine numbers and distribution of live and dead birds. In 1980, similar aerial surveys (pilot and one observer) were conducted over the Manitoba area.

In order to measure the speed of carcass disappearance through scavenging, 17 geese dead of avian cholera were marked with wing and web tags in 1979 and replaced in locations similar to those in which they had been found. These carcasses were then checked periodically from a distance.

To test an hypothesis that the infra-orbital sinus might be a site at which the bacterium could reside in carrier birds, goose heads were collected in October 1980 from persons in Kindersley and Kerrobert, Saskatchewan, who pluck geese for hunters. The heads were refrigerated until brought to Saskatoon, where the sinuses were opened and cultured for P. multocida by routine methods.

Results

Saskatchewan — 1978

On 6 May, a conservation officer observed at least 16 dead and six apparently sick white geese near Luse-
land. Avian cholera was diagnosed in five dead SG and one RG submitted for necropsy. On 19 May three
dead SG and one RG collected from the same wetland had died of avian cholera; another adult female SG had severe degeneration of skeletal and heart muscle. On 16 May, after almost all geese had migrated from the area, five SG that were unable to fly were captured and found to have a variety of traumatic injuries, including shoulder luxation (Wobeser et al. 1981); *P. multocida* was not isolated from any of the geese.

**Saskatchewan — 1979**

Ground searches for birds were conducted on a 5200 km² area (51°15'-52°10'N, 109°-109°40'W) near Kindersley on 27 days between 10 April and 11 May. SG were found dead of avian cholera within 2 days of their arrival on 13 April, and during the study period 127 dead or moribund birds of 11 species were collected (Table 1). A further 9 de birds collected (Table 1) and was largely restricted to white geese, although other waterfowl were abundant. The estimated population of white and dark geese [Canada Goose (*Branta canadensis*) with lesser numbers of White-fronted Geese (*Anser albifrons*)] increased steadily (Table 2) until approximately 11 May, when almost all white geese left the area. RG were not seen on the area until 20 April, but thereafter made up an increasing proportion of the white geese. Two of 14 white geese found dead prior to 25 April were RG; 25 of 79 found after that date were RG. Three of 69 SG (4.4%) found dead of avian cholera were immature; between 20 April and 10 May birds with immature plumage comprised 5.5% of 2677 SG in 15 flocks examined with a telescope. Males comprised 55% of adult SG found dead.

Disease in individual geese ran a rapid course from onset to death. Only two sick birds were observed and both of these died within 15 minutes of first observation. On four occasions birds were found dead in the morning on small wetlands where none had been the previous evening, indicating that the birds had been able to fly not more than 14-16 h prior to death. All geese found dead of avian cholera were in excellent body condition and many had fed recently; food was present in the upper alimentary tract of 33 of 54 SG and 17 of 22 RG. In all but one case, the food material consisted of grain (wheat, barley or wild oats).

Eight of the 17 marked goose carcasses disappeared or were dismembered beyond recognition by routine search methods within 4 days, and all had disappeared within 6 days. Six avian and four mammalian species were known to have fed on geese dead of avian cholera (Table 3). Three potential scavengers: two Ring-billed Gulls (*Larus delawarensis*) and one California Gull (*L. californicus*), were found dead of avian cholera 17 to 27 days after the first dead goose was found. These birds were emaciated and the lesions present suggested a less rapid action of the disease than in geese.

**Saskatchewan — 1980**

There was little spring runoff on the area in 1980. In April and May, mean daily temperatures were 6.1° and 3.8°C warmer than normal and precipitation was only 39 and 27% of normal, respectively (Environ-

**Table 1.** Number of birds found sick or dead of various causes in west-central Saskatchewan during April-May 1979

<table>
<thead>
<tr>
<th>Species</th>
<th>Avian Cholera</th>
<th>Trauma</th>
<th>Gout</th>
<th>Not Determined</th>
<th>Total Examined</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lesser Snow Goose</td>
<td>69</td>
<td>4</td>
<td>1</td>
<td>10</td>
<td>84</td>
</tr>
<tr>
<td><em>Anser caerulescens</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ross' Goose</td>
<td>24</td>
<td></td>
<td></td>
<td>5</td>
<td>29</td>
</tr>
<tr>
<td><em>Anser rossii</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>White-fronted Goose</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td><em>Anser albifrons</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Whistling Swan</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td><em>Olor columbianus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ring-billed Gull</td>
<td>2</td>
<td></td>
<td></td>
<td></td>
<td>2</td>
</tr>
<tr>
<td><em>Larus delawarensis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>California Gull</td>
<td>1</td>
<td></td>
<td></td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td><em>Larus californicus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mallard</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td><em>Anas platyrhynchos</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>American Wigeon</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>Anas americana</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Green-winged Teal</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td><em>Anas crecca</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

* most of these were extensively dismembered carcasses

* shoulder luxation
Table 2. Estimated numbers of white geese (Lesser Snow and Ross’) and dark geese (Canada and White-fronted) on the study area in west-central Saskatchewan in spring of 1979, as determined by aerial survey.

<table>
<thead>
<tr>
<th>Date</th>
<th>White Geese</th>
<th>Dark Geese</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>19 April</td>
<td>46 500</td>
<td>9 600</td>
<td>56 100</td>
</tr>
<tr>
<td>26 April</td>
<td>46 000</td>
<td>11 400</td>
<td>57 400</td>
</tr>
<tr>
<td>2 May</td>
<td>89 400</td>
<td>22 700</td>
<td>112 100</td>
</tr>
<tr>
<td>9 May</td>
<td>114 800</td>
<td>48 100</td>
<td>162 900</td>
</tr>
<tr>
<td>17 May*</td>
<td>2 000</td>
<td>400</td>
<td>2 400</td>
</tr>
</tbody>
</table>

*only two-thirds of area was surveyed because of low number of birds present.

Table 3. Frequency of observation of scavenging on dead geese in west-central Saskatchewan by various species in the spring of 1979

<table>
<thead>
<tr>
<th>Species</th>
<th>Number of Observations</th>
</tr>
</thead>
<tbody>
<tr>
<td>Common Crow (Corvus brachyrhynchos)</td>
<td>45</td>
</tr>
<tr>
<td>California Gull (Larus californicus)</td>
<td>4</td>
</tr>
<tr>
<td>Swainson’s Hawk (Buteo swainsoni)</td>
<td>2</td>
</tr>
<tr>
<td>Marsh Hawk (Circus cyaneus)</td>
<td>2</td>
</tr>
<tr>
<td>Peregrine Falcon (Falco peregrinus)</td>
<td>1</td>
</tr>
<tr>
<td>Unidentified gull (Larus sp.)</td>
<td>1</td>
</tr>
<tr>
<td>Black-billed Magpie (Pica pica)</td>
<td>1</td>
</tr>
<tr>
<td>Coyote (Canis latrans)</td>
<td>4*</td>
</tr>
<tr>
<td>Striped Skunk (Mephitis mephitis)</td>
<td>3*</td>
</tr>
<tr>
<td>Red Fox (Vulpes vulpes)</td>
<td>1*</td>
</tr>
<tr>
<td>Mink (Mustela vison)</td>
<td>1*</td>
</tr>
</tbody>
</table>

*Indirect observation by sign.

Table 4. Numbers of birds found sick or dead of various causes in west-central Saskatchewan during April-May 1980

<table>
<thead>
<tr>
<th>Species</th>
<th>Cause of morbidity/mortality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lesser Snow Goose</td>
<td>Avian Cholera</td>
</tr>
<tr>
<td>(Anser c. caerulescens)</td>
<td>82</td>
</tr>
<tr>
<td>Ross’ Goose</td>
<td>(Anser rossii)</td>
</tr>
<tr>
<td>Sandhill Crane (Grus canadensis)</td>
<td>2</td>
</tr>
<tr>
<td>Canada Goose</td>
<td>(Branta canadensis)</td>
</tr>
<tr>
<td>Whistling Swan (Olor columbianus)</td>
<td>1</td>
</tr>
<tr>
<td>Pintail</td>
<td>(Anas acuta)</td>
</tr>
<tr>
<td>Lesser Scaup (Aythya affinis)</td>
<td>1</td>
</tr>
<tr>
<td>Blue-winged Teal</td>
<td>(Anas discors)</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Trauma</td>
</tr>
<tr>
<td></td>
<td>2*</td>
</tr>
<tr>
<td>Not Determined</td>
<td>8</td>
</tr>
<tr>
<td>Total Examined</td>
<td>92</td>
</tr>
</tbody>
</table>

*most of these were severely dismembered carcasses
*shoulder luxation

ment Canada 1980). Many wetlands used by geese in previous years were dry. Ground search of wetlands was conducted on 12 days between 8 April and 7 May and aerial surveys were flown on 16 and 30 April. One hundred and six birds of seven species were found dead; avian cholera was diagnosed in 84% of these (Table 4).

Four SG found sick or dead had sinusitis (bilateral in two birds, unilateral in two), a lesion that had not been observed previously. P. multocida was isolated from the sinuses of all of these birds.

The number of white geese present on the area in late April was less than in 1979. Approximately 30 000 were seen during a survey on 30 April, compared with 89 000 on 2 May 1979. SG left the area earlier in 1980 than in 1979, and on 7 May almost all white geese present were RG.

None of the 116 hunter-killed SG and 69 RG examined in the fall of 1980 had grossly visible sinusitis and P. multocida was not recovered from the sinus of any of these birds.

Saskatchewan — 1981

Observations in the spring of 1981 were limited to two days of ground search. Drought conditions continued and less wetland area was available than in 1980. On 17 April seven SG and two RG were found dead on six of the larger wetlands. Eight of these birds had avian cholera. Two SG and two RG found dead on 24 April by a conservation officer also had avian cholera. On 3 May most of six SG and three RG found on four wetlands had been dead for a considerable
period of time: *P. multocida* was isolated from five of six that were cultured for bacteria.

**Northwest Territories**

On 30 August 1979 several hundred dead SG were observed near the Maguse River (61°33'N, 93°58'W, about 3 km inland from the west shore of Hudson Bay) during an aerial survey by R. Decker, Northwest Territories Wildlife Service (NWTWS). Most of the birds were concentrated in and around two small pools of less than 100 m² surface area. The number of dead birds decreased with distance from this focus, but occasional dead birds were seen up to 12 km away. It was estimated that mortality there exceeded 2000 birds. C. Gates, NWTWS, visited the site on 5 September and estimated 5-8 dead geese/ha of suitable nesting habitat with one 4 ha site containing approximately 700 dead birds. A sample of dead birds examined consisted of 80 juvenile and 54 adult SG, 1 Canada Goose, 4 Herring Gulls (*Larus argentatus*) and 1 Pintail. Five adult and 11 juvenile SG, the Canada Goose and the Pintail were sent to Saskatoon for examination. The specimens consisted of dehydrated skin and skeleton with little or no visceral or muscle tissue remaining. The adult birds were estimated to have died in early July because they had not begun the moult. On the basis of feather measurements, the juvenile birds were approximately 35-45 days of age at the time of death, so these birds probably died during the first half of August [A. Dzubin, Canadian Wildlife Service (CWS), personal communication].

Examination was limited to bacteriologic culturing from the bone marrow of each bird, and histologic examination of a small portion of kidney remaining in one juvenile bird. *P. multocida* was isolated from four of five adult SG and from the Canada Goose and Pintail, but not from any of the juvenile birds. Numerous coccidial organisms were present in the small specimen of kidney examined from one gosling.

**Manitoba**

On 21 October 1979, dead SG were reported on a small wetland near Manitou, and 90 and 30 dead birds were collected on 22 and 23 October, respectively, by CWS personnel. A sample of these birds was submitted to the Veterinary Services Branch, Manitoba Department of Agriculture, Winnipeg (VSB), and avian cholera was diagnosed.

On 26 October E.C. Whitney, CWS, with one of us (G.W.), collected all visible dead birds (39 SG, 2 Canada Geese, 1 Pintail) in the area. The major flocks had left the region, and only a few hundred live geese were present. Thirty-four SG (20 immature, 14 adult) and 2 Canada Geese were taken to Saskatoon for necropsy. Of these, 24 birds, including the Canada Geese, had gross lesions typical of avian cholera, and *P. multocida* was isolated from each of 10 birds that were cultured for bacteria. Ten other geese had gunshot wounds. Two juvenile SG had lesions unlike those of avian cholera. One of these birds had fibrin covering its viscera and the other had a swollen liver, *Pasteurella anatis*, a bacterium that causes disease in domestic ducks, was isolated from both birds.

In the spring of 1980, aerial surveys were flown south from Brandon to the vicinity of Waskada, then east parallel to, and a few kilometers north of, the U.S. border to Snowflake. Wetlands in the area bounded by the U.S. border, Snowflake, Manitou, Pilot Mound and Crystal City were examined intensively. Approximately 200, 24,000 and 0 SG were seen on surveys on 11 and 22 April and 4 May, respectively. No sick or dead geese were observed from the air. One SG dead of traumatic injuries was found during five days of ground search on this area.

**Discussion**

**Saskatchewan**

Our observations in Saskatchewan from 1977 (Wobeser et al. 1979) to 1981 indicate that avian cholera is enzootic, i.e. occurring at "a low incidence but . . . constantly present in a given community" (Arey et al. 1957) or with "predictable regularity in a population unit with only relatively minor fluctuations in its frequency pattern over time" (Schwabe et al. 1977), in SG and RG on this portion of the spring staging area. The total mortality on this area in any year is unknown, as our collections were not complete; we estimate that several hundred birds died annually. Avian cholera was diagnosed in SG near Lethbridge, Alberta, in the spring of 1980 (H. Weaver, Alberta Department of Energy and Natural Resources, personal communication). This suggests that the disease may be widespread over the spring staging area of that species, of which our study area covered only a small part.

Avian cholera was the only significant mortality factor identified and mortality was confined largely to SG and RG, although other species were abundant. There may have been a greater probability of finding the conspicuous white birds, but it seems unlikely that large numbers of dead individuals of other species would have escaped detection during the intensive ground searches in 1979 and 1980.

Avian cholera has occurred in California, the wintering area for most of the SG (Dzubin 1979) and RG (Melinchuk and Ryder 1980) that migrate through this area of Saskatchewan, each winter since 1944 and losses in individual years have been as high as 70,000 waterfowl (Titche 1979). In the years 1961-1969, White-fronted Geese, American Wigeon (*Anas ame-
icana) and American Coots (Fulica americana) suffered the heaviest mortality relative to the populations present (Rosen 1969). Many SG also died of the disease during these years, but their relative loss was less. In the winter of 1970-1971, approximately 1.5% and 7.3% of the wintering SG and RG, respectively, died of avian cholera (Rosen 1972).

The pattern of disease is western Saskatchewan, i.e. death of a few individuals each day over an extended period in a population of thousands of birds, has not been reported in other areas. This may be because of the covert nature of such mortality rather than absence of the disease elsewhere. Individual dead birds do not elicit much concern or curiosity among the few people who visit wetlands, and these birds are removed rapidly by scavengers. Dead white geese should be very conspicuous, particularly in open wetlands on agricultural land as was often the case in this area. However, during this study there was only one report of dead geese by a member of the public. Avian cholera may have been present but unrecognized on the area prior to 1977. Cote (1979) reported that increased surveillance with collection and examination of all birds found dead resulted in the recognition of avian cholera in several areas of California previously thought free of the disease.

Rapidly fatal disease is typical of avian cholera epizootics in which a large number of waterfowl die in a short period of time. It seems paradoxical that this same form also occurs when overall mortality is low. The means by which the disease is perpetuated and occurs at a low but regular incidence in migrating geese awaits elucidation.

If this enzootic form of mortality is general throughout the entire spring staging area in Saskatchewan and Alberta several thousand birds may die of avian cholera each year. The suggestion that the disease also occurs on the nesting grounds (Rosen 1972) deserves investigation.

The enzootic nature of the disease, the apparent low rate of mortality and the large size of the staging area all argue against carcass collection and disposal or other disease control efforts at this time. However, regular monitoring of the area by aerial surveys to detect changes in disease pattern would seem advisable, bearing in mind the speed of carcass removal by scavengers.

Manitoba and Northwest Territories

Sporadic epizootics of avian cholera have occurred in the U.S.A in the population of SG that migrates through Manitoba (e.g. Vaught et al. 1967), but the disease had not been reported before 1979 among these birds in Canada. Avian cholera occurred in captive waterfowl, including SG, on a game farm in southern Manitoba in December 1978, but the serotype of P. multocida and the source of infection were not determined (B. R. Boycott, VSB, personal communication). Several thousand geese may have died on the nesting grounds on the Hudson Bay coast in summer 1979. In addition to the birds found at Maguse River, many sick or dead SG were observed near Eskimo Point in early July, and there were also reports from residents and exploration crews of a large number of dead geese in the McConnell River colony south of Eskimo Point (C. Gates, NWTWS, personal communication). Unfortunately, specimens from Eskimo Point submitted to another laboratory decomposed during transit and the cause of death was not determined.

P. multocida was not isolated from the 11 juvenile SG submitted from Maguse River whereas it was recovered from 4 of 5 adult SG and from a Canada Goose and a Pintail. This, together with the different times of death of adult and juvenile SG, suggested the presence of more than one fatal disease. The cause of death of the juvenile birds is unknown. We found one potential pathogen (renal coccidia) in the kidney of the one bird from which this tissue was available and another pathogen of young waterfowl, P. anatipes-tifer, caused the death of two juvenile birds found dead later in the autumn in Manitoba. This organism has been reported to cause disease in free-flying Black Swans (Cygnus atratus) in Tasmania (Munday et al. 1970) and Whistling Swans (Olor cumbianus) in Saskatchewan (Wobeser and Ward 1974).

The outbreak of avian cholera in Manitoba may have been a continuation of the die-off that occurred on the nesting grounds. One of two banded adult geese found dead at Manitou in October had been banded at Maguse River in August. The same serotypes of P. multocida (1 and 3) were recovered from birds at both locations (J. I. Price, U.S. Fish and Wildlife Service, personal communication) and avian cholera mortality continued to occur as these birds moved south through the U.S.A later in the autumn of 1979. No deaths due to avian cholera were detected among geese migrating north through Manitoba the following spring and no unusual mortality was reported on the nesting grounds in 1980 or 1981.

Avian cholera is a well recognized mortality factor of waterfowl on wintering and staging areas in the U.S.A. Our observations indicate that the disease also occurs on staging and nesting areas in Canada. It will be necessary to examine the disease during all parts of the migratory cycle to assess its true impact on North American waterfowl populations.

Acknowledgments

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Literature Cited

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Ivory Gulls, *Pagophila eburnea*, and Ice Edges in Davis Strait and the Labrador Sea

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The seasonal occurrence and distribution of Ivory Gulls *Pagophila eburnea* in Davis Strait and the Labrador Sea may be explained by food concentrations along the pack ice edge and by reduced light levels and biological production to the north. This species, which breeds farther north and east, was absent only during the short ice-free period from late June to late October. From February through June, and probably longer, gulls were concentrated near the ice edge, where they fed on lanternfishes (Myctophidae) during April and May in Davis Strait. Hooded Seal (*Cystophora cristata*) remains may be seasonally important. About 35,000 Ivory Gulls may have been present in Davis Strait during March.

Key Words: Ivory Gull *Pagophila eburnea*, Davis Strait, Labrador Sea, ice edges, pelagic ecology.

The Ivory Gull *Pagophila eburnea* is a circumpolar breeder known for its association with ice-strewn seas in the arctic (Bailey 1948, Salomonsen 1950, 1967, Belopolskii 1961, Godfrey 1966). Its main breeding areas are between 75° – 83°N, and even during the winter this gull is only infrequently found south of the pack ice regions of the northern oceans (Blomqvist and Elander 1981). Data on all aspects of its pelagic ecology are limited because of its remote distribution. Only a few colonies have been located in arctic Canada on Ellesmere, Seymour and northern Baffin Islands (MacDonald 1976, Frisch and Morgan 1979, D. N. Nettleship, CWS, personal communication), and in northern Greenland (Salomonsen 1967). Its main breeding concentrations are farther east in Svalbard, Franz Josef Land, North Island and Novaya Zemlya (Blomqvist and Elander 1981). Ivory Gulls from the northwest Atlantic colonies probably spend the winter in the ice-strewn waters of the western North Atlantic. We report in this paper on the seasonal distribution and spring diet of Ivory Gulls and some factors influencing these in Davis Strait and the Labrador Sea.

Methods

Aerial Surveys

Aerial surveys were made between March and November 1978 in Davis Strait and between May and October 1979 in the Labrador Sea. Procedures were similar to those described by Orr et al. (*in press*) and Nettleship and Gaston (1978). The first survey in 1978, 18 to 29 March, searched coastal areas and extensive pack ice in eastern Hudson Strait and Davis Strait. East-west transects averaging 70 km in length were flown across the ice edge every 30' of latitude between 60° and 67° N. Effort was concentrated in this region because gulls were found there during a February cruise, and also because Divoky (1976) found that Ivory Gulls in the Bering Sea were most concentrated near the ice edge. We also surveyed near the ice edge to obtain a population estimate from the Hooded Seal (*Cystophora cristata*) whelping patch (Parsons, unpublished) which was located along the ice edge between 62°30' and 63°30' N (Figure 1). Beginning on 22-23 April, 18 surveys, each requiring two days to complete, were flown at 7-10 day intervals until 4-5 October, with a final survey on 2-6 November (Figure 1). In 1979, 11 surveys were flown along four east-west transects, and along the Labrador coast between 55°30' and 59° N, at two-week intervals from 30 May through 12-13 October. In total, 58,000 km of transects was flown in 1978, and 16,580 km in 1979.

DeHavilland Twin-Otter (in 1978) and Cessna 337 (in 1979) aircraft equipped with GNS-500 Global or Omega Navigation Systems (Karant 1976) were used for all surveys. The aircraft flew 30 m above sea level (ASL) at an average speed of 180 km/h, except for some marine mammal surveys flown over the ice in March at 150 m ASL (not used for density calculations). Observers sat in the right front (co-pilot's) seat, and in the left passenger seat. All birds seen within 200 m on each side of the aircraft were counted and data on species, numbers, activities, time, and estimated ice coverage were noted on cassette tape-recorders. Densities were calculated using gull numbers over a 400 m strip transect. Observation periods did not normally exceed 2 h in order to maintain observer efficiency (Norton-Griffiths 1976). As is true for most transect surveys (Burnham et al. 1980), counts are minima only.

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Figure 1. Locations of aerial survey transect lines for Ivory Gulls in Davis Strait during March (dotted lines) and April-November (heavy solid line) 1978. Dates by light lines indicate eastern extent of pack ice in 1978.
Shipboard Observations and Feeding Studies

Data on relative abundance of Ivory Gulls were obtained during oceanographic cruises aboard the M.V. Lady Johnson II to Davis Strait and the Labrador Sea in February 1977 and 16 April – 17 May 1978. The ship's path was north along the ice edge, into nearby open water and rarely more than 10 km into dense ice. Gulls were counted during a series of 10-min watches (Brown et al. 1975) and ice coverage was estimated to the nearest tenth. During the second cruise, 16 Ivory Gulls were shot at the ice edge in southwest Davis Strait for gut-content analyses. The digestive tracts were removed and frozen for later analysis; fish otoliths were used to identify prey taxa.

Results

Seasonal Distribution — Davis Strait

Varying amounts of pack ice occurred in Davis Strait for nine months in 1978. The ice extended to a maximum of 350-400 km east of Baffin Island in March, receded west through July, and by the end of this month only local accumulations remained in NW Davis Strait. By late October ice began to reform (Figure 1). All but one of 1013 Ivory Gulls counted in aerial surveys in 1978 were present when there was ice cover (Figure 2). Mean offshore density was greatest in March (0.32 gulls/km²) and gulls were seen on the following seven surveys until the migration from Davis Strait was apparently completed after the 16-17 June survey. Ivory Gulls were first seen in the fall in early November (Figure 2).

Habitat use by gulls may be related to two features in Davis Strait: 1) the position of the Hooded Seal whelping patch in March (Figure 1), and 2) the extent and density of pack ice from March through June. In March and April when ice was both extensive (Figure 1) and dense, covering more than 80% of the water surface west of the ice edge (Environment Canada 1978), Ivory Gulls were seen only near the ice edge; none was seen more than 25 km to the west on any transects, nor near the SW Greenland coast north of 65°N, where Ivory Gulls are irregular winter visitors (Salomonsen 1967). The largest gull concentration in March was at the ice edge near the Hooded Seal whelping patch. Mean density there (62°30' to 63°30'N) on three transects totalling 294 km was (X ± s.d.) 1.90 ± 0.97 gulls/km². Gulls and seals were concentrated near the ice edge although part of the seal patch extended 100 km to the west. Gull density on the remaining seven Davis Strait transects (695 km) between 60° and 62°30'N was only 0.25 ± 0.15 gulls/km². The total area of the seal herd and adjacent waters subsampled in our surveys was about 12 500 km² based on a rectangle 50 km wide (25 on each side of the ice edge) and 250 km long, oriented NE-SW along the ice edge. The area sampled in

![Figure 2](image-url)
southern Davis Strait was about 45 000 km², larger because more ice edge and open water was surveyed. Based on gull densities in these two regions, gull numbers were estimated at 23 800 ± 12 100 near the seal herd and 11 300 ± 6 750 in south-central Davis Strait.

The February shipboard observations provided a more detailed assessment of habitat use relative to ice-cover. Gulls were most frequent over 70-90% pack ice near the ice edge (\( \bar{x} = 3.2 \) gulls/10-min watch, \( n = 22 \) watches), followed by open water near the edge (\( \bar{x} = 2.6, n = 10 \)), 10-60% pack ice near the edge (\( \bar{x} = 1.5, n = 11 \)) and open water more than 5 km from the edge (\( \bar{x} = 0.5, n = 6 \)). Gull densities were greater in April-May 1978, but these habitats were favored in identical order with respective mean densities of 16.2 (29), 6.6 (30), 3.3 (33) and 1.0 gulls/watch (51 watches) (Spearman rank test, \( p < 0.001 \)).

As the ice receded after April (Figure 1), its density also decreased (Environment Canada 1978), and coastal leads developed. Ivory Gulls were then more frequently seen on coastal transects (Figure 2) and over pack ice, although most sightings were still made near the ice edge. Coastal habitats had the highest densities of gulls in November, when ice was reforming.

**Seasonal Distribution — Labrador Sea**

Ivory Gulls were uncommon during aerial surveys in the Labrador sea because these did not begin until late May. Only 52 were seen, including 50 on an iceberg near the ice edge at 59°N on 26 June, and a single bird near the last ice remnants in the northern Labrador Sea on 14 July. This species is considered to be an uncommon summer visitor to the Labrador Sea (Brown et al. 1975, Brown 1976). Ivory Gulls were far more common during February shipboard observations, as far south as 50°N, principally over open water near the ice edge (\( \bar{x} = 6.0, n = 16 \) watches), followed by 10-60% pack ice near the edge (\( \bar{x} = 3.2, n = 31 \)), 70-90% pack ice near the edge (\( \bar{x} = 3.0, n = 35 \)) and open water more than 5 km from the edge (\( \bar{x} = 1.3, n = 18 \)). Compared to this period in Davis Strait, gulls were two or three times as frequent in all habitats in the Labrador Sea except for identical densities in the 70-90% ice category, and in both regions they became less common away from the edge. By April and May 1978, most gulls had apparently migrated north from the Labrador Sea. Only 25 were seen south of 59°N in 103 watches (0.2 gulls/watch) and densities (for shipboard observations; aerial surveys covered less of the ice edge after March, Figure 1) had increased in Davis Strait (see above).

**Food**

Fifteen of the 16 Ivory Gulls shot at the ice edge in southwest Davis Strait between late-April and mid-May had eaten lanternfishes of the family Myctophi-dae. These are small fish (< 10 cm in length), generally found in deep water, which migrate to the surface to feed at night (Leim and Scott 1968). *Protomyctophum arcticum* was found in 10 stomachs, *Benthosema glaciale* in 7 and *Lampanyctus* sp. in 4, and an unidentified fish in 1. In all stomachs, only otoliths which were presumably from recently ingested fish (Bradstreet 1980) remained. One gull stomach also contained remains of the squid *Gonatus fabricii*.

**Discussion**

The seasonal occurrence and distribution of Ivory Gulls in Davis Strait and the Labrador Sea may be explained by two physical factors which influence the gulls' pelagic food supply: winter light levels and pack ice distribution. During the arctic winter, few polynyas occur north of Davis Strait and in these biological production is probably limited by low light levels (Brown and Nettleship 1981). For this reason, only small numbers of Ross' Gulls (*Rhodostethia rosea*) and Black Guillemots (*Cepphus grylle*) remain north of Davis Strait in the winter (Renaud and Bradstreet 1980, Brown and Nettleship 1981). Eastern Davis Strait and Labrador Sea remain partly open year round because of the warmer West Greenland Drift and Gulf Current. The interaction of these water masses with the colder, less saline, Baffin and Labrador Currents (J. Booth, unpublished), and wind (Dunbar 1981), determine the position of the ice edge.

The ice edge and its associated fauna are clearly important to Ivory Gulls. Food is concentrated at ice edges where epontic flora is grazed by copepods, which in turn are eaten by such fish as Arctic Cod (*Boreogadus saida*) (McRoy and Goering 1974, Bradstreet 1980, Dunbar 1981). Lanternfishes seemed to be more important than Arctic Cod at the ice edge in Davis Strait during April and May, and dense schools of these luminous fish were seen regularly at night near the surface (D. Gillis, Imakpik Fisheries, personal communication). Ivory Gulls may feed on these fish principally during the long winter nights when lanternfishes are concentrated at the surface and highly visible. The Ivory Gull must be capable of feeding at night since parts of its winter range are in continuous darkness (Blomqvist and Elander 1981). While gulls were seen feeding during the day by shipboard observers, they were commonly found resting on ice during aerial and shipboard surveys, and gut contents of all specimens collected during the day contained only otoliths, suggesting that fish had been eaten a few hours earlier (Bradstreet 1980).

The concentration of Ivory Gulls near the Hooded Seal herd suggests that seal placenta, faeces and carrion from kills by Polar Bear (*Ursus maritimus*) may be seasonally important prey items. The longer duration and larger amount of ice edge habitat should...
make the latter the more important feeding habitat, particularly in the Labrador Sea, where winter gull densities were larger. Ice edges are also important feeding areas elsewhere for Ivory Gulls and for several other seabirds (Divoky 1976, 1979, in press; Nettleship and Gaston 1978; Bradstreet 1980; Orr et al. in press).

The ice edge and nearby waters are used extensively by Ivory Gulls for three-quarters of the year in Davis Strait and for a slightly shorter time in the Labrador Sea. During this time, gulls were found along the ice edge from 50° to 64°N, a linear distance of about 1600 km, or more than 2000 km of ice edge. Canadian and northwestern Greenland gulls begin to return to their arctic colonies in late May or early June when they can feed locally (Salomonsen 1967, MacDonald 1976). Whether most Ivory Gulls we saw were from these areas is not known, but our March estimate of gull numbers suggests that either the populations of these areas are larger than previously believed, or that Ivory Gulls wintering in the western North Atlantic include birds from other geographic locations. When pack ice is present, it should be possible to accurately predict the winter distribution of Ivory Gulls in the western North Atlantic.

Acknowledgments

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Literature Cited


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Sexual Colour Differences in Canadian Western Toads, *Bufo boreas*

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Female Western Toads, *Bufo boreas*, in Alberta and the interior of British Columbia appear dimorphic in dorsal colour; some are yellowish and others are reddish due to pigmentation on the granular glands. Males in these populations are only yellowish. The proportion of reddish females increases towards the coast. There is no evidence of dimorphism in the lower Fraser Valley or on Vancouver Island. A yellowish-reddish contrast was the first principal component of a principal components analysis of Munsell Color Notation scores of the parotoid glands of dried skins, but the scores were not bimodal.

Key Words: Western Toads, *Bufo boreas*, colouration, Munsell Notation, sexual dimorphism, toads.

Sexual dimorphism in melanic pigmentation in northern Western Toads, *Bufo boreas*, has been described by Karlstrom (1962) and Black (1971); females have a more contrasting pattern of dark spots or blotches. This paper describes colour variation in *Bufo boreas* I have observed in Alberta and British Columbia. The colours of amphibia fade in preservation, so I have data only on the relatively few specimens that I have seen alive (Figure 1).

**Materials and Methods**

I recorded the colour of living individuals in the field either as partitions based on perceived colour groups within samples (e.g. “red” and “yellow”) or by comparisons with colour standards (Smithe 1975; numbers and capitalized names of colours are from these standards). Some of the specimens collected in 1976 were photographed (National Museum of Canada [NMC] Herpetology Slide Collection 848-851). Sex was determined by dissection. I compared frequencies by G tests (Sokal and Rohlf 1969). Two samples (22 of 25 from Durieu B.C. [about 75 km W of Vancouver]; NMC 18659, and 15 of 31 from Saska- toon Island Park, near Grande Prairie, Alta.; NMC 18601) were prepared as dried skins to preserve their coloration (Schueler 1980). The colours of the paro- toid glands of the skins were matched (by Aleta Karstad in 1979) to colour standards, both by reflected and transmitted daylight, and these matches were made into six numeric variables as the Munsell notations of the colour swatches (Smithe 1975; means of colours intermediate between standards, hue coded by adding 10 for each Munsell hue range from 10 for Red to 100 for Red-Purple). The Munsell notation (Munsell 1954; McKillop and Preston 1981) describes a colour by three numbers; hue (its position on the visible spectrum), value (the relative amount of reflected light, from white to black), and chroma (the intensity of the hue).

**Results**

**Qualitative Partitions of Fresh Specimens:** Table 1 summarizes colour partitions of toads with snout-vent length greater than 30 mm. The sample from Vancouver Island was collected before I had seen “dimorphic” samples, so the coding differs from the other samples. There is no significant difference between the sexes (G=6.9, 3 d.f., p>0.05), but no males were coded as “brown” nor females as “green”, and two adult females had “rusty sides”, so larger samples might show sexual differences. Patrick Gregory (University of Victoria, personal communica-

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**Figure 1. Sample Localities.** Localities are grouped as in Table 1, and some sites discussed in the text are labelled. 1 = Coastal British Columbia, 2 = Interior British Columbia, 3 = East of the Rocky Mountains.
Table 1. Colours of *Bufo boreas* recorded in the field. These are specimens with snout-vent length > 30 mm. All are in the collection of the NMC.

<table>
<thead>
<tr>
<th></th>
<th>Red</th>
<th>Intermediate</th>
<th>Yellowish or Greenish</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Dimorphism Evident</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1) Coastal British Columbia (mouth of Quatam River; May 1977 [11 specimens], Kasiks R. [1], Kitimat [1]; July-August 1980)</td>
<td>Males</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td>2) Interior British Columbia (Mt. Revelstoke; June 1973 [2], Pine Pass to Williams Lake; August 1976 [16], Smithers [1], Beaverley [1]; August 1980)</td>
<td>Males</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Females</td>
<td>5</td>
<td>2</td>
</tr>
<tr>
<td>3) East of the Rocky Mountains (Little Smoky [3], Saskatoon Island Park [31], Alberta, Swan Lake, British Columbia [5]; August 1976)</td>
<td>Males</td>
<td>0</td>
<td>0</td>
</tr>
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<table>
<thead>
<tr>
<th></th>
<th>Red</th>
<th>Intermediate</th>
<th>Not Red</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dimorphism Not Evident</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lower Fraser Valley (Durieu; September 1976)</td>
<td>Males</td>
<td>2</td>
<td>3</td>
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<td></td>
<td>Females</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Vancouver Island (Cameron Lake, June 1973)</td>
<td>Olive Brown</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>Gray Brown</td>
<td>3</td>
<td>2</td>
</tr>
</tbody>
</table>

Saskatoon Island, Alta.

![Diagram of skin colouration]

**Figure 2.** Histograms of scores of *Bufo boreas* skins on the first Principal Component of Variation in Munsell notations of parotoid gland colour. Each square represents a specimen; those marked ‘M’ are male, and the females marked ‘R’ were called ‘red’ in the field. The stars mark the means of the samples. Yellowness increases to the right, and the positions of the five colours most frequently referred to in comparisons are plotted as the score a specimen would have if its parotoid glands were the indicated colour by both reflected and transmitted light.

gives a highly significant overall G, and significant interactions between colour and sex (G=125, with 2 d.f., p<<0.005), and between colour and area (G=99.6, with 4 d.f., p<<0.005). Considering only the females (since all males are yellowish), there is a strong relationship between colour and area (G=99.6, with 2 d.f., p<<0.005). The 4 intermediate specimens from the interior were immature, so the distinctiveness of the red morph may increase with age.

In a sample of smaller toads (svl<30 mm; NMC 18612 from Pine Pass, BC) only females were "red"; 3 and 4 of 10 females were "red" and "gray-brown with red warts," which is perhaps different from 0 and 2 in these colour classes among 8 males (G=5.64, 0.05 < p < 0.075). In two samples of newly transformed toads with poorly differentiated gonads (NMC 18620; Hush Lake, north of Quesnel, and NMC 18636; 8 km SW Williams Lake, BC) females were more often reddish than males, but many were unsexable.

In the dried skins the reddish colour is confined to the granular glands, and is found on both isolated glands and those that form the warts and parotoid glands. Variation in the overall reddness of the skin is due to the intensity of the pigmentation of the glands.

In the skins of "red" specimens from Saskatoon Island the glands are coloured Cinnamon-Rufous to Amber, and beneath melanic pigmentation they appear Chestnut to Maroon. In the yellowish skins the glands match the Olive shades (colours 28-30, 42, 43, 48) of the rest of the skin. Occasionally there is a reddish gland on a yellowish female, and the reddest Saskatoon Island male (Figure 2; called "yellowish-green" in the field) has Antique Brown to Tawny...
glands. Other than the colour of the glands the only difference between the morphs appears to be the middorsal line, which is more frequently obscure or pale yellowish in the yellowish specimens, and more often sharp-edged and neutral greyish in the red specimens.

In the field I recorded adult red specimens as "pale Olive Gray with dark Maroon warts" (Little Smoky, Alta.), "pale grey with rusty or maroon warts and spots", and "Cinnamon-Rufous" (Saskatoon Is.), and adult yellow specimens as "Citrine" (Little Smoky) and "bright yellow-green with dark grey spots and mottles" and "Olive-Yellow" (Saskatoon Is.).

Principal Components Analysis of Colours of Dried Skins:

The principal components (PCs) of the correlations of the colour variables were determined with the expectation that red vs not-red differences would be a major component of variation, and would be highly correlated with the colour separations made in the field. The first PC accounts for 62% of the variation, and is strongly correlated with hue (0.91 [transmitted], 0.88 [reflected]), value (0.84, 0.61), and chroma (-0.71, -0.73). The second and third PCs account for 14 and 12%, and together separate the samples on the basis of whiter reflected value and paler reflected chroma of the Saskatoon Island specimens. High values of the first PC result from colours with yellowish hue, light value, and weak chroma. The two samples had similar means (Sask. Is. = 8.96, Durieu = 7.76) and very similar standard deviations (1.89, 1.83). Saskatoon Island specimens called "red" in the field have lower scores than any others from there, and the few males cluster with the yellowish females. In the Durieu sample some males are among the reddest individuals. There is no clear evidence of bimodality in the Saskatoon Island scores, but their distribution does differ from that of the Durieu sample (two-sided, two-sample Kolmogrov-Smirnov test on mean-centred data, n = 37, D = .955, p < 0.01; Steel and Torrie 1980). The difference is due to the predominance of red individuals from Durieu, and of yellow ones from Saskatoon Island.

Discussion

There are reddish forms in other northern or high altitude toads, but in contrast to northern Bufo boreas the rusty morph of the Canadian Toad, B. americanus hemiophrys, is equally frequent in each sex (Cook 1964). Among skins of the American Toad, B. a. americanus, from northern Ontario and Quebec there is no association between redness and sex (Schueler, unpublished). Females have more dark markings in all of these toads (Karlstrom 1962; Cook in press; Wright and Wright 1949). This sexual dimorphism in dark pigmentation is strongly evident in the Yosemite Toad, B. canorus, of the Sierra Nevada of California, a close relative of B. boreas, which is especially similar to northern and montane B. boreas, and in which red coloration is characteristic of females and greenish is characteristic of males (Karlstrom 1962; Black 1970). Like northern populations of B. a. americanus (Schueler 1973), B. canorus and B. canorus–like B. boreas are quite diurnal in habits (Karlstrom 1962; Hodge 1976; Mullanly and Cunningham 1956).

Male toads remain at breeding sites longer than females, so it seems likely that they suffer more predation there than females, and thus better match the relatively uniform muddy bottoms of these places (Karlstrom 1962). Females and northern populations must forage more extensively in daylight (the former because they must find the food to make ova and the latter because northern nights are short and cold), and thus are optimally cryptic with a more contrasting colour pattern (Endler 1978). Red coloration may enhance and diversify this contrast, and match the redder litter of coniferous forests; it is my impression that the frequency of red B. boreas (Table 1) parallels the change in ground cover from yellowish grass in the interior to reddish conifer litter on the coast. The apparent absence of red toads from the coniferous forests of Vancouver Island suggests that the variation is more complex than this, and that quantitative measurement of the colour and contrast of toads and their habitat (Papageorgis 1975; Endler 1978) might be worthwhile.

Acknowledgments

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Literature Cited


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Migratory Peregrine Falcons, *Falco peregrinus*, Accumulate Pesticides in Latin America during Winter

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⁴Patuxent Wildlife Research Center, Laurel, Maryland 20708


Blood samples from 433 Peregrine Falcons (*Falco peregrinus*) during fall and spring migrations, 1976-80, indicated that most of their pesticide burden, primarily DDE, was accumulated on wintering grounds in Latin America. DDE in spring migrants returning from Latin America for the first time declined significantly from 1979 to 1980. Only about 10% of breeding-age females contained organochlorine residues likely to adversely affect reproduction. The organochlorine pesticide threat in Latin America may be diminishing.

Key Words: Peregrine Falcon, *Falco peregrinus*, environmental contaminants, DDT, migration.

The Peregrine Falcon has suffered population declines in much of the Northern Hemisphere. It had disappeared in the eastern United States by the mid-1960’s, only remnant populations existed in many western states, and the population was reported declining in Alaska (Hickey 1969; Peakall et al. 1975; Peakall 1976). Similarly, two of the three subspecies were reported declining in Canada (Fyfe 1977). Those declines corresponded temporally with the use of DDT and resultant decreases in peregrine eggshell thickness (Ratcliffe 1967a, 1980; Peakall 1974). The present status of northern breeding populations, those wintering in Central and South America (White 1968), is the least understood, with conflicting viewpoints reported, i.e., stable (Beebe 1976) or declining (Peakall et al. 1975; Fyfe 1977; Fyfe et al. 1976).

We initiated a study of migratory Peregrine Falcons in 1976. Our approach involved capturing peregrines during fall and spring migrations at Assateague Island, Maryland/Virginia, and Padre Island Texas, and collecting blood samples for analyses of organochlorine contaminants. All spring samples were obtained in Texas. We used the plasma residues of DDE, the relevant metabolite of DDT, from adult females to predict residues in their eggs (Henny and Meeker 1981). In this way, residue information could be related to reproductive potential; Peakall (1976) tentatively concluded that 15-20 ppm (wet weight) DDE in peregrine eggs was the level above which hatching failure occurred. Thus, our study was designed (1) to determine organochlorine contaminant burdens in migrating Peregrine Falcons, (2) to determine when and where the contaminants were being accumulated, and (3) to evaluate the impact of the contaminants detected on reproductive potential.

Methods

Captured peregrines were assigned to three age classes: HY (Hatching year, known to have hatched during the calendar year it was captured), SY (Second year, known to have hatched in the calendar year preceding the year of capture and in its second calendar year of life), and ASY (After second year, known to have hatched earlier than the calendar year preceding the year of capture).

Blood was collected from the brachial vein. The 1 ml plasma samples were stored frozen, then homogenized with anhydrous sodium sulfate and extracted with hexane in a Soxhlet apparatus for 7 h. To minimize background interferences, we ignited the sodium sulfate at 675°C for 3 h and all glassware was rinsed with 15 percent ethyl ether in hexane. For each set of 10-13 samples, a procedural blank of sodium sulfate was run through the entire analytical process. Notwithstanding, the backgrounds in some of the procedural blanks prevented estimation of the generally low levels of polychlorinated biphenyls (PCBs). The extracts of all samples were cleaned up on a partially deactivated Florisil column (Cromartie et al. 1975). Pesticides and PCBs were separated on a silicaAR column into four fractions (Kaiser et al. 1980). Our recoveries of pesticides from fortified Mallard (*Anas platyrhynchos*) blood using these procedures averaged 88%. Residues reported were not corrected for recovery. Due to a lack of SilicaAR, silica gel column chromatography with the same eluting solvents was substituted in the analysis of the 1979 fall samples. To avoid endrin losses, we selectively eluted dieldrin and endrin from the Florisil column before silica gel column chromatography. We quantified residues using a gas-liquid chromatograph equipped with an
electron capture detector and a 1.5% OV-17/1.95% QF-1 or a 1.5% SP-2250/1.95% SP-2401 column. Identifications of residues in 24 samples were confirmed by mass spectrometry. The lower limit for reportable residues was 0.02 ppm wet weight.

We used an ANOVA with three factors called TIME, WINTER and SEX. TIME occurred at three levels (never to Latin America, one winter in Latin America, and one winter in Latin America and a summer on breeding grounds) and WINTER at four levels (to coincide with which winter birds were exposed). To circumvent the difficulty of empty cells (0 birds), we did not test for the usual ANOVA hypotheses but instead developed a group of contrasts and tested their significance based on the Bonferroni multiple comparison procedure (Speed and Hocking 1976). All data were log transformed and the significance level was 0.05.

Results and Discussion

**DDE in First Year Migrants**

From 1976 to 1980 we captured and bled 433 Peregrine Falcons during migrations, including three birds produced in captivity and released as nestlings along the Atlantic Coast (Cade and Dague 1980). A high percentage (85%) of the peregrines bled during the fall were HY birds making their first migratory flight from northern areas. Residues of DDE were extremely low in HY birds of each sex from both locations (Table 1). The three HY females released along the Atlantic Coast in summer and captured in the fall at Assateague Island contained DDE residues (geometric mean and 95% C.I., 0.25 ppm [0.15-0.41]) that were higher than in HY female northern migrants trapped at the same location (0.06 ppm [0.05-0.09]).

**Source of DDE Contamination**

We reasoned that the difference in contaminant concentrations between fall and spring samples would reflect residues accumulated between migrations. Northern peregrine breeding grounds are known from field surveys (e.g., Fyfe et al. 1976), while band recoveries and museum specimens show that the birds winter widely in Central and South America (Enderson 1965; White 1968). Previously banded peregrines captured during this study in Texas included two from the Yukon River, Alaska, one from northeastern Kee-watin (Calef and Heard 1979), one captive-bred bird released by the Canadian Wildlife Service in northern Alberta, and one banded during the previous fall in Mexico. Two peregrines captured at Assateague Island had been banded at their nest in Yukon Territory. Recoveries south of the United States include three banded in Texas that were encountered in the Yucatan Peninsula, Mexico, in El Salvador, and in Argentina.

A substantial concentration of migrating peregrines was discovered at Padre Island, Texas, in April 1978. We surveyed the island intensively for eight days in mid-February 1980 and saw only one peregrine. Therefore, almost all peregrines captured in April and May on this south Texas barrier island were assumed to have recently arrived from wintering areas in Latin America. Of 162 SY and ASY peregrines captured and bled during this study, only four (2.5%) were males. Thus, the residue data for the SY and ASY age classes are only for females. We assume that differen-

<table>
<thead>
<tr>
<th>Year</th>
<th>Maryland/ Virginia</th>
<th>Texas</th>
<th>Maryland/ Virginia</th>
<th>Texas</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (95% C.I.)</td>
<td>n</td>
<td>Mean (95% C.I.)</td>
<td>n</td>
</tr>
<tr>
<td>HY♀♀</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1976-77</td>
<td>0.11 (0.07-0.19)</td>
<td>15</td>
<td>0.05 (0.03-0.08)</td>
<td>15</td>
</tr>
<tr>
<td>1978</td>
<td>0.04 (0.02-0.08)</td>
<td>25</td>
<td>0.03 (0.02-0.07)</td>
<td>20</td>
</tr>
<tr>
<td>1979</td>
<td>0.07 (0.05-0.10)</td>
<td>36</td>
<td>0.05 (0.04-0.07)</td>
<td>74</td>
</tr>
<tr>
<td>Totals</td>
<td>0.06 (0.05-0.09)</td>
<td>76</td>
<td>0.05 (0.04-0.06)</td>
<td>109</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>HY♂♂</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1976-77</td>
<td>0.08 (0.05-0.14)</td>
<td>9</td>
<td>0.16</td>
<td>2</td>
</tr>
<tr>
<td>1978</td>
<td>0.03 (0.01-0.10)</td>
<td>8</td>
<td>0.06 (0.03-0.09)</td>
<td>16</td>
</tr>
<tr>
<td>1979</td>
<td>0.08 (0.06-0.11)</td>
<td>26</td>
<td>0.05 (0.04-0.08)</td>
<td>22</td>
</tr>
<tr>
<td>Totals</td>
<td>0.07 (0.05-0.09)</td>
<td>43</td>
<td>0.06 (0.04-0.08)</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SY♀♂</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fall</td>
<td>0.82 (0.44-1.53)</td>
<td>11</td>
<td>0.28 (0.01-0.75)</td>
<td>4</td>
</tr>
<tr>
<td>1976-78</td>
<td>0.64 (0.38-1.07)</td>
<td>6</td>
<td>0.27 (0.02-3.91)</td>
<td>3</td>
</tr>
<tr>
<td>1979</td>
<td>0.75 (0.50-1.13)</td>
<td>17</td>
<td>0.28 (0.07-1.16)</td>
<td>7</td>
</tr>
<tr>
<td>Totals</td>
<td>0.71 (0.14-3.67)</td>
<td>5b</td>
<td>0.33 (0.14-0.77)</td>
<td>12</td>
</tr>
<tr>
<td>Spring</td>
<td>1978-79</td>
<td></td>
<td>0.40 (0.22-0.72)</td>
<td>18</td>
</tr>
<tr>
<td>1980</td>
<td>0.60 (0.36-1.00)</td>
<td>27</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td></td>
<td>0.67 (0.55-0.83)</td>
<td>84</td>
</tr>
</tbody>
</table>

*Excludes 3 HY♀♀ that were released along East Coast by Cornell University biologists.

*bIncludes one sample from 1978.
tual timing of migration or alternate migration routes account for the low numbers of males observed and captured.

The population comparisons were of two types: (1) comparing a population of HY birds enroute to Latin America the first time in the fall with SY birds returning from Latin America for the first time in the spring, and (2) comparing adult (ASY) birds caught in the fall of one year with those caught in the spring of the following year.

Assumptions necessary to include the two comparisons in a combined linear model would probably not be met because of adult birds having multiple exposure to the presumed perturbation, i.e., multiple winters in Latin America. In addition to testing for acquisition of contaminants in Latin America during the winter, we also tested for reduction of contaminants during the summer on the breeding grounds.

The DDE concentration in SY birds returning from Latin America in the spring was significantly higher than that HY birds captured in Texas in the fall enroute to Latin America. No significant reduction of DDE was found for the period on the breeding grounds, although the DDE concentration in SY birds returning from Latin America in the spring was somewhat higher than in SY birds on the migration to Latin America the next fall. A residue decrease during the summer could result if peregrines purge their system of pesticides during the egg-laying process (Henny and Meeker 1981; Bogan and Newton 1977), but few, if any, SY female peregrines lay eggs (Ratcliffe 1980). The hint of reduced DDE residues in the fall SY females, if true, probably resulted from consuming less contaminated prey on the breeding grounds. DDE in pigeons (Columba livia) on an uncontaminated diet had a half life of 8.3 months (Bailey et al. 1969). ASY females from Texas also had higher residues in the spring (returning from the wintering grounds) than in the fall, but again the difference was not significant. Most peregrine researchers had anticipated that the wintering period in Central and South America was an important time and location for DDE accumulation. But we did not expect that residue concentrations nearly equal to those in adult females would be accumulated by young females during the first winter (Table 1). Concentrations of DDE in seven peregrines recaptured and bled several times in subsequent seasons in Texas provided additional support for the pesticide patterns observed. Furthermore, the recaptures, especially the fall-to-spring recaptures in Texas, strongly suggest the same population was studied in both fall and spring.

Trends in DDE Contamination

The difference in DDE concentrations between HY females enroute to Latin America in the fall and SY females returning in the spring was significantly higher in the winter of 1978-79 than in the winter of 1979-80. Similarly, the DDE concentrations in SY spring migrants (birds about 10 months old) in 1979 was significantly higher than in SY spring migrants in 1980. No significant differences were noted for adults between years.

Other Pesticides

Residues of DDE were detected in 99% of the ASY, 98% of the SY, and 82% of the HY peregrines, but 12 other organochlorine pesticides or their metabolites (including DDT and DDD) and PCBs were detected. However, the generally low levels of PCBs were incompletely estimated (see methods) and are not presented. Among the other pesticides, dieldrin and heptachlor epoxide were most commonly detected (see Appendix Table).

DDE in Early vs Late Migrants

Data from SY and ASY females in spring (5 April - 4 May) were used to evaluate the hypothesis that early migrants were more contaminated than later migrants. Based on phenology, we assumed falcons that nest at more southerly latitudes migrate north earlier. We correlated DDE residues in plasma (log transformed) with date of capture. Years were evaluated separately since annual differences were found for SY spring migrants. Spearman's Correlation Coefficients showed no significant relationship between capture date and DDE in ASY females in either year (r = -0.193, P = 0.44, n = 18; r = -0.018, P = 0.89, n = 62); however this relationship in SY females, though not significant in 1979, (r = -0.607, P = 0.15, n = 7) was highly significant in 1980 (r = -0.604, P < 0.01, n = 19). Early SY migrants were more contaminated than falcons captured later. Temporal patterns of selected contaminants in spring migrants are illustrated in Table 2 by subjectively dividing the spring into three categories. The patterns observed may result from population segments at different wintering and breeding areas migrating on slightly different schedules.

Some birds from more southern breeding areas in Canada may have migrated before our spring sampling began. Arrival dates on territory in southern Alberta (51°N) include 9 April (male), 11 April (pair), 15 April (male), and in northern Alberta (58°N) 16 April (male), 21 April (pair); these Alberta birds are among the most contaminated in Canada and Alaska (R. W. Fyfe, Canadian Wildlife Service, personal communication).

Significance of Pesticides on Reproduction

We estimated the DDE residues in eggs of ASY females from DDE residues in their blood plasma. The egg residue estimates were based on a post-laying
Table 2. Organochlorine pesticides in blood plasma of female Peregrine Falcons captured in Texas during segments of the spring migration, 1979 and 1980.

<table>
<thead>
<tr>
<th>Age and date</th>
<th>n</th>
<th>Geo. mean</th>
<th>Samples with pesticide (%)</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>DDE</td>
<td>DDT</td>
<td>HE</td>
<td>Dieldrin</td>
<td>Mirex</td>
</tr>
<tr>
<td>SY</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5-15 April</td>
<td>11</td>
<td>0.95 ppm</td>
<td>(18%)</td>
<td>4(36%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>16-25 April</td>
<td>10</td>
<td>0.71 ppm</td>
<td>0</td>
<td>7(70%)</td>
<td>6(60%)</td>
<td></td>
</tr>
<tr>
<td>26 April-4 May</td>
<td>6</td>
<td>0.18 ppm</td>
<td>0</td>
<td>3(50%)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>ASY</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5-15 April</td>
<td>23</td>
<td>0.65 ppm</td>
<td>(9%)</td>
<td>8(35%)</td>
<td>8(35%)</td>
<td>6(26%)</td>
</tr>
<tr>
<td>16-25 April</td>
<td>37</td>
<td>0.75 ppm</td>
<td>(3%)</td>
<td>14(37%)</td>
<td>22(59%)</td>
<td>10(27%)</td>
</tr>
<tr>
<td>26 April-4 May</td>
<td>20</td>
<td>0.66 ppm</td>
<td>(10%)</td>
<td>12(60%)</td>
<td>13(65%)</td>
<td>6(30%)</td>
</tr>
</tbody>
</table>

*HE = heptachlor epoxide

The equation for fall-captured females, whereas both pre- and post-laying equations were used for spring-captured females (Henny and Meeker 1981). If we follow Peakall's (1976) estimate that hatching failure occurs when DDE residues in peregrine eggs reach 15-20 ppm (weight), and the adjustment equations of Henny and Meeker (1981), only 7 (6.6%) of 106 adult female peregrines sampled contained sufficient concentrations of DDE to affect reproduction adversely.

Heptachlor epoxide (HE) and dieldrin may also affect reproduction in peregrines. Ratcliffe (1967b) presented organochlorine residues in sample eggs from 18 peregrine eyries, excluding 9 with high DDE residues (> 15 ppm in egg) that failed. Eyries with the four highest HE residues (0.8 to 4.1) were all successful in fledging young; eyries with the four highest dieldrin residues (1.1 to 1.8) included two failures. Because none of our projected egg residues of HE were above 2.7 ppm, we doubt that HE had an impact on our sampled peregrine population. If dieldrin levels ≥ 1.3 ppm affect reproduction, two to four of the peregrines in our sample, depending upon adjustment equations, may have been inimically affected by dieldrin.

Interpreting egg residues and reproductive success requires caution. The nesting pair, rather than the egg, is the biological unit upon which the organochlorines operate. Failure may result from the direct action of toxic residues on the embryo or chick, from shell thinning or other changes in the shell, or because of behavioral changes in the parents (A. S. Cooke, Nature Conservancy Council, Great Britain, personal communication). Also, the combined effects of the residue burden may be crucial. Our best estimate, not allowing for combined effects, is that reproduction is affected adversely by organochlorine pesticides (primarily DDE) at the present time in less than 10 percent of the ASY female population of northern peregrines. This may reflect an improvement over 10 years ago because DDE burdens in our SY female sample declined during this study.

Although we believe the future looks optimistic for the northern population in general, the birds affected by pesticides might not be randomly distributed throughout the breeding range. A pattern of reduced contaminant burdens and improved reproduction has been documented for several avian species in the United States, including Ospreys ( Pandion haliaetus ), and Bald Eagles ( Haliaeetus leucocephalus ) (Henny 1977; Spitzer et al. 1978; Postupalsky 1978). However, the northern peregrine differs from Ospreys and Bald Eagles because Central and South America are its primary sources of contaminant uptake. The United States was the primary source for the Osprey (Henny and Van Velzen 1972), and probably the sole source for the Bald Eagle, which seldom migrate south of the border (Brown and Amador 1968). The former Peregrine Falcons of the eastern United States likewise did not migrate outside the country (Hagar 1969), and captive-bred birds are now nesting successfully in that region (Cade and Dague 1980). Migratory habits are important; DDT was banned in the United States and Canada in the early 1970's, but it is still used in many Central and South American countries (Weir and Schapiro 1981).

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Literature Cited


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Accepted 14 May 1982
APPENDIX TABLE. Other organochlorine pesticides in blood plasma of Peregrine Falcons captured at Assateague Island, Maryland/Virginia and Padre Island, Texas, 1976-80.

<table>
<thead>
<tr>
<th>Category</th>
<th>Number analyzed</th>
<th>DDT</th>
<th>DDD</th>
<th>HE*</th>
<th>Dieldrin</th>
<th>OXCH</th>
<th>CICH</th>
<th>Mirex</th>
<th>HCB</th>
</tr>
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<tbody>
<tr>
<td>Texas</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fall HY♂♂</td>
<td>40</td>
<td>—</td>
<td>—</td>
<td>2(0.03)♭</td>
<td>4(0.03)</td>
<td>1(0.02)</td>
<td>3(0.03)</td>
<td>—</td>
<td>1(0.03)</td>
</tr>
<tr>
<td>Fall HY♀♀</td>
<td>109</td>
<td>—</td>
<td>—</td>
<td>3(0.07)</td>
<td>6(0.08)</td>
<td>1(0.02)</td>
<td>2(0.04)</td>
<td>1(0.02)</td>
<td>2(0.03)</td>
</tr>
<tr>
<td>Spring SY♀♂</td>
<td>27</td>
<td>2(0.38)</td>
<td>—</td>
<td>16(1.1)</td>
<td>13(0.30)</td>
<td>—</td>
<td>—</td>
<td>1(0.05)</td>
<td>—</td>
</tr>
<tr>
<td>Fall SY♀♀</td>
<td>7</td>
<td>1(0.04)</td>
<td>—</td>
<td>2(0.04)</td>
<td>2(0.20)</td>
<td>2(0.03)</td>
<td>—</td>
<td>1(0.05)</td>
<td>—</td>
</tr>
<tr>
<td>Spring ASY♀♂*</td>
<td>84</td>
<td>5(0.44)</td>
<td>2(0.07)</td>
<td>35(0.44)</td>
<td>46(0.65)</td>
<td>13(0.13)</td>
<td>2(0.06)</td>
<td>22(0.17)</td>
<td>1(0.03)</td>
</tr>
<tr>
<td>Fall ASY♀♀</td>
<td>18</td>
<td>1(0.09)</td>
<td>1(0.02)</td>
<td>11(0.17)</td>
<td>10(0.13)</td>
<td>5(0.05)</td>
<td>2(0.03)</td>
<td>3(0.12)</td>
<td>2(0.03)</td>
</tr>
<tr>
<td>Maryland/Virginia</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fall HY♂♂</td>
<td>43</td>
<td>4(0.08)</td>
<td>—</td>
<td>2(0.02)</td>
<td>2(0.07)</td>
<td>—</td>
<td>2(0.02)</td>
<td>—</td>
<td>1(0.02)</td>
</tr>
<tr>
<td>Fall HY♀♀*</td>
<td>76</td>
<td>7(0.27)</td>
<td>2(0.05)</td>
<td>4(0.04)</td>
<td>8(0.08)</td>
<td>3(0.05)</td>
<td>6(0.12)</td>
<td>3(0.07)</td>
<td>1(0.04)</td>
</tr>
<tr>
<td>Fall SY♀♂*</td>
<td>17</td>
<td>2(0.05)</td>
<td>1(0.08)</td>
<td>6(0.10)</td>
<td>11(0.36)</td>
<td>7(0.11)</td>
<td>1(0.02)</td>
<td>6(0.15)</td>
<td>4(0.15)</td>
</tr>
<tr>
<td>Fall ASY♀♀</td>
<td>5</td>
<td>—</td>
<td>1(0.04)</td>
<td>3(0.08)</td>
<td>3(0.12)</td>
<td>3(0.07)</td>
<td>1(0.03)</td>
<td>2(0.10)</td>
<td>—</td>
</tr>
</tbody>
</table>

*HE = heptachlor epoxide; OXCH = oxychlordane; CICH = cis-chlordane; HCB = hexachlorobenzene.

*Number of samples with detections, i.e., ≥0.02 ppm wet weight; the highest residue detected ( ). Note: trans-nonachlor not evaluated all years and not presented.

*One contained endrin (0.02 ppm).

*One contained cis-nonachlor (0.05 ppm).

*One contained toxaphene (0.05 ppm), one contained cis-nonachlor (0.08 ppm).
Notes

Determining Age of Coyotes, Canis latrans, by Tooth Sections and Tooth-wear Patterns

W. DON BOWEN

Department of Zoology, University of British Columbia, Vancouver, British Columbia.


Accuracy of age determination in Coyotes (Canis latrans) from tooth-wear patterns was compared to that from cementum annuli of first premolars and canines. Age determined from first premolar and canine sections agreed in 14 of 19 specimens. Although the use of canine teeth is preferred because of better definition of lines, first premolars and canines from the same animal differed by only one or two annuli. Thus first premolars may be used to determine age when extraction of a canine is not feasible. Tooth-wear patterns reliably gave the age of pups and yearlings only. In older Coyotes this method generally underestimated age by about one or two years.

Key Words: Coyotes, Canis latrans, Alberta, age, premolar, canine, tooth-wear, Jasper National Park

Two methods are commonly used to determine the age of Coyotes (Canis latrans): tooth-wear patterns of incisors and canines (Gier 1968) and incremental cementum annuli (Linhart and Knowlton 1967). The first method requires only visual inspection of the teeth, is simple, and allows rapid age determination of live animals in the field. The principal disadvantages of this method are that individual and geographic variation in the rate of tooth wear may vary with the type of food eaten, and the method is subjective. Those difficulties are largely overcome by the use of cementum annuli in age determination. Although the cementum procedure is relatively expensive and time consuming, it is generally regarded as the most reliable method (Linhart and Knowlton 1967, Jensen and Nielson 1968, Klevecz' and Kleinenberg 1969, Roberts 1978, Grue and Jensen 1979). A tooth must be extracted to use cementum annuli for age determination. As the canine tooth is preferred, this presents a problem in behavioural studies, because removing a canine from an animal that is to be released for further study may have harmful consequences.

At present there are two solutions to this problem. One is to extract another tooth, for example, the first premolar, a small and largely non-functional tooth in canids. This approach was used by Willey (1974) in his study of Black Bears (Ursus americanus) and by Craighead et al. (1970) in their work on the ecology of Grizzly Bears (Ursus arctos). The second approach is to use the tooth-wear method in the field, but to recalculate this technique using more accurate information derived by counting cementum annuli of teeth collected from Coyotes killed in the same area.

In this paper, I compare age determination in coyotes from tooth-wear patterns and cementum annuli of first premolars, with age determined for the same Coyotes based on counts of cementum annuli of canine teeth.

Methods and Materials

The teeth from 30 road-killed Coyotes, collected in Jasper National Park, Alberta between 1974 and 1977, were studied. Seven of these Coyotes had been tagged at birth, hence their true age (ranging from 6 to 23 months) was known. The age of each Coyote was first estimated to the nearest month (assuming 1 April birth date) using the tooth-wear chart of Gier (1968). Both a lower canine and a first premolar were extracted from 19 Coyotes and a lower canine only from 11 by boiling the jaws for approximately one–two hours. The first premolar was lost or damaged in 11 animals that had been killed by vehicles. Recent experience by dental histologists indicates that better preparations can be made from teeth which are handled and preserved wet than can be produced from traditional boiled material (Scheffer and Myrick 1980). However, jaws have been boiled to facilitate extraction of teeth in all previous studies on age determination in Coyotes using dental annuli (Linhart and Knowlton 1967; Allen and Kohn 1976; Nellis et
al. 1978; Roberts 1978). Tooth sections were prepared following the method of Linhart and Knowlton (1967), but tooth roots were sectioned longitudinally at 24 μm instead of 16 μm. Two to four sections of each tooth were then air-dried and mounted in Permount. I examined canine and premolar sections in blind trials.

Results and Discussion

A lack of known-aged Coyotes approaching 2 years of age led Linhart and Knowlton (1967) to speculate that the first cementum annulus forms when Coyotes are between 20 and 23 months of age. Recently, Allen and Kohn (1976) reported that five 18-month-old coyotes from North Dakota each had one clearly visible cementum annulus. However, Nellis et al. (1978) found the first incremental line appearing at 20 months of age. In Jasper, three 6 to 12-month-old Coyotes and two 15-month-old individuals had closed root canals and no cementum annuli. However, two 23-month-old Coyotes had 1 annulus near the exterior edge of the cementum.

The factors responsible for the formation of incremental lines in the cementum of Coyotes and in other mammals are poorly understood. Grue and Jensen (1979) reviewed the available data on 52 species of terrestrial mammals and concluded that the formation of primary incremental lines is governed to a considerable degree by endogenous factors which are coupled to the animal’s overall pattern of growth and metabolism. External factors may modify line formation to a greater or less extent in different species or in the same species in different areas.

At present there are insufficient data to judge the relative importance of seasonal variation in food and climate and endogenous rhythms in the formation of cementum annuli in Coyote teeth. The sex and age of Coyotes studied from Jasper had no apparent effect on the formation or clarity of cementum lines. These observations agree with the general conclusions of Grue and Jensen (1979). However, considerable subjectivity was involved in interpreting the lines in some teeth, as previously noted by Nellis et al. (1978). Roberts (1978) has reported variation in the clarity of lines in the cementum of canine teeth of Coyotes collected from different areas.

The maximum number of annuli in both premolars and canines was usually found near the apex of the tooth root where the cementum deposit is thickest. Because canine cementum was considerably thicker than that found in premolars, canine cementum annuli were more widely spaced and thus generally easier to count. Nevertheless, for the seven known-aged animals there was complete agreement in the number of incremental lines counted in the canine and premolar of the same individual. From these data it is not possible to state which tooth would be most reliable in general, as the oldest known-aged animals examined were only 23 months.

Overall, the number of cementum annuli counted in the first premolar and canine of the same individual agreed in 14 of 19 specimens (Table 1). In Coyotes up to and including age 3 (¼ 2 annuli), the first premolar agreed with the canine in 12 of 15 (74%) specimens. However, beyond the estimated age of 3 only 2 of 4 premolars agreed with canines. Knudsen (1976) working in Idaho and Utah, found that 73% of 43 individuals were assigned the same age based on both the first premolar and canine. However, Roberts (1978) reported that these teeth agreed in only 4 of 8 (50%) Coyotes collected from south Texas. Where the age of an animal differed based on counts of cementum lines in canines and premolars, the premolar estimate was less than the canine estimate three times (4–3:C–PM, 6–4, 2–1) and greater twice (2–4, 2–3). Roberts (1978) also found no tendency for the premolar to over- or under-estimate the age of an animal when compared to the estimate from canines. My results and the results of these other studies support the view that, where possible, the canine should be used in age determination (Roberts 1978). Incremental lines in canines were more widely spaced, more easily counted and hence, likely to be more reliable. However, there is a clear need for studies of known-aged animals 3 years old and older to assess the comparative reliability of different teeth in age determination of Coyotes.

Coyotes were assigned the same age (to the nearest year) using both tooth-wear patterns and counts of canine cementum annuli in only 17 of 30 (57%) individuals (Figure 1). Tooth-wear patterns accurately estimated the age in 15 of 20 specimens aged 1 and 2 years by cementum annuli in canines. However, age as

<table>
<thead>
<tr>
<th>Number of annuli</th>
<th>Canine and premolar</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Agree</td>
</tr>
<tr>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>1</td>
<td>5</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>4</td>
<td>-</td>
</tr>
<tr>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>-</td>
</tr>
<tr>
<td>7</td>
<td>-</td>
</tr>
<tr>
<td>8</td>
<td>1</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>14</strong></td>
</tr>
</tbody>
</table>
determined by tooth-wear patterns agreed with counts of cementum annuli in only 2 of 10 specimens 3 years old and older. Tooth-wear patterns generally under-estimated the age of 3+ coyotes by one or two years. Linhart and Knowlton (1967) also reported that ages assigned by relative tooth-wear classes generally under-estimated the age of older animals (i.e., 5+).

To summarize, where high accuracy in age determination is required, as for example in studies of population dynamics, analysis of the canine tooth is preferred. However, the first premolar may be used when extraction of a canine is not feasible, as for example in long-term studies of behavioural ecology (Bowen 1978, 1981). Tooth-wear patterns were reliable only in determining the ages of pups and yearlings. In older coyotes this method generally under-estimated age by about one or two years. In general, the use of first premolars and tooth-wear patterns are good techniques, if an estimate to within one or two years is adequate.

Acknowledgments
I would like to thank Daphne Hards for sectioning coyote premolars and canines. Jack Plekhitis and Doug Stewart assisted with the field work. I am grateful to Dr. I. McT. Cowan for his support of this work. The research was funded by Dr. I. McT. Cowan from the National Research Council of Canada.

Literature Cited

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Bones from an Arctic Fox Den on Knight's Hill in Northern Manitoba

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Examination of bones surface-collected at entrances to an Arctic Fox (Alopex lagopus) den on Knight's Hill in northeastern Manitoba in the summer of 1979 suggests heavy reliance by den residents on the nearby and abundant Lesser Snow Goose (Anser c. caerulescens) colony, with a focus on very young individuals during the season of their availability.

Key Words: Northern Manitoba, Arctic Fox, Alopex lagopus, faunal analysis, food habits, Lesser Snow Goose, Anser c. caerulescens.

Two surface collections of animal bone lying at entrances to the Knight's Hill fox den were made in 1979: on July 7 by one of the authors (JCC) and on August 24 by R. Hurst and M. Leonard of the Churchill Northern Studies Centre.

Knight's Hill lies some 25 miles east of Churchill and 10 miles west of Cape Churchill, in the Hudson Bay lowlands, approximately ½ miles from the Hudson Bay coast to the north and east (see Figure 1 of Cooke et al. 1975). A glacial feature, this isolated hill with its truncated top and steep banks at the northern portion, is associated with the gravel ridge of an esker that extends, through low-lying semi-flooded tundra, some five miles in a general north-south direction from Watson Point. As a site on a stable surface deposit of silt and sand, well vegetated, elevated and gently sloping, the Knight's Hill den is typical of that described by Macpherson (1969) as favoured denning habitat for Arctic Fox populations in the central District of Keewatin, N.W.T.

Within a circle of approximately 20 metres in circumference, Hurst and Leonard discovered a total of 18 den entrances, many of which were at least partially hidden by dwarf willows (Salix spp.). They judged that six of these entrances had not been used for a number of years, but that others had been utilized within recent weeks or days, and concluded that at least some portions of the den were then in current use. Although no Arctic Foxes were seen at the time of either visit to the site, Fred Cooke (personal communication 1980) confirms that they occupied the den in 1979 but notes that they were wiped out, presumably by trapping, in 1980 and that the den was reported to have been taken over by Red Fox (Vulpes vulpes).

The 111 bones in the sample represent all bone visible on the surface of the ground at four entrances, only one of which appeared to have been used recently, and no scats were encountered. Identification to the lowest possible taxon is summarized by age classification in Table 1, from which it may be seen that the sample was 88.3% avian and 11.7% mammalian.

Based on bone morphology and cortical development, 52 of the avian bones (53%) represented individuals immature or juvenile and this accounts for the inability to identify most of them to species; the juveniles in this group (N=41) indicate chronological age up to approximately three or four months, but many of the bones appear to have come from individuals either just hatched or even not yet hatched. These findings, and the fact that some 60% of the avian bones identified were goose species, are not surprising since the abundant ground-nesting bird life in the Knight's Hill area includes both Canada Goose (Branta canadensis interior) and Lesser Snow Goose (Anser c. caerulescens), with a large colony of the latter less than two miles distant at La Pêrouse Bay. The report (U.S. Fish and Wildlife Service) on a band retained on the left tarsometatarsus of a skeletally immature Lesser Snow Goose indicated that it was a male banded on July 21, 1977 at La Pérouse Bay when it was too young to fly. Dr. Cooke (personal communication 1980) notes that many bands from the goose colony have been recovered at this den.

Goose bones categorized as immature or older include young of the year very late in the reproductive season as well as adults; the latter would be most susceptible to predation during the flightless molt period, usually in mid-summer. Of the eleven partridge bones present, only one exhibited skeletal immaturity; this may suggest fox predation between September and May when geese are unavailable. In this event, predation by Arctic Fox would most likely have occurred between the time dens are occupied about the end of March (Bansfield 1974) and the arrival of the geese, but other months cannot be excluded since some dens may be inhabited all winter (Macpherson 1969). However, there is no conclusive evidence for
Table 1. Summary of the Knight's Hill Fox Den Faunal Sample: Absolute Bone Frequencies Separated by Age Classification, and Estimated Minimum Numbers of Individuals

<table>
<thead>
<tr>
<th>Age Category*</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>Total</th>
<th>MNI</th>
</tr>
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<tbody>
<tr>
<td>Phenacomys intermedius</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Heather Vole</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Dicrostonyx torquatus</td>
<td></td>
<td></td>
<td>8</td>
<td>8</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>Collared Lemming</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Ondatra zibethicus</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Muskrat</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Canis</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>cf. Wolf</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Alopex lagopus</td>
<td></td>
<td></td>
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<td>1</td>
</tr>
<tr>
<td>Arctic Fox</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Pusa or Phoca sp.</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>cf. Ringed or Harbour Seal</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>1</td>
</tr>
<tr>
<td>Mammalian Total</td>
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<td>0</td>
<td>0</td>
<td>12</td>
<td>13</td>
<td></td>
</tr>
<tr>
<td>Branta canadensis</td>
<td></td>
<td></td>
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<tr>
<td>Canada Goose</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Anser caerulescens</td>
<td></td>
<td></td>
<td>23</td>
<td>29</td>
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</tr>
<tr>
<td>Snow Goose</td>
<td></td>
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</tr>
<tr>
<td>Anserinea</td>
<td></td>
<td></td>
<td>23</td>
<td>29</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td>* goose</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Anas sp. (small)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>cf. teal</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Anas sp. (large)</td>
<td></td>
<td></td>
<td>1</td>
<td>4</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>cf. Mallard/Black Duck</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
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<td>1</td>
</tr>
<tr>
<td>American Widgeon</td>
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</tr>
<tr>
<td>Somateria mollissima</td>
<td></td>
<td></td>
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<td></td>
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<td>1</td>
</tr>
<tr>
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<td></td>
<td>1</td>
<td>1</td>
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<tr>
<td>Anatidae</td>
<td></td>
<td></td>
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</tr>
<tr>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Lagopus sp.</td>
<td></td>
<td></td>
<td>1</td>
<td>10</td>
<td>11</td>
<td></td>
</tr>
<tr>
<td>cf. Willow/Rock Ptarmigan</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Avian unidentified</td>
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<td></td>
<td></td>
<td></td>
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<td>1</td>
</tr>
<tr>
<td>Avian Total</td>
<td>41</td>
<td>2</td>
<td>9</td>
<td>46</td>
<td>98</td>
<td></td>
</tr>
<tr>
<td>Sample Total</td>
<td>42</td>
<td>2</td>
<td>9</td>
<td>58</td>
<td>111</td>
<td></td>
</tr>
</tbody>
</table>

*1 = juvenile; 2 = juvenile to immature; 3 = immature; 4 = immature or older and adult.

This suggestion since the ptarmigan sample could not be separated with confidence into either Willow Ptarmigan (Lagopus lagopus) available year round, or Rock Ptarmigan (L. mutus) available between late October and the end of May (Jehl and Smith 1970).

Within the small mammalian sample, Collared Lemming (Dicrostonyx torquatus) dominates numerically, with a minimum of the three individuals present. Although the Meadow Vole (Microtus pennsylvanicus) is by far the commonest small mammal in the area (F. Cooke, personal communication 1980), it did not appear. This may be due to sampling error, but could also suggest that the sample represents a period of lemming abundance or that den residents en route to and from the Lesser Snow Goose colony at the coast tend to favour the higher and drier esker preferred by the Collared Lemming.

Although the time depth represented by the Knight's Hill sample and the percentage it represents of the total number of bones actually present on the entire den site are both unknown, it certainly contains the remains of more than one season and may well include bones deposited during more than a single year. Unfortunately, time was not available for a systematic collection at all den entrances, let alone excavation of the site. Under these circumstances, the species composition of the sample may not be representative of that for the entire den and its small size precludes any statistical analysis. As a consequence of small sample size the minimum number of
individuals present (MNI), calculated using both the most frequently-occurring bone and age categories, is also small (see Table 1), with many species represented by only a single bone. As an extension of these calculations, combining all goose (N=59) and all duck (N=16) bones gave MNIs of 6 and 4 respectively. It cannot, of course, be proved that all bones recovered are the remains of Arctic Fox predation when the time depth of the sample is unknown and the possibility exists that the den may have been occupied by Red Fox at some time prior to 1979. However, the information extracted from this sample may prove useful to workers researching predation patterns in general, while future studies of the subsistence strategies of Red Fox at this site may perhaps demonstrate characteristics that permit conclusions to be drawn regarding the agent(s) of the bone accumulation examined here.

Acknowledgments
For their valuable comments on a draft of this note, we thank Lorraine Brandson, Paul Catling, Fred Cooke, Allan Keast and Jim Rising.

Literature Cited
Macpherson, A. M. 1969. The Dynamics of Canadian Arctic Fox Populations. Canadian Wildlife Service Report Series No. 8, Department of Indian Affairs and Northern Development, Ottawa, pp. 8-10.

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Distribution and Breeding Status of Forster's Tern, *Sterna forsteri*, in British Columbia

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Forster's Tern (*Sterna forsteri*) was previously considered an accidental visitor in British Columbia. Four nests with eggs or young were found near Creston, British Columbia, in 1980, and at least seven others in 1981. Nesting began possibly in 1976, following the creation of suitable marsh nesting habitat. The provincial status of Forster's Tern should be rare, local summer resident.

Key Words: Forster's Tern, *Sterna forsteri*, British Columbia. distribution, breeding status.

Forster's Tern (*Sterna forsteri*) characteristically breeds in marshes from Texas to the Prairie Provinces and from Virginia to California (Bent 1921; Godfrey 1966). It has occurred casually or accidentally in British Columbia (Godfrey 1966; A.O.U. 1957; Campbell 1977, Checklist of British Columbia Birds, British Columbia Provincial Museum, Victoria), but has previously not been known to nest in Canada west of the Rocky Mountains. This paper reviews sight records and documents the first breeding record in British Columbia. We are aware of only seven occurrences of Forster's Tern in British Columbia besides those seen near Creston (Table 1). More than 40 sightings of Forster's Terns were made in the Creston Valley Wildlife Management area west of Creston, British Columbia, from May through August 1980. Maximum number seen on one occasion was 21 at Duck lake on 25 May 1980, but most sightings were of fewer than three birds.

White terns have been seen in the vicinity of Duck Lake near Creston since 1974 and there are observations which suggest nesting may have occurred there from 1976. Nests of white terns were found at Duck Lake as follows: two on 1 June 1976, and single nests on 7 June 1977 and 18 June 1979. On 26 July 1979, adult and juvenile Forster's Terns were first identified at the south end of Duck Lake in the company of Common Terns (*Sterna hirundo*).

The first identified Forster's Tern nest and eggs were found in a 370 ha Typha marsh at the south end of Duck Lake, 15 km northwest of Creston, on 31 May 1980. Another four Forster's Tern nests were found nearby, about 85 m south of the Duck Lake cross dyke. One was empty, predation had occurred at

**TABLE 1. Locations of Forster's Tern seen in British Columbia.**

<table>
<thead>
<tr>
<th>Location</th>
<th>Date</th>
<th>Numbers (Age)</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>Okanagan Lake</td>
<td>24 June 1928</td>
<td>3</td>
<td>Brooks (1942)</td>
</tr>
<tr>
<td>Nelson</td>
<td>Autumn 1943</td>
<td>18 (immatures)</td>
<td>W. J. Merilees (pers. comm.)</td>
</tr>
<tr>
<td>Osoyoos Lake</td>
<td>10 June 1974</td>
<td>1</td>
<td>R. A. Cannings (pers. comm.)</td>
</tr>
<tr>
<td>Vancouver</td>
<td>7-8 September 1974</td>
<td>1 (immature)</td>
<td>B. Kautsk (unpublished notes)</td>
</tr>
<tr>
<td>Lightning Lake</td>
<td>20 September 1974</td>
<td>2 (immatures)</td>
<td>Crowell and Nehls (1975)</td>
</tr>
<tr>
<td>Nicola Lake</td>
<td>20 September 1978</td>
<td>2 (2 adults, 3 immatures)</td>
<td>D. W. Goudie (unpublished notes)</td>
</tr>
<tr>
<td>Shuswap Lake Region</td>
<td>Before 1979</td>
<td>No data</td>
<td>J. E. V. Goodwill (unpublished notes)</td>
</tr>
<tr>
<td>Vancouver</td>
<td>21 August 1979</td>
<td>1</td>
<td>Becham et al. (1979)3</td>
</tr>
</tbody>
</table>

1Creston sightings not included

2Godfrey (1966) reported this sighting as 3 August 1938; however, this latter date was Brooks' (1942) record for Franklin's Gull (*Larus pipixcan*) (W. E. Godfrey, personal communication).

another (eggshell in British Columbia Provincial Museum, BCPM No. 1982), the third held two luke-warm eggs and the fourth nest contained three warm eggs. The two-egg clutch was lost by 15 June, but the three-egg clutch pipped on 19 June and hatched two young on 20 June. Those two chicks were dead in the nest on 23 June and were collected (BCPM No. 16721). Nests of *Equisetum* sp. stems on grassy hummocks were located in 12-22 cm of water. Nearest internest distances were 5.6 m, 7.0 m, 7.8 m, and 26.0 m (mean 11.6 m). A fifth nest, found on 16 June, held three abandoned eggs. Those three eggs were collected (BCPM No. 1982). At least five other nests of white terns, some with eggs, were found by Stushnoff on 9 June 1980 in another part of the same marsh.

Photographs of eggs and chicks have been deposited in the British Columbia Provincial Museum photo-duplicate file (No. 530) (Campbell and Stirling 1971).

One immature Forster’s Tern was seen at Duck Lake on 12 and 13 August and fifteen more were seen on 28 August at the south end at Kootenay Lake.

In 1981, at least nine nests were found. Four nests were known to contain three eggs, two with two eggs and one with none (B. Chapman and S. Roberts, personal communication). The status of two other nests is unknown. Only two nestlings were observed, one in each of two nests, and one of these young is known to have died (B. Chapman, personal communication). One immature was observed by Stushnoff at Duck Lake on 8 July.

Forster’s Tern is a common summer resident in southern Idaho and occurs less commonly in eastern Washington (Jewett et al. 1953, Burleigh 1972). Burleigh (1972) gave no breeding or migration records of this tern in northern Idaho, but Rogers (1972) reported a sighting at the Kootenai National Wildlife Refuge (NWR), Idaho, about 35 km south of the Canada-United States border and 50-60 km from Duck Lake. Two individuals were seen on the same Refuge on 30 May 1980 (Rogers 1980). One of the major factors restricting Forster’s Tern distribution in the Cordilleran region may be suitable breeding habitat (Jewett et al. 1953, Burleigh 1972). Although there were extensive natural wetlands in what is now the Creston Valley Wildlife Management Area, Forster’s Terns were probably prevented from colonizing by the annual June flooding of the Kootenay River. Dying and water control to prevent flooding and enhance wildlife habitat appears to have provided suitable nesting habitat for Forster’s Tern in the Creston Valley. Impoundment of the marsh at Duck Lake was initiated in 1970-71, and by 1973 major stands of Common Cattail (*Typha latifolia*) and Reed Canary Grass (*Phalaris arundinacea*) had appeared in wet sites (B. Stushnoff, unpublished report). The latter date is close to the first observation of white terns in the area.

The present observations extend the known breeding range of Forster’s Tern. The nearest nesting records are Stobart Lake, Alberta (Salt and Salt 1976), some 310 km northeast of Duck Lake, Nine-pipe NWR, Montana (270 km SE), and at Brook and Moses Lake, Washington (280+ 300 km SW).

We suggest that the status of Forster’s Tern in British Columbia is now that of a rare, local summer resident.

**Acknowledgments**

The Creston Valley Wildlife Management Authority allowed Goossen and Butler access to the Duck Lake nesting area. R. W. Campbell provided museum specimen and photoduplicate numbers. M. K. McNicholl advised us on field studies. Various drafts were typed by B. Goossen. D. R. Flook, J. B. Gollop and J. Grant provided comments to improve the publication. We thank all of you.

**Literature Cited**


Brooks, A. C. 1942. Additions to the distributional list of the birds of British Columbia. Condor 44: 33-34.


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A Brown Bear (*Ursus arctos*)-Human Encounter in the Brooks Range, Alaska

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A Brown Bear (*Ursus arctos*)-human encounter involving physical contact ended with no injury, and several observations of Brown Bear threat posture and behavior were documented.


Large carnivore-human encounters involving physical contact are infrequent and only a few eyewitnessed accounts exist in scientific literature. Bardack (1967) described an encounter with a Brown Bear (*Ursus arctos*) that resulted in physical contact but with little injury, and Munthe and Hutchison (1978) reported a Wolf (*Canis lupus*) encounter involving physical contact. The following account describes a Brown Bear-human encounter where the human initiated the physical contact.

The incident occurred on a steep hill near the confluence of the Glacier and the North Fork of the Koyukuk rivers (67°20'N, 150°40'W). The hill was appointed with numerous rock outcroppings and covered primarily with *Dryas* sp., a variety of lichens, and alder bushes. About half way up the hill I noticed a Brown Bear approaching at a gentle gallop from behind an outcrop at about 75 m distance. I was armed only with a small explosive device designed to startle roosting birds. This device had worked well when used to dispatch other Brown Bears, but in this instance it proved ineffective. Within moments the bear had approached to within 10 m. The bear was not fully grown, weighing in my estimation 80 to 90 kg and measuring 1.4 to 1.5 m from nose to tail.

When the bear began its first approach, I maintained my position, shouted and waved my hands overhead. This had no deterrent effect. As the bear came within 4 m, I threw several softball-sized rocks toward it. The bear retreated briefly but approached again, circling me with a radius of about 4 m. While circling with its head held low, it began to hiss and gnash its teeth audibly. Suddenly the bear directed an attack toward an alder bush, and with a guttural growl, shredded the bush with its fore-paws. Then the bear retreated slowly, and turning, sat on its haunch, and watched me from 15 m away. I took this opportunity to back slowly down the hill. When I had about doubled the distance between us, I turned and began bounding down the hill. I soon realized that this was not an effective strategy; the bear gave chase and was gaining ground. I turned and held my position again and the bear repeated its circling, hissing and gnashing behavior. After seemingly redirecting its aggression toward another alder bush, it began circling again but with an ever-decreasing radius, and soon was within arms reach. Out of desperation, I sharply slapped the bear across the snout with an open, gloved hand. The bear turned and ran about 15 m uphill where it turned, sat on its haunch, and stared at me.

About 30 sec later the bear began to approach again and I expected a direct attack. I drew a small folding knife, assumed a low stance with feet apart, knees bent, arms out-stretched, and maintained continuous eye contact. The bear circled and attacked yet a third bush. But after several revolutions it again retreated uphill 15 m, turned and watched me for about 30 sec, then retreated another 15 m. I maintained my position and eye contact. It continued its retreat in increments of about 15 m, stopping only to glance backwards. Within minutes the bear was over a ridge and out of sight.

Encouragement to write this article was offered by R. M. Mengel and R. S. Hoffman of the Natural History Museum of the University of Kansas, and review of the first draft was provided by R. M. Mengel.

**Literature Cited**


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Terrestrial Amplexus in the Wood Frog, *Rana sylvatica*

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Amplexus pairs of the Wood Frog, *Rana sylvatica*, were observed on land at three sites in eastern Ontario on nights in 1981 and 1982 when large numbers of frogs were moving towards aggregations of calling males. Terrestrial amplexus is a hitherto unreported aspect of the breeding behaviour of this species.

Key Words: Wood Frog, *Rana sylvatica*, breeding behaviour, amplexus.

The breeding behaviour of Wood Frogs (*Rana sylvatica*) has been well-studied, but pairs have only been reported to occur in the water (Banta 1914, Noble and Farris 1929, Berven 1981). Banta (1914) noted unsuccessful pursuit of females by males on land, but the observations reported here are the first record of terrestrial amplexus in this species.

In the evening of 1 April 1981 (2000-2030 hrs) many *Rana sylvatica* were breeding in a swampy maple (*Acer rubrum-A. saccharinum*) forest along Leeds County Road 6, 3.5 km NNW of Brockville, Ontario. The air temperature was 11.4°C and the water 10°C, the sky was overcast, and it had rained earlier in the afternoon. We saw hundreds of calling males and dozens of amplexant pairs in several aggregations in the 30-40 cm deep water on the west side of the road, but heard no calling from the swamp east of the road. We found 1 Blue-spotted Salamander, *Ambystoma laterale*; 2 Spring Peepers, *Hyla crucifer*; 1 American Toad, *Bufo americanus*; 1 Leopard Frog, *Rana pipiens*; and 29 *R. sylvatica* on the road. Among the *R. sylvatica* there were 4 amplexant pairs (all moving west across the road; NMC 21208-24-29), 9 unpaired males, and 12 unpaired females. All of the females had ovulated eggs in their oviducts. The road is raised about a metre above the level of the water, so the pairs were this much above, and at least several metres from, the water. We surmise that the females were clasped by silent males outside the groups of calling males, and then continued overland towards the calling. These pairs may well have formed in the water east of the road, so pair formation need not have been terrestrial.

Alerted by the 1981 observation, FWS observed terrestrial amplexus at two Grenville County, Ontario, sites on 16 April 1982. This was the first warm, sunny day of the spring, and *R. sylvatica* bred eruptively at many sites. Near Limerick Forest, 3 km SW of McReynolds, at 2200-2220 hrs, air temperature 16.5°C, *R. sylvatica* bred in a flooded pasture across a gravel road from a mixed swampy forest. Frogs were leaving the forest and crossing the grassy verge of the road to reach the chorus. Of 84 taken along the road, there were 12 amplexant pairs on land, 46 other males, and 13 other females. Six or 7 of the 13 females were in amplexus in shallow ditches and puddles along the road, and 3 or 4 of these were at the very edge of the water, so more than half of the females were paired before they were within 75 m of the breeding site. No calling was heard from the woods (which were not very flooded), so it seems likely that many of these pairs had formed on land. One *Ambystoma laterale* was also on the road, and many *Hyla crucifer* were calling from the flooded pasture.

Later that night (0130 hrs; air 14.5°C) another pair was found on a grassy road embankment 1.3 km NE of Oxford Station. It was 2 m above the surface of a pond bisected by the road, and there were choruses of *R. sylvatica* and Striped Chorus Frogs, *Pseudacris triseriata* in both halves of the pond.

The calls of a chorus of *R. sylvatica* presumably transmit information about a better-than-average oviposition site. Massed egg deposition increases the temperature and developmental rate of the eggs by trapping solar heat (Hassinger 1970), and may locally satiate egg predators (Cory and Manion 1953). It would be advantageous for a female to proceed to a chorus to lay eggs even after she had acquired a mate. The advantage to a male of obtaining a mate before entering the breeding mêlée is obvious.

Terrestrial amplexus is frequent among North American anuran species in which the male calls from terrestrial sites, presumably because females find males at their calling sites (many hyliids, some spadefoot toads, *Scaphiopus*; Wright 1914, 1932, Bragg 1965), but is rarely observed in those species which call only from the water (most *Bufo*, *Rana*, some *Scha-phiopus*; Wright 1914, 1932; Wright and Wright 1949; Bragg 1965; Licht 1969). Exceptions include pairs on land during frenzied breeding of *Bufo americanus* and Pickerel Frogs, *Rana palustris* (Wright 1914). FWS has observed a terrestrial pair of Western Toads, *Bufo
boreas (9 km E of the mouth of the Quatam River, B.C., 1 May 1977, NMC 18776), and Licht (1969) observed a Red-legged Frog, Rana aurora, × Spotted Frog, R. pretiosa, pair.

Among European species, most female Common Toads, Bufo bufo, arrive at the breeding ponds already clasped by a male (Davies and Halliday 1978), and arrival as pairs is frequent in Common Frogs, Rana temporaria (Savage 1934; Steward 1968), a species otherwise much like R. sylvatica in its breeding behaviour. This difference may be due to the more gradual onset of the European spring, as both European species are active before breeding, and may spend several days in amplexus before spawning. R. sylvatica and B. americanus breed more eruptively upon emergence from hibernacula, and terrestrial amplexus may occur only when spring breaks so suddenly that large numbers of both sexes are moving towards the breeding sites simultaneously.

Literature Cited


Steward, J. W. 1968. Arrival of frogs (Rana t. temporaria) and toads (Bufo b. bufo) at a breeding site. British Journal of Herpetology 4: 59–60.


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An Additional Morphological Character Useful in Distinguishing Two Similar Shrews Sorex monticolus and Sorex vagrans.

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Sorex monticolus and Sorex vagrans from southern British Columbia were found to differ in the number of small paired digital callosities. This character is potentially useful as an additional means of identification in areas of sympathy.

Key Words: Dusky Shrew, Sorex monticolus, Wandering Shrew, Sorex vagrans, identification, morphology.

The Dusky Shrew (Sorex monticolus) and the Wandering Shrew (Sorex vagrans) are morphologically similar and have for a long time been difficult to distinguish in certain areas where the two species occur sympatrically. The apparent lack of a clear-cut character separating the two and the convergence in size and color in areas of overlap were interpreted by Findley (1955) as evidence of introgression between the two forms and led him to the conclusion that they were conspecific.

Since then Hennings and Hoffmann (1977) described a diagnostic character involving the size and position of the small median cusp of the upper incisors relative to the red pigmentation of the tooth. In addition to this character, Hawes (1977) used tail length, color and odor of breeding males to distinguish the
species in the field in southwestern British Columbia.

All these characters have their limitations as discriminators. Hennings' and Hoffmann's tooth character for example is difficult or impossible to use in old adults with heavily worn teeth. Moreover in some areas of British Columbia, e.g. on Vancouver Island, the tooth pigmentation is very pale and reduced in some specimens. Tail length and color likewise have their limitations. It is true that in areas of sympatry in British Columbia the larger long-tailed subspecies of _S. monticolus_ can usually be distinguished from the smaller short-tailed _S. vagrans_ with a certain degree of probability. A comparison of tail lengths of _S. m. isolatus_ and _S. v. vancouverensis_ from Vancouver Island, and _S. m. setosus_ and _s. v. vagrans_ from the mainland of southwestern British Columbia revealed a probability of misidentification in the range of 0.08 to 0.11, or approximately one wrong identification out of 9 to 13 (van Zyll de Jong, unpublished data). Farther to the east in British Columbia, where _S. v. vagrans_ converges with the smaller shorter-tailed _S. m. obscurus_, the probability of misidentification using tail length increases to approximately 0.30, or one out of three incorrect identifications. It is obvious that the use of an additional morphological character to identify these two species would be desirable.

While examining samples of _S. monticolus_ and _S. vagrans_ from southern British Columbia in the collection of the National Museum of Natural Sciences, I found that the toes of _S. monticolus_ are relatively longer and possess a greater number of small paired digital callosities or friction pads than those of _S. vagrans_. This is especially evident in the toes of the hind feet (Figure 1). In _S. monticolus_ there are five or six paired friction pads on the second to fourth digit. In _S. vagrans_ the number never exceeds four. This character is easily seen in fresh or liquid preserved specimens, but is not well preserved and often difficult to discern in study skins as a result of drying.

I have not had an opportunity to study this character over the entire range of the two species and geographic variation in the number of paired friction pads is of course a possibility. The purpose of this note is to draw attention to this character so that others might evaluate it in other parts of the distributional range of the two species.

**Literature Cited**


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**Figure 1.** Left hind foot of _Sorex vagrans_ (left) and _Sorex monticolus_ (right) from British Columbia showing the difference in the number of paired digital friction pads.


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Common Twayblade, *Listera ovata* (Orchidaceae), in Wellington County, Ontario: A Second North American Record

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A locality with seven plants of the Common Twayblade, *Listera ovata*, in Puslinch Township, Wellington County, is 200 km SSE of the only other fully documented record of this species in North America. The new site differs in light intensity, soil type, moisture and temperature from the previous one.

Key Words: Common Twayblade, *Listera ovata*, Orchidaceae, new record, habitat.

On July 27, 1980, the authors discovered seven plants of Common Twayblade, *Listera ovata*, in the southwest corner of Puslinch Township, Wellington County. The colony was 70 m north of Galt Creek and 1.5 km southeast of Puslinch Lake, (43°24′N, 80°15′W). This site was approximately 200 km south-south-east of the original location, Red Bay in the Bruce Peninsula, where this species was first reported in North America (Elliott, 1969; Elliott and Cook, 1970).

The plants were growing on a gentle slope in deep cedar litter in full shade beneath White Cedars (*Thuja occidentalis*) approximately 8 m from the southern edge of a cornfield. No other companion species grew within 2 m of the colony, but nearby were occasional plants of Black Snakeroot (*Sanicula marilandica*), Helleborine (*Epipactis helleborine*), and White Birch (*Betula papyrifera*). On the date of discovery, the soil was dry. However, due to the close proximity of Galt Creek, the soil would likely be subject to seasonal fluctuations in water content.

The Puslinch Township site differed in light intensity, soil type, moisture and temperature, from the Red Bay locality. At the latter location some plants grow in full sunlight, the soil is sandy and consistently moist, and the temperature is cooler due to the close proximity of Lake Huron. One of us (A.B.A.) has found this species growing in a number of different habitats in Britain including railway embankments, roadsides and hedgerows. Luer (1975) recognizes the Common Twayblade as a “robust, aggressive and exceedingly common orchid weed found in many kinds of habitat” throughout Europe and Asia.

The largest of the four fruiting plants was 61 cm in height and bore 46 flowers. Two sterile plants were separated by 1.5 m from the main clump of five orchids. A specimen consisting of two flowers and a photograph were deposited in the University of

Guelph Herbarium (OAC 57717). *Listera ovata* is the largest of the *Listera* species found in North America with an inflorescence often exceeding 50 cm in height. Reference to Luer's key on *Listera* species will alleviate any confusion between depauperate specimens of this species and any of the native *Listera*.

It is unlikely that the orchids in Puslinch Township were derived from Red Bay as prevailing winds are from the west and probably would carry seed well to the north-east of Puslinch Township.

A previously unreported occurrence of *Listera ovata* in Wellington County is documented by a herbarium specimen (OAC 5806) but bears only the following data: *Listera convallarioides* (SW) Tor., Twayblade, moist woods. Underneath the label in pencil is written: *Listera convallarioides*, Twayblade, Wellington Co. This sheet was annotated to *Listera ovata* (L.) R. Br. by Paul Catling in 1976. Although the data for this earlier collection is incomplete with regard to collector, date of collection and locality, it possibly represents an earlier colony from which the Puslinch Township population established itself. The colony at Red Bay has spread only locally, several hundred meters downwind of the location where this species was first discovered in 1968.

Apart from its adventive existence in North America, *Listera ovata* occurs throughout most of Eurasia from Ireland and Great Britain eastward to Siberia, and from Scandinavia southward to India. Helleborine (*Epipactis helleborine*), another Eurasian species of orchid, was first found in North America at Syracuse, New York, in 1879, spread to Toronto in 1890 and subsequently has spread to or established itself in most areas in central North America. If *Listera ovata* follows the same pattern of spread as did Helleborine, it can be expected to appear in a number of locations, spreading locally at first and then becoming more widespread. However, the initial pattern of spread of *Listera ovata* in rural areas differs from that of *Epipactis helleborine* which was first observed close to urban localities. Its future in North America presumably will be determined by specific requirements for mycorrhizal fungi and by reproductive factors.

**Acknowledgments**

We thank Dr. D. M. Britton for reviewing an earlier draft of this note and Mr. R. E. Whiting for measurement data. We also acknowledge the assistance of Mr. E. W. Eaton, of the Pathology Department, University of Guelph, for photographic prints.

**Literature Cited**


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Fraie du Touladi (Salvelinus namaycush) en très faible profondeur

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Nous décrivons la distribution des œufs en fonction de la profondeur sur une frayère de Touladi située au lac David dans le sud-ouest du Québec. Des œufs furent trouvés sous 12 à 95 cm d'eau, dans un épais substrat de moellons. Les densités maximales furent observées dans moins de 60 cm d'eau. Les données recueillies suggèrent le fait que l'épaisseur du substrat peut influencer le choix des sites de fraie.

Mots clés: Touladi, Salvelinus namaycush, frayères

We describe egg distribution in relation to depth on a Lake Trout spawning ground located at David Lake in southwestern Québec. Eggs were found in 12 to 95 cm of water in a thick rubble bottom. Maximum densities were observed in water less than 60 cm. Data seem to indicate that thickness of the substrate can be important in the choice of spawning ground.

Key Words: Lake Trout, Salvelinus namaycush, Spawning ground

La fraie du Touladi a déjà fait l'objet de nombreuses descriptions. Bien que, dépendant du plant d'eau, une large gamme de profondeurs (0,2-110 m) et de substrats (argile, gravier, moellons, blocs) soient utilisés, le Touladi préfère généralement des sites dont la profondeur est inférieure à 10 m et le substrat de gravier et de moellons (Scott et Crossman 1974; Machniak 1975; Martin and Olver 1980). Des observations faites au lac David, dans le sud-ouest du Québec, permettent d'élargir la gamme des profondeurs utilisées et apportent des précisions sur l'importance de l'épaisseur du substrat.

Aire d'étude et méthodes

Le lac David (comté de Pontiac; 46°29'N, 76°27'O) est un lac profond (Z_{max} = 50 m), de superficie moyenne (757 ha) dont le littoral est en pente généralement très abrupte. Un inventaire des sites potentiels de fraie sur les premiers 10 m de profondeur fut réalisé par deux plongeurs au cours de l'été 1980. Vingt km de berge furent couverts en 12 heures de plongée. Le nombre de sites répertoriés fut très limité. Le fond du lac est généralement sablonneux; les zones d'enrochement sont très rares et de superficie restreinte.

L'utilisation de ces sites ne fut confirmée que pour un seul de ceux-ci par des observations visuelles au moment de la fraie. Les observations se firent de nuit, à la lumière artificielle, et de jour, en plongée, les 20 et 21 octobre 1980 (T° de l'eau de surface: 9,5°C). Nous avons ainsi pu délimiter la frayère, décrire le substrat et estimer la densité relative des œufs en fonction de la profondeur de l'eau. Les décomptes d'œufs furent faits de la manière suivante. Les roches étaient soulevées une à une et le plongeur estimait d'après cinq calses de densité (0, aucun; 1, entre 1 et 5; 2, entre 6 et 10; 3, entre 11 et 20; 4, plus de 20) le nombre d'œufs qu'il était en mesure de voir dans le champ visuel délimité par l'opposition des pouse et index de chaque main. La figure ainsi formée à l'allure d'un pique de carte à jouer et une superficie approximative de 60 cm².

Résultats et discussion

La frayère localisée a une superficie d'environ 400 m². Elle est située sur la rive est du lac, à même la beine. Il s'agit d'une étroite bande, d'environ 3 m de large, légèrement dentelée. Elle est exposée aux vents originant du nord, de l'ouest ou du sud. La pente y est moyenne (15 à 20°). Elle devient par contre très abrupte immédiatement au large de la frayère. La profondeur maximale du site avant la modification de la pente est de 1,2 m. Le substrat est principalement

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TABLEAU 1. Distribution des œufs de Touladis en fonction de la profondeur.
composé d'un mélange en proportions égales de moëllons de 8 à 10 cm et de 15 à 20 cm de diamètre. L'épaisseur de ce substrat atteint 40 à 50 cm au bord et diminue graduellement jusqu'à devenir nulle dans la partie la plus profonde. Aucun des autres sites répertoriés n'offrait ces caractéristiques. Le substrat y était ou de gravier, ou, au contraire, de blocs de grande taille.

Le patron de distribution des œufs en fonction de la profondeur apparaît au tableau 1. Bien que le nombre d'observations soit limité, il y est clairement démontré que les plus fortes densités, qui correspondent à plus de 3,5 œufs/10 cm², se trouvaient dans moins de 60 cm d'eau et que même entre 12 et 20 cm, cette densité était assez élevée (2,5 à 3,5 œufs/10 cm²). Ces densités sont de beaucoup supérieures aux densités moyennes rapportées par Martin (1957) pour les lacs du parc Algonquin (0,5 œuf/10 cm²) et par Royce (1951) pour le lac Otsego (0,2-0,5 œuf/10 cm²). La profondeur minimale à laquelle nous avons trouvé des œufs fut 12 cm. Plusieurs groupes de deux à cinq géniteurs de grande taille (>T70 cm) furent d'ailleurs aperçus longeant la rive immédiatement au bord, le dos complètement hors de l'eau.

D'après nos observations, les œufs s'infiltraient profondément dans le substrat; nous en avons trouvés jusqu'à 35 cm environ. La petite taille et la forme arrondie des pierres sur la frayère favorisent cette infiltration. La densité relative des œufs diminue à mesure que la profondeur de l'eau augmente et que l'épaisseur de dépôt de roches diminue. Il est généralement reconnu que la nature du substrat influe sur le choix des sites de fraie. Les observations faites au lac David suggèrent le fait qu'il peut en être ainsi de son épaisseur. La détermination de cette dernière par le poisson est possible puisqu'il est en mesure de percevoir des changements de réflexion des ondes acoustiques sur le substrat (Brown 1957).

Remerciements
Nous tenons à remercier nos collègues F. Cotton, M. Dubreuil et H. Fournier pour la critique du manuscrit initial et D. Chartrand pour sa participation aux travaux sur le terrain.

Références

Reçu le 4 avril 1981
Accepté le 5 juillet 1982

Range Extensions for Eight Species of Plants in the Lake Iliamna Region, Alaska

ALBERT G. WESTERMAN

Thomas Hunt Morgan School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506


Collections from four sites in the Iliamna Region, Alaska, made in August 1978 and 1979, contained 107 species of plants. Eight were new to the area.

Key Words: Flora, Iliamna, Alaska, range extensions.

Eight of 107 species of plants collected at four sites in the vicinity of Lake Iliamna, Alaska, were new to the area. Collections were made in August 1978 and 1979 and voucher specimens deposited in the herbarium of the Thomas Hunt Morgan School of Biological Sciences, University of Kentucky, Lexington, Kentucky 40506. Sources used to delineate known ranges were Osgood (1904), Martin and Katz (1912),
Smith (1917), Williamson and Peyton (1962) and Hulten (1968).

Collections were made at two sites near Iliamna Village and two on islands in Lake Iliamna, approximately 59° 45' N, 154° 45' W, as follows: I, Iliamna Village, within a 3.2 km radius of the village at an elevation ranging from 36-61 m; 2, Portage Road, within 400 m of the road and along its 12.9 km length at elevations of 61-122 m; 3, Rabbit Island, 4.3 km by 1.6 km at elevations of 36-50 m; and 4, Porcupine Island, within a 2 km radius of the Fisheries Research Institute of University of Washington Biological Station at elevations of 45-61 km.

Range extensions were as follows: Lycopodium c. clavatum (Common Club Moss), 257 km E; Equisetum fluviatile (Swamp Horsetail), 241 km N; Hordeum jubatum (Squarreltail Grass), 338 km SW; Urtica iuryllii (Lyall Nettle), 209 km W; Actaea rubra (Baneberry), 64 km SE; Heuchera glabra (Alpine Alumroot), 96 km W; Empetrum nigrum (Crowberry), 241 km NE; and Cassiope stelleriana (Alaska Moss Heath), 177 km N. Nomenclature and systematics follow Hulten (1968).

James Petranke and Doris Westman assisted with the collections in 1979.

Literature Cited

Received 12 December 1980
Accepted 2 September 1981

Interactions Between Purple Martins, Progne subis, and Tree Swallows, Iridoprocne bicolor, in Quebec

JEROME A. JACKSON, BETTE J. SCHARDIEN, OPAH H. DAKIN, AND GEORGE C. KULESZA

Department of Biological Sciences, Mississippi State University, Mississippi State, Mississippi 39762


Purple Martins, Progne subis, and Tree Swallows, Iridoprocne bicolor, were observed defending nesting boxes at Drummondville, Quebec. At least one pair of Tree Swallows had a nest though apparently was not yet incubating. First-year male and female Purple Martins were searching for nest sites and defended one nest box against Tree Swallows in spite of the entrances being too small for the martins to enter. The nesting Tree Swallows physically attacked a martin that perched at their apartment entrance and pulled it from the perch.

Key Words: Purple Martin, Progne subis, Tree Swallow, Iridoprocne bicolor, nest site, interspecific territoriality.

On 10 June 1981 between 0700 and 0800 we watched numerous interactions between Tree Swallows (Iridoprocne bicolor) and Purple Martins (Progne subis) in Des Voltigeurs Park, Drummondville, Quebec. At least six Tree Swallows and six Purple Martins (females and first-year males) were present. The interactions took place at three multi-apartment bird houses which had entrances varying from approximately 2.6 to 3.8 cm in diameter as measured by holding a 2.5 cm wide stick at entrances. Purple Martins normally require cavity entrances greater than 5 cm in diameter (Wade 1966), and none was able to enter any apartment in spite of numerous and persistent efforts to do so by at least four of the martins. With each attempt the martin pushed vigorously with its feet as it flailed the air with its wings. Four martins defended one apartment house against Tree Swallows, not allowing them to land on it, in spite of the inability of the martins to make use of the apartments. A pair of Tree Swallows vigorously defended a second house against a lone first-year male martin as it tried to enter each apartment. The martin
was physically attacked by both Tree Swallows and pulled from the perch beneath the swallows' nest entrance (Figure 1). When the martin finally fell, it was pursued by the swallows, but quickly returned to perch elsewhere on the apartment house. Its head was missing many feathers and appeared to be bleeding.

Defense by both martins and swallows included aerial chases and much vocalization. In addition to the physical attack on the martin by the Tree Swallow pair, Tree Swallows repeatedly dove at martins perch behind the two houses not dominated by the martins. Throughout the observations a pair of House Sparrows (*Passer domesticus*) worked at constructing a nest in the house that was so strongly defended by the Tree Swallow pair. At least one Starling (*Sturnus vulgaris*) was also present within 10 m of the bird houses. In no instance did either martins or swallows interact with these other cavity competitors.

Tate (1963) reported a pair of Tree Swallows in Michigan that successfully nested in an apartment house which also contained two active Purple Martin nests. He discovered the association when there were small Tree Swallow young in the nest, and he noted no interactions between the species during three afternoons of observation. In that instance, the martins and swallows nested on opposite sides of the apartment house. During our observations the swallows had a nest and may have been laying, but we observed no indication of incubation or presence of young. The martins were obviously still searching for nest sites and were investigating all available apartments — including that occupied by the Tree Swallows. Thus, both species were at stages in the nesting cycle when time and "inclinations" for territory invasion and defense would have been greater than for the birds observed by Tate. In spite of the smaller size of Tree Swallows (ca 22 g vs ca 49 g; Hartman 1955), one might have expected them to prevail in the encounter with the martin because of their greater investment in the nest site. Competitive encounters of this type may

**Figure 1.** Two Tree Swallows attacking a first-year male Purple Martin perched at the swallows' nest entrance (left) and successfully pulling the martin from the perch (right).
indeed be a cause for the arrival of Tree Swallows on
the nesting areas before other swallow species (Tyler 1942). Tree Swallows are well known as feisty cavity
defenders (and usurpers) against other cavity nesting

Perhaps the most intriguing aspect of these observa-
tions was that the martins persisted with intense
competition for a resource that they could not use. All
male martins in the group were first-year birds, which
one might expect to be less successful in intraspecific
competition for nest sites and thus relegated to infe-
rior housing; they also might have less insight with
regard to nest site competitors and appropriateness of
nest sites. At Drummondville Purple Martins are near
the northern limit of their range (Godfrey 1966) and
scarcity of suitable nest sites may be a factor limiting
their distribution. Tree Swallows, however, extend
much farther north into Quebec and Labrador and are
probably much more abundant than Purple Martins
at the latitude of Drummondville. Erskine (1979) dis-
cusses the relative frequency of use of various types of
nest sites by both species and points out that martins
are now almost totally dependent on nest boxes in
eastern North America. In contrast, Tree Swallows
commonly use sites other than nest boxes. These dif-
fences in nest sites used seem to be related to the
coloniality of the martins, their requirements for
larger cavity entrances, and human destruction of
old-growth trees which might provide the multiple
woodpecker holes which would allow colonial nest-
ing. Thus, it would seem that if man is to provide
nesting boxes for either species, certainly the Purple
Martin has the greater need; the Tree Swallows will
use boxes with the larger entrances.

**Literature Cited**

Bird-Banding 6: 45–57.

Erskine, A. J. 1979. Man’s influence on potential nesting
sites and populations of swallows of Canada. Canadian

Museum of Canada Bulletin no. 203.

Hartman, F. A. 1955. Heart weight in birds. Condor 57:
221–228.

Hersey, F. S. 1933. Notes on Tree Swallows and Bluebirds.
Auk 50: 100–110.

Tate, J., Jr. 1963. Tree Swallow nesting in martin colony.
Wilson Bulletin 75: 278.

Tyler, W. M. 1942. *Iridoprocne bicolor* (Viellot). Tree
Swallow. Pp. 384-400, in *Life Histories of North Ameri-
can Flycatchers, Larks, Swallows, and Their Allies*. By

Wade, J. L. 1966. What you should know about the Purple

Zeleny, L. 1976. The Bluebird. Indiana University Press,
Bloomington, Indiana.

Mink, *Mustela vison*, Attacks Trumpeter Swan,
*Cygnus buccinator*, Cygnet

TIMOTHY D. SIFERD

Alberta Environment, 9926 111 Avenue, Grande Prairie, Alberta T8V 4C3
Present address: Box 51, Oyen, Alberta T0J 2J0


Attempted predation by a Mink, *Mustela vison*, upon a young Trumpeter Swan, *Cygnus buccinator*, is documented
apparently for the first time. It was unsuccessful because of defense by parents and the size of the cygnet.

Key Words: Mink *Mustela vison*, Trumpeter Swan, *Cygnus buccinator*, predation.

Mink (*Mustela vison*) are potential predators of
Trumpeter Swans (*Cygnus buccinator*; Hansen et al.
1971; Shea 1979). But such an event apparently has
not been documented. This note describes an attack
by a Mink upon this species.

On 17 August 1979, I was observing a family group
of Trumpeter Swans (two adults, three cygnets) on
Dickson Lake (53°31’N, 119°52’W), 140 km north-
west of Grande Prairie, Alberta. The swans were
observed at a distance of 800 m with a 40x spotting
scope. The 8-week old cygnets were approximately
two-thirds adult size.

At 1320 (MDT), the cygnets were feeding < 1 m
apart near emergent vegetation (*Carex* spp.) which
bordered the open water. The adult female (identified by a neck collar) was loafing 20 m away, and her mate was feeding 5 m from the cygnets. The behavior of the swans appeared normal.

At 1321, one cygnet turned quickly and swam toward open water; a Mink was biting the side of its head. The cygnet held its head close to the water and flapped its wings towards the Mink.

The adult male responded to the attack by assuming a threat posture (wings spread without flapping; Johnsgard 1965) as he approached the cygnet. The male made one attempt to hit the Mink with his breast; then the adult female repeatedly attempted to hit the Mink with her breast and wrists. Based on the positions and activities of the adults, it appeared that the female drove off the Mink, which presumably escaped into the emergent vegetation.

Following the defence of the cygnet, which had lasted approximately 40 s, the adult swans performed a triumph ceremony (Johnsgard 1965). The male then patrolled the attack area for 30 s while maintaining a threat display. Finally, the family swam away from the area, but apparently did not avoid the emergent vegetation which had harbored the predator. The attacked cygnet remained < 1 m from the female for approximately 2 h, and did not feed. By 1530, the behavior of all the swans again appeared to be normal.

During the attack, the cygnet sustained a cut approximately 3 cm long behind the right eye and, within 1 h, a noticeable lump developed near the cut.

However, when the cygnet was banded 26 days later, there was no obvious scar tissue so apparently it had not been seriously injured by the Mink.

This observation suggests that Mink may opportunistically prey upon large cygnets. However, successful predation by Mink probably occurs mainly when a cygnet is small enough to be killed quickly (as suggested by other authors), or possibly when a large cygnet is not defended by its parents (see Shea 1979).

Acknowledgments

This observation was made while I was employed by Alberta Environment, Planning Division (Grande Prairie). I thank G.R. Holton, M.R. Lein, M. Rothfels and anonymous referees for reviewing drafts of this manuscript.

Literature Cited


Received 1 December 1981
Accepted 12 May 1982.
News and Comment

Call for nominations for the Council of the Ottawa Field-Naturalists' Club

A nominating committee has been chosen by the Council to nominate persons for election to offices and membership of the Council for the year 1983, as required by the Constitution.

Club members may also nominate candidates as officers and other members of Council. Such nominations require the signatures of the nominator and seconder, and a statement of willingness to serve in the specified position by the nominee. Nominations should be sent to the Nominating Committee, The Ottawa Field-Naturalists' Club, Post Office Box 3264, Postal Station C, Ottawa, Ontario K1 Y 4J5, to arrive no later than 15 December 1982.

The Committee will also consider any suggestions for nominees which members wish to submit to it by 15 December 1982. It would be helpful if some relevant background on the proposed nominees were provided along with the suggested names.

W. K. GUMMER
Chairman, Nominating Committee

The Biographical Dictionary of North American Environmentalists

The *Biographical Dictionary of North American Environmentalists*, edited by Keir B. Sterling of Pace University, Pleasantville, New York, is scheduled for publication by Greenwood Press in 1984. The work will cover Canada, the United States and Mexico, and will include detailed biographical sketches of some 700 individuals prominent in the environmental sciences and related fields from 1500 to 1970. They need not have been native to North America, but the major portion of their careers should have been closely identified with it.

The individuals listed will include: explorers responsible for published works on the geography and natural history of North America, geographers, conservationists, wildlife management specialists, park planners, administrators of national parks and forests, other government officials concerned with environmental matters, museum officials whose work had to do with environmental questions, ecologists, biogeographers, mammalogists, ornithologists, herpetologists, ichthyologists, entomologists, invertebrate zoologists, botanists, and naturalists.

While some Canadian subjects have been identified, there are a number of others who are deserving of inclusion. There are undoubtedly many of whom the editor is unaware, but who should be listed. The editor welcomes suggestions of suitable subjects and the names of those willing to write the sketches of them. Very modest compensation can be arranged. Please write Sterling at 31 Chestnut Street, Rhinebeck, N.Y., 12572, USA.

Notice of The Ottawa Field-Naturalists' Club Annual Business Meeting

The 104th Annual Business Meeting of the Ottawa Field-Naturalists' Club will be held in the auditorium of the Victoria Memorial Museum Building, Metcalfe and MacLeod Streets, Ottawa on Tuesday, 11 January 1983, at 2000.

FRANK POPE
Recording Secretary

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Grants Available for Bird Projects

The James L. Baillie Memorial Fund for Bird Research and Preservation invites applications for grants to support projects on Ontario birds in 1983.

The Fund's aim is to encourage field studies by amateur naturalists and to support projects which increase or disseminate knowledge of birds in their natural environment or contribute to their preservation. Priority will be given to projects which draw on the resources of volunteer naturalists in conducting research or fieldwork and to applicants who do not have access to other sources of support.

Two types of grants will be offered in 1983: (a) Project Grants and (b) Atlas Fieldwork Grants. Any project which has a volunteer component and otherwise meets the Fund's objectives is eligible for a type (a) grant. Type (b) grants provide partial support for travelling expenses to remote central and northern areas for fieldwork on the Ontario Atlas of Breeding Birds.

Grants do not normally exceed $750. Applications for Project Grants are due by 31 December 1982 and for Atlas Fieldwork Grants by 21 February 1983. All applications should be submitted on forms obtainable from the Secretary, The James L. Baillie Memorial Fund, c/o Long Point Bird Observatory, P.O. Box 160, Port Rowan, Ontario N0E 1M0.

The James L. Baillie Memorial Fund approved 10 Project Grants totalling $5071 and five Atlas Fieldwork Grants totalling $2000 in 1982. The Fund is financed in part from proceeds of the Baillie Birdathon. Donations to the Fund are tax deductible and may be sent to the address given above.

Errata


On page 69 in line 1 of abstract, “. . . studied on Elk Island . . .” should read “. . . studied in Elk Island . . .”

On page 71 (left column) in line 37, “. . . each 25-m transects . . .” should read “. . . each 25-m transect . . .”.

On page 71 (left column) in line 43, “. . . analyses of variances” should read “. . . analyses of variance”.

On page 72 (left column) in line 24 of Results, “. . . development of” should read “. . . development on”.

On page 73, Table 2 under “Moose pellet group density” within “Lowland” habitat and the row for “Total” distance from trails, a horizontal line should appear under 6 and 4 (i.e. 6 4) between “Light” and “Heavy” levels of human use.

On page 73, Table 2 in footnote 1, “. . . pp. 71-72” should read “. . . p. 71”.

On page 74, Table under “Relative Moose track density” within “All habitats” and the column for “Total” level of human use, a vertical line should appear to the right of 4 and 6 (i.e. 4 6) between “1-500” and “501-1600” distance from trials.

On page 74, Table 3 in footnote 1, “. . . p. 72” should read “. . . p. 71”.

On page 75, Table 5 in footnote 1, “. . . p. 9” should read “. . . p. 71”.
Report of Council to the 103rd
Annual Business Meeting of
The Ottawa Field-Naturalists’ Club
12 January 1982

Minutes of the 102nd Annual Business Meeting of The Ottawa Field-Naturalists’ Club

Auditorium, Victoria Building, National Museum of Natural Sciences, Metcalfe Street, Ottawa; 13 January 1981, 2000 h,

Chairman: Dr. R. Taylor, President, Ottawa Field-Naturalists’ Club.

Others Present: The meeting was called to order with 46 members in attendance, satisfying the requirements for a quorum. The ultimate attendance was 53.

1. Minutes of the Previous Meeting:
   D. F. Brunton, Recording Secretary, read the minutes of the 101st Annual Business Meeting. It was moved by F. Pope, (2nd, P. Hall) that the minutes be approved, with the following amendments:
   — pg. 2, 6th last line — Ewen, not Ewan.
   — pg. 2, last line — Vice-president, not Vice-chairman.

   (Motion carried)

2. Business Arising From the Minutes:
   (a) OFNC Assets — R. Taylor directed members to the discussion of this in the Annual Report of Council. Council is examining a variety of possible OFNC projects which would utilize these assets, including the establishment of a permanent OFNC office and the establishment of an OFNC scholarship.
   (b) Macoun Autobiography — although sold initially for $10.00 to members, the book is now priced at $12.50.
   (c) Nakkertok Ski Club — a number of OFNC members have visited the land in question and enjoyed the experience. There seems to be little interest in formalizing the relationship between Nakkertok and the OFNC.

3. Correspondence:
   (a) Ottawa Valley Mineral Association — notice has been received that their next meeting would be held on 15 January 1981 and that OFNC members would be welcomed.
   (b) Ontario Provincial Parks Council — notice has been received that a conference to discuss the future of Ontario Provincial Parks will be held in May 1981 at Waterloo.

4. Finance:
   (a) The auditor’s report (prepared by F. M. Brigham) was presented.
   (b) The overall financial situation of the OFNC is good and the club has enjoyed another successful year.
   (c) H. Thomson queried the figure of $156 listed for life members. Henson suggested that this was probably related to the CFN allocation formula.
   (d) W. Gummer moved (2nd, Gilliatt) that the financial statement be approved.

   (Motion carried)

5. Report of Council:
   R. Taylor and OFNC Vice-president H. L. Dickson read the Report of Council for those present. It was moved by E. Dickson (2nd, D. Laubitz) that the report be accepted with the following amendment:
   — there were 5 (not 4) issues of Trail & Landscape in 1980.

   (Motion carried)

6. Nominations
   (a) C. Gilliatt read out the slate of 1981 Council nominations (as prepared by the Nominations Committee) as follows:
      President — R. Taylor
      Vice-president — H. L. Dickson
      Treasurer — B. Henson
      Recording Secretary — F. Pope
      Corresponding Secretary — W. Gummer
   Other Members:
      F. Bell C. Gilliatt
      R. Bedford F. Goodspeed
      D. Bewley J. Jackson
      D. F. Brunton D. Laubitz
      W. J. Cody A. Mason
      S. Darbyshire C. Montgomery
      E. Dickson K. Strang
      K. Taylor
   It was moved by C. Gilliatt (2nd, D. Bewley)
that the slate of nominations be approved.

(Motion carried)

(b) E. Dickson noted that at least one nomination was offered from the membership at large.

(c) R. Taylor thanked retiring Council members R. A. Foxall, P. Hall, J. D. Lafontaine and H. Mackenzie for their efforts on behalf of the OFNC. He noted that Foxall and Mackenzie were past-presidents of the club and also performed important services as chairman of the Ad Hoc Publications Committee and Centennial Committee respectively.

(d) R. Taylor thanked D. F. Brunton, who is retiring from the Recording Secretary position, for his efforts in that regard.

(e) R. Taylor introduced the new members of Council to the membership and also offered particular thanks to W. J. Cody, the longest sitting member of Council.

7. Nomination of Auditor:
C. Gilliatt moved (2nd, K. Taylor) that F. M. Brigham be appointed OFNC auditor for 1981.

(Motion carried)

8. New Business
(a) Raccoon dogs — R. Taylor reported that recent information has exposed the fur farmer wishing to hold these animals as an agent for a Finnish company (Supi). This is apparently a common ploy used to get around Foreign Investment Review Board regulations. There is reason to be optimistic that these potentially dangerous animals will yet be returned to Europe. Strong legislation, intended to avoid such situations developing in the future, is presently being drafted. The role of the OFNC in this issue has been very important and has significantly affected the proceedings.

(b) G. McGee — R. Taylor reported that former OFNC President and OFNC Honorary Member George McGee, had recently been quite ill, but was recovering nicely and “... is up and ranin to go...”.

(c) Study Groups — H. L. Dickson reported that over 150 members have signed up for membership in one or more of the study groups and that meetings will commence shortly. The response has been tremendous.

(d) Acknowledgments — R. Taylor thanked E. Evans and her group for so successfully providing refreshments at all the OFNC meetings during this past year. He also thanked H. L. Dickson in particular and Council members in general for their assistance throughout 1980.

9. Adjournment:
It was moved by C. Gilliatt (2nd, D. Laubitz) that the meeting adjourn.

(Motion carried) 2115 h

Following the Business Meeting, individual OFNC members narrated the showing of their own natural history slides. Over 200 slides, beautifully illustrating subjects from throughout Canada, were presented. Following this splendid and well-received program, a social gathering was held downstairs in Activity Room 3, where refreshments were served.

D. F. Brunton,
Recording Secretary.

Auditor's Report

To: Members of The Ottawa Field-Naturalists' Club

I have examined the balance sheet of The Ottawa Field-Naturalists' Club as at September 30, 1981, and the related Income Statements for the year then ended. My examination included a general review of the accounting procedures and such tests of the records and supporting vouchers as considered necessary under the circumstances.

In my opinion, these financial statements present fairly the financial position of the organization as at September 30, 1981, and the results of its operations for the year then ended in accordance with generally accepted accounting principles.

January 4, 1982

(Signed) F. Montgomery Brigham

The Ottawa Field-Naturalists' Club Balance Sheet

as of September 30, 1981

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The Ottawa Field-Naturalists' Club: Statement of Income and Expenditure

for the year ended September 30, 1981

**Income**

<table>
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<tr>
<th>Description</th>
<th>Amount</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apportionment of Membership Fees</td>
<td></td>
</tr>
<tr>
<td>Annual</td>
<td>$7,548.75</td>
</tr>
<tr>
<td>Life</td>
<td>240.00</td>
</tr>
<tr>
<td></td>
<td>$7,788.75</td>
</tr>
<tr>
<td><em>Trail &amp; Landscape</em> — Subscriptions</td>
<td></td>
</tr>
<tr>
<td></td>
<td>192.00</td>
</tr>
<tr>
<td>Back numbers</td>
<td>216.00</td>
</tr>
<tr>
<td></td>
<td>408.00</td>
</tr>
<tr>
<td>The <em>Shrike</em> Subscriptions</td>
<td></td>
</tr>
<tr>
<td>Donations</td>
<td>571.50</td>
</tr>
<tr>
<td></td>
<td>234.25</td>
</tr>
<tr>
<td></td>
<td>9,002.50</td>
</tr>
<tr>
<td>Interest</td>
<td>1,695.51</td>
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<tr>
<td></td>
<td>$10,698.01</td>
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</table>

**Expenditure**

<table>
<thead>
<tr>
<th>Description</th>
<th>Amount</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Trail &amp; Landscape</em></td>
<td></td>
</tr>
<tr>
<td>Publishing</td>
<td>$5,050.30</td>
</tr>
<tr>
<td>Circulation</td>
<td>206.09</td>
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<tr>
<td>Editing and Office</td>
<td>373.36</td>
</tr>
<tr>
<td>Honoraria</td>
<td>253.00</td>
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<tr>
<td></td>
<td>$5,882.75</td>
</tr>
<tr>
<td>The <em>Shrike</em> Publishing and Expenses</td>
<td>540.11</td>
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**Committee Activities — Net**

<table>
<thead>
<tr>
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</thead>
<tbody>
<tr>
<td>Excursions and Lectures</td>
<td>40.20</td>
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<tr>
<td>Membership</td>
<td>1,147.52</td>
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<tr>
<td>Macoun Club</td>
<td>93.80</td>
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<td>Conservation</td>
<td>278.10</td>
</tr>
<tr>
<td>Bird Records</td>
<td>289.24</td>
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<tr>
<td>Bird Feeders</td>
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<td>Publications</td>
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<td>Study Groups</td>
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<td></td>
<td>$2,873.65</td>
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<tr>
<td>Baldwin Scholarship</td>
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<tr>
<td>Special Activities</td>
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<td>Council Expenses</td>
<td>1,153.80</td>
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<td>Office Assistant</td>
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<tr>
<td>Office Supplies and Expenses</td>
<td>853.11</td>
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<td>Miscellaneous</td>
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<td>2,725.42</td>
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<td>12,021.93</td>
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**Excess of expenditure over income**

<table>
<thead>
<tr>
<th>Description</th>
<th>Amount</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>$ 1,323.92</td>
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</table>
The *Canadian Field-Naturalist*: Statement of Income and Expenditure

for the year ended September 30, 1981

**Income**

<table>
<thead>
<tr>
<th>Description</th>
<th>Amount</th>
</tr>
</thead>
<tbody>
<tr>
<td>Apportionment of Membership Fees</td>
<td></td>
</tr>
<tr>
<td>Annual</td>
<td>$5,033.00</td>
</tr>
<tr>
<td>Life</td>
<td>160.00</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>5,193.00</strong></td>
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<tr>
<td>Subscriptions</td>
<td>15,246.75</td>
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<tr>
<td><strong>Total Income</strong></td>
<td><strong>20,439.75</strong></td>
</tr>
<tr>
<td><strong>Publication</strong></td>
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<tr>
<td>Reprints</td>
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<tr>
<td>Plates and Tab Settings</td>
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<tr>
<td>Extra Pages</td>
<td>11,139.00</td>
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<tr>
<td>Back Numbers</td>
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<tr>
<td><strong>Total Publication</strong></td>
<td><strong>20,326.99</strong></td>
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<tr>
<td>Other</td>
<td></td>
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<tr>
<td>Interest</td>
<td>5,676.28</td>
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<tr>
<td>Exchange</td>
<td>1,461.77</td>
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<tr>
<td><strong>Total Other</strong></td>
<td><strong>7,138.05</strong></td>
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<tr>
<td><strong>Total Income</strong></td>
<td><strong>$47,904.79</strong></td>
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**Expenditure**

<table>
<thead>
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<tr>
<td>Publishing</td>
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<tr>
<td>Circulation</td>
<td>2,749.04</td>
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<td>Honoraria</td>
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<tr>
<td><strong>Total Expenditure</strong></td>
<td><strong>47,553.07</strong></td>
</tr>
</tbody>
</table>

**Excess of income over expenditures**

$351.72
Statement of Centennial Project Revenue and Expenditure

for the year ended September 30, 1981

<table>
<thead>
<tr>
<th>Description</th>
<th>1979-81</th>
<th>1981</th>
<th>Difference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recording — Songs of the Seasons</td>
<td>$9,980.26</td>
<td>$2,092.81</td>
<td>$7,887.45</td>
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<tr>
<td>Revenue</td>
<td>8,017.56</td>
<td>1,962.70</td>
<td>1,050.70</td>
</tr>
<tr>
<td>Expenditure</td>
<td></td>
<td>$1,042.11</td>
<td></td>
</tr>
<tr>
<td>Club Pin</td>
<td>218.40</td>
<td>11.20</td>
<td></td>
</tr>
<tr>
<td>Revenue</td>
<td>1,188.36</td>
<td>(969.96)</td>
<td></td>
</tr>
<tr>
<td>Expenditure</td>
<td></td>
<td></td>
<td>11.20</td>
</tr>
<tr>
<td>Bird record cards</td>
<td>183.00</td>
<td>13.25</td>
<td></td>
</tr>
<tr>
<td>Revenue</td>
<td>405.95</td>
<td>(222.95)</td>
<td></td>
</tr>
<tr>
<td>Expenditure</td>
<td></td>
<td></td>
<td>13.25</td>
</tr>
<tr>
<td>Hasti notes</td>
<td>78.40</td>
<td>16.80</td>
<td></td>
</tr>
<tr>
<td>Revenue</td>
<td>89.07</td>
<td>(10.67)</td>
<td></td>
</tr>
<tr>
<td>Expenditure</td>
<td></td>
<td></td>
<td>16.80</td>
</tr>
<tr>
<td>Macoun autobiography reprint</td>
<td>5,143.55</td>
<td>2,443.55</td>
<td></td>
</tr>
<tr>
<td>Revenue</td>
<td>10,404.09</td>
<td>(5,260.54)</td>
<td></td>
</tr>
<tr>
<td>Expenditure</td>
<td></td>
<td>324.59</td>
<td>2,118.96</td>
</tr>
<tr>
<td>CFN Index</td>
<td>741.00</td>
<td>516.00</td>
<td></td>
</tr>
<tr>
<td>Revenue</td>
<td>10,509.50</td>
<td>(9,768.50)</td>
<td></td>
</tr>
<tr>
<td>Expenditure</td>
<td></td>
<td>25.00</td>
<td>491.00</td>
</tr>
<tr>
<td>Club T-shirts</td>
<td>156.25</td>
<td>146.25</td>
<td></td>
</tr>
<tr>
<td>Revenue</td>
<td>185.90</td>
<td>(29.65)</td>
<td></td>
</tr>
<tr>
<td>Expenditure</td>
<td></td>
<td></td>
<td>146.25</td>
</tr>
<tr>
<td>Orchids of the Ottawa District</td>
<td>(2,317.62)</td>
<td>(1,244.73)</td>
<td></td>
</tr>
<tr>
<td>Publication of Conference Papers in</td>
<td></td>
<td>(1,700.00)</td>
<td></td>
</tr>
<tr>
<td>The Canadian Field-Naturalist</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Projects completed in prior periods</td>
<td>(1,761.77)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Revenue over (under) expenditure</td>
<td>$(18,378.96)</td>
<td>$894.84</td>
<td></td>
</tr>
</tbody>
</table>
Report by Council to The Ottawa Field-Naturalists' Club for the Year 1981

In general, Council continued the programs established in previous years. A notable event during the year was the change in editor of The Canadian Field-Naturalist from Dr. Lorraine Smith to Dr. Francis Cook. Membership remained stable but costs rose, prompting Council to increase fees for 1982 to avoid an operating deficit.

Membership for the 1981 Council was as follows:
President: R. Taylor
Vice-President: L. Dickson and D. F. Brunton
Recording Secretary: E. F. Pope
Corresponding Secretary: W. K. Guummer
Treasurer: B. C. Henson


(Award)

Awards Committee

In 1981 the Awards Committee created and defined awards in recognition of service and achievement by Club members. Four new awards were proposed to Council and accepted.

1) Member of the Year Award
   To be given annually to the member who is judged by the Committee to have contributed the most to the OFNC in the previous year.

2) OFNC Service Award
   To be given in recognition of a member who has contributed significantly to the smooth running of the Club over several years.

3) The Anne Hanes Natural History Award
   This award is given to a Club member who, through independent study or investigation, has made a worthwhile contribution to knowledge, understanding and appreciation of the natural history of the Ottawa Valley.

4) Conservation Award
   To be given in recognition of a member who has made a recent outstanding contribution to the cause of natural history conservation.

The following guidelines were established:

1) Nominations are open to all OFNC members in good standing. Officers of the Club are excluded from Member of the Year Award and OFNC Service Award.

2) All awards are to be made annually if a suitable candidate is found.

3) Nominations by the Awards Committee for all awards will be subject to approval by Council.

4) The OFNC Service Award, the Anne Hanes Natural History Award and the Conservation Award may be awarded jointly for cooperative activities on a single project.

5) The Awards Committee will consult with chairmen of other committees for information on members who are active in the club.

6) A call for nominations for all Club awards will be made by the Awards Committee annually in both The Canadian Field-Naturalist and Trail & Landscape.

7) The Awards Committee will inform the membership of recipients of Club awards through CFN and T & L.

8) Presentation of these awards will follow the tradition set by the Honorary Member Award and be made at the annual dinner or soirée. A document describing the Club's recognition of the contribution, which is suitable for framing, will be given to each recipient.

9) The evaluation of Honorary Member nominations has been included in the duties of the Awards Committee.

The Natural History Award was renamed the Anne Hanes Award for Natural History to commemorate Anne who died on 17 October 1981. She was a very active member of the Club and the first editor of Trail & Landscape. Donations have been received in memory and they will be used to pay for a trophy. The Committee will be soliciting the membership for drawings, paintings, or sculptures that could be used as a trophy to be kept by each winner for a one year period.

(Firstly)

Birds Committee

The reorganization of the Committee that was undertaken in 1980 has had time to settle in and appears to be having the desired effects. The Committee has distributed its work load among subcommittees and thereby has been able to exercise its responsibilities for coordinating Club birding activity more effectively.

The Ad Hoc Subcommittee established to examine the OFNC role in running bird counts made its report this year and after some revision and considerable discussion, the document has been accepted as the basis for count guidelines. During the year we conducted Spring and Christmas Counts (the Fall count
has been dropped for the time being at least) as well as a new event, the Owl Census. The latter program was particularly successful, with several hundred owls being noted. A general Club meeting in the spring was held to go over the results of this census (and also the Spring Count) and was well received. Special thanks are due to Bernie Ladouceur for his efforts in coordinating the Spring Count and Christmas and Owl Censuses.

The Committee was involved (with the Conservation Committee) in developing OFNC positions on the questions of Gyrfalcon and Henslow’s Sparrow conservation, and participated in a provincial identification of endangered and/or threatened bird species.

The OFNC feeders are again maintained by our volunteers this year, although the Anderson Road feeder was not set up this winter. Our thanks to Jean Hastie for her terrific efforts of the past number of winters in that regard. We held a ‘Seedathon’, a money raising effort whereby two teams of birders were sponsored so many cents per bird during a ‘big-dayrun’ in September, and it was a great success. Over 100 contributors donated in excess of $800, all of which is to go to the OFNC bird feeders. Our thanks to Bruce Dilabio, Jim Harris, Bernie Ladouceur, Dan Brunton and OFNC President Roger Taylor who did the field work for this, and to Vi Humphreys who came up with the idea in the first place. The generosity of contributors, coupled with the excess seed resulting from the bulk purchase last year, means that we do not have to request any funds for bird seed this year.

The Bird Records Subcommittee had a quiet year but was able to cover their end of things, including the resolution of a number of rare bird reports. The remaining reports will be dealt with early in the new year.

The Ottawa Rare Bird Hotline appears to be close to reality and we look forward to its establishment early in 1982. The Rare Bird Alert system was revised in the fall by Bruce Dilabio and has been altered somewhat to more effectively represent rare records.

Several contributions or archival materials were processed this year, including important data sets from the 1940's and 1950's by the late Walton Groves and from the 1880's by the late A.G. Kingston.

The Committee has increased the number of bird contributions in Trail & Landscape this year, with articles appearing on the Christmas and Owl Censuses, the archival materials received, the Seedathon effort and the regular seasonal summaries. We are also involved in the ongoing Ontario Breeding Bird Atlas project (with Bruce Dilabio coordinating the effort).

The progress and achievement of Bird Committee efforts in 1981 was most satisfying and we seem to be well set up to continue this momentum into the 1980's.

The Committee has continued to advise *The Shrike* editors on technical matters and on the basis of feedback received from the general readership. We hope to increase and formalize such contacts in the new year.

(D. F. Brunton)

**Centennial Committee**

There was little activity by this Committee in 1981. A final report is expected next year.

**Conservation Committee**

Like the preceding year, 1981 was a busy time for the Conservation Committee. The Committee involved itself in numerous local concerns and also tackled several broader issues.

**National Issues**

The Committee was perturbed by the Northwest Territories' decision to allow the capture of gyrfalcons for commercial export since it had not been shown that the population could sustain a harvest. The Committee sent several letters outlining this point.

Canada's withdrawal from the International Whaling Commission also aroused the Committee's concern. We have not yet received reassurance that this action will leave Canada any opportunity to protect these valuable creatures.

In September 1980, 30 male and 100 female raccoon dogs were imported by an Ontario fur rancher. These animals could become a severe pest species should they escape and establish themselves in the wild. Conservationists' hopes were raised when the Foreign Investment Review Agency rejected the application. The provincial government refused the federal government's offer to split the cost of buying the animals so the threat still remains.

We are continuing to monitor the Baffin Island Oil Spill Program.

**Provincial Issues**

The Committee responded to many requests for input. Some of these were: The Fitzroy Provincial Park Master Plan, the Point Pelee National Park Draft Master Plan, the Pukaskwa National Park Draft Master Plan and the Strategic Land Use Plan for Northern Ontario.

 Destruction of part of the rare Henslow's sparrow breeding site at Tiny Marsh by the Ontario Ministry of Natural Resources (OMNR) aroused our concern. This type of mismanagement by the OMNR is disturbing to the Committee, especially since much of the environmentally significant land in Ottawa-Carleton is, or will be, managed by the OMNR. Our concerns were expressed to both OMNR and the regional government.
The Committee also responded to the Lennox generating station bird kill. Over 10,000 migratory birds were killed because of the lighting of the stack during nights last fall. Ontario Hydro and the Ministry of Transportation and Communications have agreed that harmless strobe lights should be installed to avoid future disasters.

A member of the Conservation Committee attended the wetlands conference sponsored by the Federation of Ontario Naturalists in September. At the conference the Ontario government released a discussion paper on wetland policy. The Committee is preparing a response to this paper.

Local Level

We opposed the proposal to build a flood control structure on the Jock River on the grounds that the environmental impact had not been fully assessed. Regional politicians rejected the proposal on the grounds that the financial benefits were not worth the construction cost.

The Committee commented on the Gatineau Park Master Plan.

We appointed one of our members to the recently formed Marlborough Forest Management Advisory Committee. This Committee will oversee the well-known Richmond fen complex.

In March the regional government decided not to allocate funds for the purchase of “Natural Environment Areas.” The Committee initiated a letter writing campaign which may have contributed to the partial revision of the decision in April.

The regional government adopted an amendment concerning land designation and use along the Ottawa and Rideau rivers covering several local environmentally significant areas. The Committee provided a lot of the input for the production of this amendment.

In April the Club opposed a proposal to develop the area known as the South March Highlands. This area is a part of the Natural Environment Areas concept in the official plan. The Regional Council decided to make an amendment that would allow the developer to go ahead. We joined several other groups, including the Ontario Ministry of Natural Resources, in a request for an Ontario Municipal Board hearing, which was granted.

While 1981 was a busy and challenging year we look forward to an equally challenging 1982.

(S. Gawn)

Education and Publicity Committee

The role of the Education and Publicity Committee is to inform the people of the Ottawa area about the OFNC and its various activities. The Committee carries this mandate by publicizing Club meetings and outings through local newspapers, radio and T.V., by setting up displays, and by providing speakers and “outing” leaders to interested groups in the Ottawa district.

In 1981 the Federation of Ontario Naturalists (FON) celebrated its 50th anniversary. The Education and Publicity Committee helped them celebrate by setting up an OFNC exhibit at the FON annual meeting in London, Ontario. Closer to home the Committee set up a display at the Ottawa Duck Club annual show.

Again this year the Ottawa Field-Naturalists’ Club under the coordination of the Education and Publicity Committee, awarded a $100 cash prize and a subscription to Trail & Landscape to a deserving life science exhibitor at the Ottawa Regional Science Fair.

1982 should be a busy year for the OFNC with the activities of the “study groups” gaining momentum. This could result in more work for the Committee, but it could also provide us with needed resources. Display material and interesting, knowledgeable speakers are always welcomed by the Education and Publicity Committee.

(K. Taylor)

Excursions and Lectures Committee

The Committee organized the usual nine monthly meetings (excluding the annual business meeting), the new Soirée, and 45 other functions, principally outings. For many there were two highlight events of the year: the Members’ Soirée, which replaced the annual Banquet, and the lecture and slide presentation by the famous artist Robert Bateman.

The Soirée at the RA Centre replaced the more formal annual Banquet. The food was reduced to wine and cheese and punch, so as to give more time to visit with old and new friends, and to view the many exhibits of nature art, photos, and collections submitted by Club members. In addition, there were special displays by OFNC individuals and groups, and a record number of displays by Macouners, some of which were recipients of newly created awards. The outstanding presentation by Robert Bateman — arranged by non-committee member Dan Brunton — was attended by a record crowd which overflowed into the balcony. Although this was an exceptional meeting, the attendance at the Monthly Meetings continues to increase.

Bird related functions — 18 outings, a special meeting concerning the results of the owl and the spring census, and a bird song workshop — as usual, dominated the “Excursions”. Next in popularity were botany related functions — seven outings and a workshop. The Mammalogy and Herpetology collections at the National Museum were visited. A new feature in
1981 was the conducting of two joint outings with the Catharine Traill Naturalists' Club of the western suburbs of Montreal. Both were to the C.I.P. Harrington Nature Centre, the one on Labour Day weekend being overnight.

Space prohibits mentioning all of the outings and thanking all the members of the Committee and of the Club whose efforts made the year a memorable one for "E & L". And as usual we are greatly indebted to the National Museum of Natural Sciences for the use of meeting facilities and of the Dynobus.

(F. Bell)

Finance Committee

Two Finance Committee meetings were held during 1981.

At the first meeting on 2 March, a number of requests for additional funds were considered, amounting in all to about $1450. $240 of this was for the CFN and $1200 for the OFNC. These additional expenditures were recommended to Council and subsequently approved. This resulted in a forecast deficit of about $700.

There was a further consideration of the minimum level of reserve funds for the OFNC. It was agreed to recommend a level of $2000 rather than the $12 000 figure previously agreed upon. Thus the total reserve funds deemed necessary for both the CFN and the OFNC were $20 000 plus $2000 or $22 000. This was considered to be an absolute minimum and not an optimum figure.

At the meeting on 2 November 1981, the Treasurer outlined the financial position of the Club. The deficit for the year was estimated to be about $1200. This was brought about primarily as the result of additional costs for the publication of T & L. The deficit for CFN was originally forecast to be about $5000, but in fact revenue was about equal to expenditures.

Although the financial position of the Club was still very good it was agreed that the Club should not continue to operate at an increasing deficit. Therefore, a budget was drawn up based on a proposed 50 per cent increase in membership fees. This would have resulted in a surplus of about $1000 for the OFNC but a continuing deficit for the CFN unless pagination or other changes were increased. A 30 per cent increase in membership fees was subsequently approved by Council.

Mr. Barry Henson decided to step down as Treasurer and will be replaced next year.

(C. Gilliatt)

Macoun Field Club Committee

The Macoun Field Club went through a number of changes in 1981. Chairman Arnet Sheppard announced that he could no longer meet the time commitment required to run the Club. In the past years he has relied on a more independent senior group but this year the senior enrolment was down. Arnet continued to organize the senior group with assistance from Andrew MacFarlane. Sharon Gowan and Sharon Smith, two OFNC members, volunteered to organize the Saturday meetings of the Junior and Intermediate groups.

Dr. F. R. Cook of the National Museum of Natural Sciences has agreed to sit on the Macoun Field Club Committee and will help to act as a liaison between the two co-sponsors.

Unfortunately due to numerous delays, the Club's annual publication Little Bear is two years behind. All the material submitted by members over the past two years is together and now being typed in final draft. This combined issue should be completed early in 1982. There have been no contributions for this year's Little Bear to date but it is hoped that there will be enough submissions for the 1981-82 issue at the usual time in June.

During the organization of the Club library a number of old and rare books have been catalogued and researched by workers at the National Museum Library. Thirty-three volumes were considered of significant value and warrant safer storage. These books have been moved to the NMNS library at 2086 Walkley Road where they will be kept in safe storage for the Macoun Field Club and be available to Club members for viewing.

(S. Darbyshire)

Membership Committee

The membership of the Club has remained virtually constant over the past year with approximately 150 to 160 new members replacing a similar number who elected to drop their membership. The total membership at 1 December 1981 was 1223, compared with 1220 a year ago. This figure includes 284 family memberships (an increase of 23) which would increase the number of actual members by at least several hundred. Following is a table comparing the numbers and types of memberships for 1980 and 1981.

<table>
<thead>
<tr>
<th>Year</th>
<th>Honorary</th>
<th>Executive, Committee, Chairmen</th>
<th>Editors of CFN and T &amp; L</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td>1980</td>
<td>100</td>
<td>200</td>
<td>400</td>
<td>300</td>
</tr>
<tr>
<td>1981</td>
<td>115</td>
<td>210</td>
<td>410</td>
<td>310</td>
</tr>
</tbody>
</table>

Two distinguished Club members were elected honorary members in 1981, namely, Louise de Kiriline Lawrence and Sheila C. Thomson.

Many members have volunteered their services on the membership renewal forms in the past couple of years, or when they first joined the Club on the application form. This information has been compiled and distributed to the Executive, Committee Chairmen and the Editors of the CFN and T & L. The lists display all of the information supplied by the volunteers and we have identified 193 local volunteers, 29 from other areas in Canada and 13 from other coun-
tries. These lists have been annotated to identify volunteers whose services are being utilized and they will be updated as new members indicate their willingness.

I wish to thank all members of the Committee: Ellaine Dickson, Louella Howden, Vi Humphreys, Aileen Mason and Ken Strang, for their work this year and to add a thank you to Patricia Narraway who has spent a great deal of time and effort overseeing our computer programs and recently converting our records to a more versatile system.

(F. Goodspeed)

Publications Committee

The Committee is responsible for overseeing the publications of The Ottawa Field-Naturalists’ Club which comprise The Canadian Field-Naturalist, Trail & Landscape, The Shrike and, from time to time, special publications.

Three issues, Volume 95 (1, 2, 3) of The Canadian Field-Naturalist were published in 1981 with a total of 402 pages, 41 articles, 27 notes, 53 book reviews, and 249 new titles. In addition, five symposium papers that were first presented orally at a Centennial Symposium on 19 May 1979, were published in 95(1). It is expected that 95(4) will appear in January, 1982. Long-time (nine years) editor, Dr. Lorraine Smith, decided in January not to accept reappointment, her duties to be concluded with the appearance of 95(3). The Committee, on behalf of all of the membership, thank Lorraine for her excellent service as editor. Her successor, Dr. Francis Cook, was appointed June 8. No financial assistance from fund granting organizations was required to meet 1981 publication expenses, nor has any been applied for in 1982.

Trail & Landscape was published as Volume 15, Issues 1-5 to a total of 264 pages. This was substantially more pages than heretofore. A second associate editor, Peter Hall, was appointed during the year.

The Shrike continues to provide seasonal summaries of bird sightings in the Ottawa region and news of interest to local birders. Five issues appeared in 1981 (Volume 55, 6 and Volume 61-3). With Volume 6, a new approach was begun. In addition to a written commentary on highlights of bird sightings, all of the data obtained is summarized in both graphical and tabular form. Recent issues have also been highlighted by some remarkable drawings by Jacques Cantin. A newly appointed editorial staff consists of Roger Taylor, editor, and Tom Hanrahan and Frank Bell, associate editors.

Reports of sales of Special Publication No. 1 (Autobiography of John Macoun) are encouraging. Special Publication No. 2 (Transactions of the Ottawa Field-Naturalists’ Club and The Ottawa Naturalist — Index) which appeared in late 1980, is expected to be of long-lasting value to professional biologists.

The Committee wishes to thank the editorial and production staffs of all of these publications for their excellent work.

(R. Bedford)

Natural History Study Groups

The study groups established by former Vice-president Loney Dickson in 1980 are now in operation and have proven to be phenomenally popular. Some two hundred members indicated an interest in one or more of the groups. When the dust had settled, study groups for birds, botany, sound recording, butterflies, other insects, nature art and photography were established and active. There are still some growing pains being experienced while different interest groups work out their programs and projects, but the results to date are most encouraging. The participants are encouraged to develop their own work (the groups are not to be extensions of the excursions and lectures program but are intended to serve as skill-developing workshops) and a number of interesting and worthwhile projects are under way. As time goes by, we hope to see the results of some of these efforts being written up in Trail & Landscape.

(D. Brunton)
Book Reviews

ZOOLOGY

Checklist of Albertan Birds


We tend to think of checklists as being bare (or simply annotated) lists of the birds of a particular area that are only of real use as a field check for birders. This list is more than that, as it provides a considerable amount of rather detailed information on the status of Alberta birds.

The list describes (by use of various easy-to-follow symbols and codes) the breeding and migration status of the 364 known species in each of five major natural regions. These include the grasslands, the parkland, the foothills, the boreal forest, and the mountains. That immediately makes the data available for use in the eastern British Columbia mountain region, the grasslands of northern Montana, and the grasslands, parkland, and boreal forest of western Saskatchewan.

Species data is further sub-divided to include separate descriptions for easily recognizable sub-specific taxa — such as Blue/Snow Goose, Myrtle/Audubon's Warbler, Northern/Bullock's Oriole, etc. This excellent feature not only is a service to birders but it helps to accentuate the distinctiveness of these taxa and provides useful insurance against future taxonomic 'lumping' or 'splitting'!

With literally hundreds of individual datum, it is easy to find minor areas of disagreement. Audubon's Warbler, for example, is certainly more plentiful than "Uncommon" in the mountain region and Bohemian Waxwing is a common to abundant early spring migrant there (not a common winter visitor). These are relatively trifling concerns, however, and do not take away from the list's over-all excellent value.

The status categories are very subjectively defined (e.g. Fairly Common — not as frequently observed as Common; Uncommon — not as frequent as Fairly Common). Even with the obvious limitations of this approach, it is still probably the most practical way of labelling status for these purposes. I am less satisfied with the frequent use of Accidental ("not to be expected"). One could argue that, if the species isn't extinct, it could well be expected. After all, birds have wings . . .!

The hypothetical list includes some rather bizarre reports (such as California Condor and Great White Heron) which surely are too improbable to even be offered that status. In addition, some species (e.g. Black-throated Sparrow) are included despite very limited or quite inadequate documentation. This not only is a questionable practice but confuses the limits between Accidental and Hypothetical records. That is particularly the case when some species are noted as requiring further data (a nice feature) while other (questionable) reports are not so qualified.

The introduction is somewhat too casually written (causing confusion between the terms 'sporadic' and 'accidental', for example) and contains at least one spelling error ("species"). Over-all, this checklist is terrific and is a 'must' for anyone interested in the status of birds in western Canada. It is clearly the best such publication of its kind in Canada and should serve as a model for subsequent provincial lists across the country. At its present price, it is also a very good value.

Daniel F. Brunton

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A Cottager's Guide to the Birds of Muskoka and Parry Sound


Another volume can be added to the growing list of regional bird books being produced throughout Canada — and this one is excellent. It follows a well-established format, beginning with a general introduction to the study area (in central Ontario), followed by a detailed list of contributors and data sources and a species-by-species discussion of the status, distribution, nesting characteristics and migration patterns of the 264 known species. The maps of each District, illustrating township boundaries, followed by alphabetical listing of key locations (each of which is referenced to the appropriate township), are useful and interesting additions. The book concludes with an adequate index and a brief biography of the author.

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It's a soft-cover book, but is well produced and should stand up to frequent use. The type-face is clear, readable and well-printed. Generally excellent line-drawings are found occasionally in the text and provide a pleasing interruption to the copy. (The rather crude Northern Oriole on the cover is an unfortunate exception to this pattern.)

Each species discussion is surprisingly readable, considering the large number of facts and figures presented. The standard approach for each, starting with status, then migration data, then breeding information and concluding with various historical and incidental notes, would have benefited from sub-titles. This does not reduce its readability significantly, however.

The author has gone to considerable pains to uncover unpublished literature sources (such as provincial parks inventories and park naturalists' files) and has utilized these data very well. His literature citations are quite thorough and the information developed from these sources has been supported by specimen records from the appropriate provincial collections.

The text appears to be essentially free of typographical and factual errors; the reader develops increasing confidence in the author's statements as he proceeds through the work.

This is not a "cottager's guide"; it is too technical (and too good!) for that. I suspect that the author, who financed this book personally, added this to the title to increase its marketability. He needn't have worried; the quality shows . . . and quality sells.

Not only is this a fine contribution to existing regional bird studies in Ontario, but it indicates that a keen individual can produce an authoritative and high quality publication without institutional support and for a reasonable price. Perhaps most remarkable about the production of this book is the fact that the author accomplished the research, field work, design and publication quite independently and had the volume available for sale before he reached his 21st birthday! I suspect we'll see a great deal from him in coming years.

I highly recommend this book to anyone interested in the birds of southern Ontario and also to those who wish to see how an excellent regional study can be accomplished with a minimum of fuss and expense and a maximum of effectiveness.

DANIEL F. BRUNTON

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Amphibians of Canada

By Barbara Froom. McClelland and Stewart. 1982. 120 pp. illus. $12.95.

For the past two decades, Barbara Froom has been an eager and self-taught spokesperson, through articles, interviews and correspondence, for concern over what Claude Melançon termed the "inconnus et méconnus" — the unknown and misunderstood ones — of the Canadian vertebrate fauna. Throughout this period Barbara has also kept the Canadian Amphibian and Reptile Conservation Society (CARCS) viable by editing its bulletin and incorporating into the latter's pages a collage for every herpetological taste from field reports to newspaper fillers.

Her latest book is a companion for Snakes of Canada (1972) and Turtles of Canada (1976) and essentially completes her popular survey of the Canadian herpetofauna. Only the lizards are missing. As only five species of these occur in Canada they probably will remain neglected.

Amphibians of Canada begins with a forward in which Barbara has delightfully incorporated some personal anecdotes to trace the origins of her interest in these animals. One is missing because an overzealous editor, perhaps apprehensive of the reaction of her own children, expurgated Barbara's refusal, when a child, to eat tapioca pudding on realizing that it resembled masses of frog eggs. A brief but comprehensive acknowledgments section is followed by an "Introduction" which defines amphibians. Four chapters touch on "The Origin of Amphibians", "Myth and Legend", "Physical Characteristics and Adaptations", and "Classification". Chapter five gives 10 accounts of the 19 species of salamanders and Chapters six and seven give 12 accounts of the 21 species of anurans (including the Tailed Toad, Spadefoot Toads, true toads, treefrogs, and true frogs). The final chapters cover "Amphibians as Pets" and "Conservation", and the book concludes with two pages of references.

The general sections do not struggle for comprehensive coverage of the subject material but focus on highlights which most interested the author. A balance is struck in the species accounts between widespread and rare species and even those which are not given full treatment are at least mentioned in passing. Several accounts combine similar species effectively. Amphibians of Canada is an attractive book. The
cover is striking with its three colour photographs — Wood Frog, American Toad, and Tiger Salamander. These are repeated among 19 colour plates that are inserted between the table of contents and the text. Black-and-white photographs head the species accounts and only the Tailed Toad appears to be a duplicate from the colour section. In all, 26 of the 40 species of Canadian amphibians are illustrated. In the colour section the “Spotted Frog” may actually be a Red-legged Frog. The black-and-white illustration in the Tiger Salamander account is a western specimen from Ninette, Manitoba, misleadingly placed above a caption referring to the eastern race.

My checklist from the CARCS Bulletin (18(2): 1-6, 1980) has been reproduced without mention of editorial deletions from the original. The removal of most species names from above their included subspecies in this version produced some unexplained abbreviations such as Rana c. melanota and Acris c. blanchardi. A “p.” in what should have been Desmognathus f. fuscus slipped passed the proof-reading.

Style is both a strength and a pitfall throughout this book. In maintaining a personal and lively approach the author sometimes turns out statements which are unintentionally misleading or superficial. The Lepto- dactylidae, merely stated to be “found in parts of the southern United States” are also widespread in Central and South America, the West Indies, and Australia. They are one of the most abundant (in terms of numbers of species) families of frogs in the world. The implication that laying eggs on land, sucker-like disks on their bellies, and lack of webbing are characteristic of all members of this family and that such characters are primitive is questionable. Similarly, poor expression is evident in “South America and Guianas” and “the most familiar of the true toads are those of the Bufonidae family”. Sometimes emotional expressions intrude: the description of the distress call of a frog sometimes leading a “guilt-ridden captor to release it”. In opinions authoritatively credited to “herpetologists” or “biologists” these titles are often bestowed uncritically. Although the text generally restricts itself to Canadian data some very discordant references to life histories in the United States intrude, such as Spring Peepers calling in January on Long Island. The breeding season of the Bullfrog is given as “March to July” but here March was meant to read May.

Outright errors of fact are few. The statement that the Tailed Toad has been found in south-central Alberta near the United States border is an obvious lapsus as this mountain-stream species could hardly be expected in the prairies. Records for Chilliwack and Cultus lakes for the Pacific Giant Salamander were from the 1900’s not the 1800’s. The Eastern Tiger Salamander is also known from a collection taken in 1915 from Point Pelee. The Spring Salamander (Gyrinophilus not Grinophilus) record from opposite Buffalo was published in 1926 but actually collected in 1877, and the Britannia record was based on a larva collected in 1934 not 1954. Some errors have crept in because of reliance on outdated literature. Spring Peepers probably do not take “three to four years” to reach maturity. The Spotted Frog does have a distinctive mating call. Tadpoles first identified as the latter species from Saskatchewan were shown 20 years ago to be indistinguishable from those of the Leopard Frog so lack of subsequent reports of Spotted Frogs from that province is hardly worth the mention. The Plains Spadefoot, although restricted to prairies in the central provinces, is not “rare” within this area, simply hard to find outside of its brief breeding periods. Auditory records have been made of hundreds of individuals after heavy late-spring rains.

Despite lapses in editing and verification this book will reach a large audience and should promote further study and conservation of Canadian amphibians. If it does, then Barbara will have partly discharged her acknowledged debt to the late E. B. Shelley Logier whose contributions to Canadian herpetology not only included his publications and collections while at the Royal Ontario Museum but also that rare commodity — the ability to instill enthusiasm in others.

FRANCIS R. COOK

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Proceedings of the Third International Symposium on Trichoptera


The Trichoptera, or caddisflies, are the seventh largest order of insects with an estimated 10,000 species in over 30 families distributed in all faunal regions of the world. Their variety, abundance, and importance have attracted workers since the time of Linnaeus. The First International Symposium on Trichoptera was held in Lunz, Austria, in 1974, and the Second was held in Reading, England, in 1977. The Third Symposium on Trichoptera was held in Perugia, Italy, from 28 July to 2 August 1980, and was attended by 63 scientists from 21 countries. The meeting was hosted by Professor Giampaolo Moretti, Director of the Institute of Zoology of the University of Perugia. As with the two previous Symposia, the Proceedings have been published by Dr. W. Junk Publishers.

The Proceedings of the Second Symposium showed a distinct improvement over the First in the overall quality of the published papers, and the Third is better still. This volume, edited by Professor Moretti, consists of 53 papers presented at Perugia, as well as the abstract and a photograph from a poster presentation on Baltic amber Trichoptera (a total of eight posters were presented). The topics covered include ecology, life history, population dynamics, sex ratios, physiology, biochemistry, cytology, morphology, ultrastructure, parasitology, systematics, phylogeny, distribution, paleontology, and pollution, and deal with these aspects in both larval and adult stages. One new family, 15 new species, and seven new subspecies are described. The great variety of topics treated and the diversity of approaches adopted by different authors reflect the widespread interests and backgrounds of the participants. This also made it impossible to group the papers by subject, so they have been arranged alphabetically by authors. Ten of the 53 papers and two of the eight posters are authored or coauthored by Moretti, who was retiring and chose the Symposium as a vehicle to demonstrate his versatility. His contributions deal with most of the subject areas listed above.

The volume is well edited and contains only a few typographical and grammatical errors. In fact, I have only two complaints: first, the literature cited section of each paper is in the abbreviated form in which journal article titles are omitted in order to save space; second, many of the line drawings failed to reproduce clearly, with the fine lines disappearing completely in some of the systematic illustrations. Since the book is printed on high quality glossy paper and carries a very high price tag, this is indeed regrettable.

These Proceedings provide a wide ranging overview of many of the areas of current research into the study of caddisflies by many of the world's leading authorities. Considering the cost of the book I would not recommend the purchase of a personal copy. However, I do urge anyone with a serious interest in Trichoptera or aquatic entomology to request his or her institution's library to obtain a copy.

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BOTANY

Guide to the Orchids of the Cypress Hills


The Cypress Hills, straddling the southern Alberta-Saskatchewan border, have been variously described as an island in a sea of grass, an oasis in the desert, and, in glacial times, an island in the ice. These terms would serve as good metaphors for the student of orchids because while fifteen species have been found in the Hills, there are very few species in the immediately surrounding prairies.

Unfortunately, until now, the student could obtain no complete and convenient field guide discussing the orchids as they occur in the Hills. Budd's Flora of the

Canadian Prairie Provinces would be heavy in a back pack, while Szczawinski's The Orchids of British Columbia does not, of course, discuss the Cypress Hills.

The present book, while its paper cover might suffer in a back pack, helps to fill the information gap and should be useful to the novice and the visitor to the Cypress Hills. The title page indicates that it includes "the most common orchids of Alberta and Saskatchewan". The buyer should realize, however, that some fifteen or so less common species of these provinces which do not occur in the Hills are not discussed.
The author has brought together, occasionally uncritically, information from various sources (some of it applying to larger regions such as the entire province of Alberta), as well as his own field observations in the Cypress Hills. The book contains a brief discussion of the Hills, the orchid family and the orchids in the Hills, and a selected bibliography. The central part of the book consists of a set of keys to the species and fairly detailed treatments of fourteen species. A pair of facing pages is devoted to each species. Line drawings by the author fill one page. On the opposite page are given, below the common and botanical names, other common names, terse descriptions of flowers, leaves and habitat as well as heights, blooming dates and occurrence. Detailed localities are not given either in the text or as distribution maps. For most species there are small colour photographs grouped in the centre pages. One other species and two varieties are discussed briefly. The layout shows a strong sense of organization with good typogaphy, and there are few typographic errors.

The reader will need to use the book with some caution, however. The weakest part of the book is the illustrations, which are of variable quality. While some of the line drawings are almost photographic in their precision and detail, others, such as Spotted Coral-root and Northern Twayblade, are confusing and difficult to recognize. The photographs compensate to some extent, but they are quite small, and some of them are not too clear because of poor lighting or focus.

The keys generally seem reasonable, but three points could cause difficulties. The Early Coral-root, *Corallorhiza trifida*, is sometimes green in colour and would not key out with the other corallorhizas as intended under "no green color". Bracted Bog Orchid is grouped with habenarias having spurred lips; however, although this species does have a spur, it is so inconspicuous that it could be overlooked easily by a novice. The Rattlesnake-plaintains *Goodyera oblongifolia* and *G. repens* are usually easy to distinguish by height and leaf pattern. Separation of the two species at heights of 15 cm usually works in eastern North America but is not reliable in the west. *G. repens* in Alberta and Saskatchewan is taller than in the east; almost half the specimens we have examined from these two provinces were over 15 cm in height. On the other hand, *G. oblongifolia* can occasionally be as short as 14 cm.

There are a few points in the species accounts which could cause problems. For example, the so-called spur on Spotted Coral-root could hardly be called "conspicuous" even in comparison with the short spurs of Bracted Bog Orchid. A *Goodyera oblongifolia* of 60 cm would not be in the normal height range of this species and should have been commented on. Heights over 40 cm would be unusual in Alberta and Saskatchewan. Similarly, a Sparrow's Egg Lady Slipper with three flowers would be rare enough to be worthy of special comment. The very rare, yellow Striped Coral-root (*var. ochroleuca*) is not, in fact, unique to the Cypress Hills but has been reported and photographed from other parts of Canada and the United States.

Some items which are peripheral to the main theme could nevertheless mislead the novice. The statement "All orchids in the northern hemisphere grow on the ground..." needs to be reworked. While Darwin did mention orchids briefly in the account of his South American travels, his great work on fertilization of orchids by insects started about twenty-five years later when he began to study British orchids. His subsequent work on tropical species was based on specimens given to him by various growers and importers. The names *Cypripedium spicerianum* and *Epipactis latifolia* will not be found in most resources available to the amateur, having been replaced long ago by *Paphiopedilum spicerianum* and *Epipactis helleborine*.

Aside from the above points, the novice or visitor to the Cypress Hills will find this book a convenient, easy-to-use and inexpensive reference for the orchids.

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**Environment**

**Urban Natural Areas: Ecology and Preservation**


As concerned naturalists become increasingly involved in the battle to preserve representative and special natural landscapes in and around the urban areas of Canada, their need for a practical, effective and authoritative guide to the 'dos' and 'don't' of urban landscape analysis and protection has grown. This book attempts to provide such a guide. The editors identify their readership as including students,
field naturalists, citizens groups, etc. It is certainly the first Canadian attempt to provide such comprehensive and detailed guidance for this audience.

The book covers a wide range of topics within its 10 chapters including techniques for designating significant areas, political strategies, biophysical inventory techniques, socio-economic analyses, and report preparation. Appendices, providing case studies and/or important base-line data, accompany many chapters. There are 18 different authors involved, each a specialist in his field, and most from the university community. Inevitably, with so many 'cooks' involved, a few 'lumps in the broth' are to be found. The varying style, format, and approach in many sections are not all that serious in a technical work such as this one. The variations which occur in the depth to which subjects are explored, in the use of technical jargon, and in the complexity of subject treatment, do present problems, however.

The book is well constructed and despite its low-budget soft-cover production, is quite durable and readable. The text appears to represent reduced type-written sheets (published by off-set processes) and is supported by numerous simple but quite effective line-drawings. Typographical errors are rather frequent, however, and suggest that the proof-reading could have been done more carefully.

The simplicity and economy that went into the physical production was not, unfortunately, carried on into the text. By and large, each specialist begins by stating how important — even vital — his particular discipline is to the whole process of natural areas protection and then proceeds to unload a package of overly-complicated and overly-technical data-gathering and analytical techniques that are guaranteed to frighten off even the most dedicated naturalists, citizens groups, and whoever else might look to this work for guidance! I found myself asking “who are these guys kidding?” as I read of the glorious opportunities for natural values protection that await us through evaluation of socioeconomic variables, regression analysis, Point Quarter vegetation analysis, delineation of drainage densities ... and so on. What is presented provides a good reference for seriously-involved individuals but fails in the very area that should be of primary importance. By and large, the contributors fail to clearly explain what their area of concern contributes to the preservation effort, why the reader should gather such data, and how the reader can utilize these data to assess natural values significance or to argue for preservation/conservation at a particular site. The book is dominated by methods (the means) rather than application (the ends). Less serious, but annoying nonetheless, are spells of academic elitism, where a few of the contributors down-play the contribution possible from “amateur naturalists” in a rather patronizing and self-inflating manner.

There is one section, however, (Chapter Four) that provides lucid, realistic and practical advice. Fortunately, it covers the critical area of developing strategies for political action.

Urban Natural Areas is a valuable contribution to the Canadian literature on natural areas protection. It achieves this, however, more from its reference value (and the absence of comparable Canadian books) than from its value as a guide for “do-ers”. Anyone interested in the protection of natural landscapes in urban areas in Canada will find it a useful reference work but will have to look elsewhere for clear, practical guidance for the collection and — more critically — application of life science data to the preservation/conservation effort. That book, unfortunately, has yet to be written.

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NEW TITLES

Zoology

*The amphibians of Canada. 1982. By Barbara Froom McClelland and Stewart, Toronto. 120 pp., illus. $12.95.


Botany


Environment


†The natural environment of Newfoundland past and present. 1981. Edited by Alan G. Macpherson and Joyce Brown Macpherson. Memorial University of Newfoundland, St. John’s. xviii + 265 pp., illus. $17.50.


Miscellaneous


Books for Young Naturalists†


Mighty mites in dinosaur land. 1981. By Emily Hearn. Owl Magazine, Toronto. 48 pp., illus. $4.95.

†A new categorization as emphasis of the importance of involving young naturalists.

*assigned for review
†available for review
Instructions to Contributors

Content

The Canadian Field-Naturalist is a medium for the publication of scientific papers by amateur and professional naturalists or field-biologists reporting observations and results of investigations in any field of natural history provided that they are original, significant, and relevant to Canada. All readers and other potential contributors are invited to submit for consideration their manuscripts meeting these criteria. As the journal has a flexible publication policy, items not covered in the traditional sections (Articles, Notes, Letters, News and Comment, and Book Reviews) can be given a special place provided they are judged suitable. Readers are encouraged to support regional, provincial, and local natural history publications as well by submitting to them their reports of more restricted significance.

Manuscripts

Please submit, in either English or French, three complete manuscripts written in the journal style. The research reported should be original. It is recommended that authors ask qualified persons to appraise the paper before it is submitted. Also authors are expected to have complied with all pertinent legislation regarding the study, disturbance, or collection of animals, plants or minerals. The place where voucher specimens have been deposited, and their catalogue numbers, should be given.

Type the manuscript on standard-size paper, if possible use paper with numbered lines, double-space throughout, leave generous margins to allow for copy marking, and number each page. For Articles and Notes provide a bibliographic strip, an abstract and a list of key words. Articles also require a running head. Generally words should not be abbreviated but use SI symbols for units of measure. Underline only words meant to appear in italics. The names of authors of scientific names should be omitted except in taxonomic manuscripts or other papers involving nomenclatural problems. Authors are encouraged to use "proper" common names (with initial letters capitalized) as long as each species is identified by its scientific name once.

We prefer the names of journals in the Literature Cited to be written out in full. Unpublished reports should not be cited here. Next list the captions for figures (numbered in Arabic numerals and typed together on a separate page) and present the tables (each titled, numbered consecutively in Arabic numerals, and placed on a separate page). Mark in the margin of the text the places for the figures and tables.

Extensive tabular or other supplementary material not essential to the text, typed neatly and headed by the title of the paper and the author's name and address, should be submitted in duplicate on letter-size paper for the Editor to place in the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2. A notation in the published text should state that the material is available, at a nominal charge, from the Depository.


Illustrations—Photographs should have a glossy finish and show sharp contrasts. Photographic reproduction of line drawings, no larger than a standard page, are preferable to large originals. Prepare line drawings with India ink on good quality paper and letter (don't type) descriptive matter. Write author's name, title of paper, and figure number on the lower left corner or on the back of each illustration.

Reviewing Policy

Manuscripts submitted to The Canadian Field-Naturalist are normally sent for evaluation to an Associate Editor (who reviews it himself or asks another qualified person to do so), and at least one other reviewer, who is a specialist in the field, chosen by the Editor. Authors are encouraged to suggest names of suitable referees. Reviewers are asked to give a general appraisal of the manuscript followed by specific comments and constructive recommendations. Almost all manuscripts accepted for publication have undergone revision — sometimes extensive revision and reappraisal. The Editor makes the final decision on whether a manuscript is acceptable for publication, and in so doing aims to maintain the scientific quality and overall high standards of the journal.

Special Charges

Authors must share in the cost of publication by paying $60 for each page in excess of six journal pages, plus $6 for each illustration (any size up to a full page), and up to $60 per page for tables (depending on size). Reproduction of color photos is extremely expensive; price quotations may be obtained from the Business Manager. When galley proofs are sent to authors, the journal will solicit on a voluntary basis a commitment, especially if grant or institutional funds are available, to pay $60 per page for all published pages. Authors may also be charged for their changes in proofs. Limited journal funds are available to help offset publication charges to authors with minimal financial resources. Requests for financial assistance should be made to the Editor when the manuscript is submitted.

Reprints

An order form for the purchase of reprints will accompany the galley proofs sent to the authors.
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12 January 1982

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- Botany: Guide to the Orchids of the Cypress Hills
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The Ottawa Field-Naturalists’ Club

FOUNDED IN 1879

Patrons

Their Excellencies the Governor General and Mrs. Edward Schreyer

The objectives of this Club shall be to promote the appreciation, preservation and conservation of Canada’s natural heritage; to encourage investigation and publish the results of research in all fields of natural history and to diffuse information on these fields as widely as possible; to support and cooperate with organizations engaged in preserving, maintaining or restoring environments of high quality for living things.

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Back Numbers and Index

Most back numbers of this journal and its predecessors, Transactions of The Ottawa Field-Naturalists’ Club, 1879-1886, and The Ottawa Naturalist, 1887-1919, and Transactions of The Ottawa Field-Naturalists’ Club and The Ottawa Naturalist — Index compiled by John M. Gillett, may be purchased from the Business Manager.

Cover: Charles Mortram Sternberg (center) with Joe Skillen (left) and Hank Shearman (right) putting finishing touches on an Upper Cretaceous duck-billed dinosaur skeleton, Lambeosaurus sp., at the Sussex and George streets Paleontology Laboratory in 1950. Photograph courtesy of the Photo-Retrieval Section, National Museums of Canada (with special thanks to Kathleen Desrochers). See tribute to C. M. Sternberg pages 483-486.
An Annotated List of Spiders Collected During the “Big Dig” Near Wawa, Ontario, 1971

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²Department of Photo Information Retrieval, National Museums of Canada, Ottawa, Ontario K1A 1M8
³10727-64 Avenue, Edmonton, Alberta T6H 1T1


An annotated list of 57 species of spiders collected over a three month period in pitfall traps near Wawa, Ontario is given. Numbers caught were not correlated with ph, % carbon or water retention capacity of the soil. Habitats, sex, and age of collected specimens are discussed.

Key Words: spiders, Northwestern Ontario, species list, ecological notes.

During the summer of 1971 the National Museums of Canada sponsored a Youth Hostel in Wawa, Ontario approximately 300 miles east of Thunder Bay on the north shore of Lake Superior. Financial assistance was obtained from the Office of the Secretary of State, housing and transportation being supplied by the Canadian Army.

The purpose of the hostel was to provide a meaningful experience to both the students who worked at the camp and the transients, acquainting them with the fields of Archaeology, Botany, Geology, Ecology and Entomology. The most extensive project was an Archaeological “dig” for native artifacts. This paper is the result of a study of the spiders near Wawa, conducted under the supervision of R. Freitag, Lakehead University. The spider fauna of northern Ontario is not well known, although Freitag et al. (1969), Freitag and Poulter (1970), Olynyk and Freitag (1977), and Graham (unpublished), have reported on their occurrence in northwestern Ontario and Stratton et al. (1978) has studied an arboreal spider community in northern Minnesota.

Materials and Methods

On 8 June 1971 six sampling stations were established near Wawa. The stations were as follows: (1) Black Spruce stand ½ mile north of Highway 101 on the south side of Twin Lakes Road; (2) Jack Pine stand 3 miles south of Wawa on the east side of Highway 17; (3) White Birch stand at the end of Mission Road approximately 1000 feet from the shore of Lake Superior; (4) Poplar stand 2 miles north of Highway 101 on the north side of Twin Lakes Road; (5) mixed forest stand 1 mile north of Highway 101 at the east end of Wawa Lake; and (6) meadow 4 miles north of Highway 17 on High Falls Dam Road on the premises of an old homestead.

Each station comprised two lines of 25 pitfall traps. Traps were constructed at 4 m intervals running east-west. Trap construction and treatment of collected material follows that described by Freitag et al., 1969. Pitfall traps were emptied daily from 13 June 1971 to 16 August 1971 inclusive.

Six soil samples were taken from each site and analyzed for pH, carbon content and ability to retain water. The samples comprised one from the end of each line and one between the 12th and 13th trap. Methods of soil analysis followed that of Atkinson et al. 1958.

In order to determine forest types in each station, all trees over 6 inches DBH (diameter at breast height) within 15 feet of each line were identified and counted.

Results and Discussion

Station 1 (BS): 88.4% Black Spruce, Picea mariana, B.S.P., 11.6% Balsam Fir, Abies balsamea; pH 3.7; carbon content 77.9%; high water retention capacity of 348.0%. This stand had little undergrowth and the ground was heavily covered with spruce needles.

Station 2 (JP): 57.5% Jack Pine, Pinus banksiana, 42.5% Black Spruce; pH 4.2; carbon content 5.1% low water retention capacity of 60.6% being sandy and
atop a hill. Undergrowth was present as well as a mat of pine needles.

Station 3 (WB): 85.0% White Birch, *Betula papyrifera* 10.0% White Spruce, *Picea glauca*, the remaining 5.0% being made up of a variety of species; pH 3.7; carbon content 15.2%; water retention capacity of 107.0%. This station was hilly, had black, damp soil, thick leaf litter and an average soil depth of less than 5 inches. Undergrowth was predominantly Moose Maple, *Acer spicatum*, and young Balsam Fir.

Station 4 (P): 63.1% Poplar, *Populus* sp. 33.5% White Birch, 2.1% Balsam Fir and 1.3% Black Spruce; pH 4.1; carbon content 7.6%; water retaining capacity of 97.9%. The soil had a hard, clay texture and a thick undergrowth of herbaceous plants.

Station 5 (MF): mixed forest consisting of 25.7% Balsam Fir, 25.0% White Spruce, 23.2% White Birch, 14.0% Mountain Ash, *Sorbus decora*, 6.8% Moose Maple, 5.3% Poplar; pH 4.1; carbon content 12.5%; water retaining capacity of 97.9%. Some undergrowth was encountered and the soil was sandy.

Station 6 (M): open field of tall grasses with no trees except around the perimeter; pH 6.5; carbon content 9.3%; water retention capacity 93.2%. The soil was hard, reddish clay and very damp.

A total of 732 adults and immatures were collected representing 11 families and a minimum of 31 genera and 43 species.

Table 1 accounts for the station description and soil analysis. There appears to be little correlation between the number of spiders caught and the pH, % carbon or water retention capacity of the soil.

Table 2 shows the habitat, sex and age of the collected specimens. At least three species were present in all six habitats, *Bathyphantes pallidus*, *Alopecosa aculeata*, and *Trobchosa terricola*, and collectively they comprised 35.3% of the total sample of 732 spiders. Sixty-six of the 100 *Bathyphantes pallidus* specimens were found in the deciduous stands (P, MF, WB) 23 in the conifers (JP and BS) and 11 in the meadow. Both *Alopecosa aculeata* and *Trobchosa terricola*, however, were concentrated among conifers where 128 of the 162 spiders were collected; 25 were from the deciduous stands and 9 from the meadow.

Sixteen species occurred in numbers which totalled less than 3.0% of the sample. These species contributed little to the population structure of this spider community.

Females with eggs or egg sacs were found throughout the sample period.

As found by Hauge (1977) and Stratton et al. (1978), the number of species of spiders collected in each habitat was fairly constant (14-20), while the number of adult individuals varied greatly (Figure 1). Poplar and Black Spruce stands had the most specimens with 28.7% and 27.3% of the total sample respectively followed by Jack Pine 16.0%, meadow 12.0%, White Birch 10.3%, and mixed forest 5.7%.

*Oreonetides* sp., *Calliopus tibialis* and *Cyrphoea montana* are uncommon in northern Ontario but more common in southern Ontario. Of the 18 specimens, only 1 was found in the Black Spruce stand, an indication of their preference for deciduous forest.

The number of captured females in each habitat generally outnumbered the males, whereas the number of immatures were less than the total adult count for each habitat (Figure 1).

While the female population remained essentially

### TABLE 1. Station description and soil analysis.

<table>
<thead>
<tr>
<th>Station</th>
<th>Tree Types (%)</th>
<th>Soil pH</th>
<th>% Carbon</th>
<th>Water Retention Capacity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Black Spruce (BS)</td>
<td>Black Spruce (88.4)</td>
<td>3.7</td>
<td>77.9</td>
<td>348.0</td>
</tr>
<tr>
<td>Jack Pine (JP)</td>
<td>Jack Pine (57.5)</td>
<td>4.2</td>
<td>5.1</td>
<td>60.6</td>
</tr>
<tr>
<td>White Birch (WB)</td>
<td>White Birch (85.0)</td>
<td>3.7</td>
<td>15.2</td>
<td>10.7</td>
</tr>
<tr>
<td>Poplar (P)</td>
<td>Poplar (63.1)</td>
<td>4.1</td>
<td>7.6</td>
<td>82.7</td>
</tr>
<tr>
<td>mixed forest (MF)</td>
<td>Balsam Fir (25.7)</td>
<td>4.1</td>
<td>12.5</td>
<td>97.9</td>
</tr>
<tr>
<td>meadow (M)</td>
<td></td>
<td>6.5</td>
<td>9.3</td>
<td>93.2</td>
</tr>
</tbody>
</table>

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### Table 2. Habitat, sex, and age of spiders collected in pitfall traps near Wawa, Ontario.

<table>
<thead>
<tr>
<th>Species</th>
<th>Habitat</th>
<th>$\sigma$</th>
<th>$\varphi$</th>
<th>Total Adult</th>
<th>Immature</th>
<th>Eggs Present</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Agelenopsis utahana</em></td>
<td>JP</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cicurina brevis</em></td>
<td>P</td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Cryphoea montana</em></td>
<td>BS, P</td>
<td>2</td>
<td>2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ambrosius borealis</em></td>
<td>JP, WB, P, MF</td>
<td>4</td>
<td>1</td>
<td>5</td>
<td>3</td>
<td></td>
</tr>
<tr>
<td><em>Calliopus euoplos</em></td>
<td>BS, JP, WB, MF</td>
<td>3</td>
<td>6</td>
<td>9</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Calliopus tibialis</em></td>
<td>WB, MF</td>
<td>1</td>
<td>7</td>
<td>8</td>
<td>4</td>
<td></td>
</tr>
<tr>
<td><em>Calliope bennetti</em></td>
<td>BS, JP, WB, P, MF</td>
<td>2</td>
<td>7</td>
<td>9</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td><em>Agroeca ornata</em></td>
<td>BS, P</td>
<td></td>
<td>5</td>
<td>5</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dictyna alaskae</em></td>
<td>BS</td>
<td>1</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ceratoclus fssiceps</em></td>
<td>P</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Ergone sp.</em></td>
<td>M</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Erigonidae sp.</em></td>
<td>M</td>
<td></td>
<td>1</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Sciasies truncatus</em></td>
<td>BS</td>
<td>1</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Zornella cultrigera</em></td>
<td>WB, MF</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Haplodrassus signifer</em></td>
<td>BS, WB</td>
<td>2</td>
<td></td>
<td>2</td>
<td></td>
<td></td>
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<tr>
<td><em>Zelotes sp.</em></td>
<td>BS, JP, P</td>
<td>4</td>
<td>2</td>
<td>6</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Zelotes subterraneus</em></td>
<td>BS</td>
<td></td>
<td>2</td>
<td>4</td>
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<tr>
<td><em>Neoantistea sp.</em></td>
<td>BS</td>
<td>1</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Agyntia sp.</em></td>
<td>P</td>
<td>1</td>
<td></td>
<td>1</td>
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<tr>
<td><em>Bathyphanes pallidus</em></td>
<td>BS, JP, WB, P, MF, M</td>
<td>10</td>
<td>85</td>
<td>95</td>
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<td></td>
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<tr>
<td><em>Bathyphanes pullatus</em></td>
<td>M</td>
<td></td>
<td>1</td>
<td>1</td>
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</tr>
<tr>
<td><em>Bathyphanes simillimus</em></td>
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<td></td>
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<td><em>Bathyphanes sp.</em></td>
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<td></td>
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<tr>
<td><em>Lepthyphantes alpinus</em></td>
<td>BS, MF</td>
<td></td>
<td>2</td>
<td>2</td>
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<tr>
<td><em>Lepthyphantes complicitus</em></td>
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<td>7</td>
<td>7</td>
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<tr>
<td><em>Lepthyphantes sp. nr. flavipes</em></td>
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<tr>
<td><em>Lepthyphantes intricatus</em></td>
<td>WB, P, MF</td>
<td>6</td>
<td>21</td>
<td>27</td>
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<tr>
<td><em>Linyphidiae spp.</em></td>
<td>BS, JP, WB, P, MF, M</td>
<td>0</td>
<td>31</td>
<td>x</td>
<td></td>
<td></td>
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<tr>
<td><em>Meioneta sp.</em></td>
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<tr>
<td><em>Oreonetides sp.</em></td>
<td>P, MF</td>
<td>4</td>
<td>4</td>
<td>4</td>
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<tr>
<td><em>Arcosta emeritoni</em></td>
<td>JP</td>
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<tr>
<td><em>Arcosta sp.</em></td>
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<td><em>Pardosa fuscata</em></td>
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<td>x</td>
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<tr>
<td><em>Pardosa hyperborea</em></td>
<td>BS</td>
<td>16</td>
<td>10</td>
<td>26</td>
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<td>x</td>
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<tr>
<td><em>Pardosa mackenziana</em></td>
<td>BS, JP, WB, P, MF</td>
<td>48</td>
<td>37</td>
<td>85</td>
<td>x</td>
<td></td>
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<tr>
<td><em>Pardosa milvina</em></td>
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<tr>
<td><em>Pardosa moesta</em></td>
<td>JP, WB, M</td>
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<td>45</td>
<td>51</td>
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<td><em>Pardosa sp.</em></td>
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<td>12</td>
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<td>50</td>
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<td><em>Pardosa xerampelina</em></td>
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<td><em>Pirata sp.</em></td>
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<td><em>Alopecosa aculeata</em></td>
<td>BS, JP, WB, P, MF, M</td>
<td>30</td>
<td>35</td>
<td>18</td>
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<tr>
<td><em>Trochosa terricola</em></td>
<td>BS, JP, WB, P, MF, M</td>
<td>21</td>
<td>22</td>
<td>43</td>
<td>66</td>
<td>x</td>
</tr>
<tr>
<td><em>Robertus riparius</em></td>
<td>BS, P</td>
<td>3</td>
<td>4</td>
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<tr>
<td><em>Robertus sp.</em></td>
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<tr>
<td><em>Theridion aurantium</em></td>
<td>MF</td>
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<tr>
<td><em>Theridion sexpunctatum</em></td>
<td>BS, JP, WB, MF, M</td>
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<td></td>
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<tr>
<td><em>Theridion sp.</em></td>
<td>JP</td>
<td></td>
<td></td>
<td>0</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td><em>Thymoites sp. nr. pallidus</em></td>
<td>M</td>
<td>1</td>
<td></td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Philodromus sp.</em></td>
<td>P</td>
<td></td>
<td>0</td>
<td>1</td>
<td></td>
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</tr>
<tr>
<td><em>Xysticus elegans</em></td>
<td>P</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**TOTAL** 172 314 486 246
constant throughout the sampling period, the male spider catch decreased noticeably after mid June (Figure 2), similar to Hauge (1977). Mid July was a peak period for the number of immatures (Figure 3). The population peak occurred in mid June for the male population as well as the total adult population. These results indicate that had the sampling period been extended to include May and September a density trend similar to that reported by Peck (1966) and MacMahon and Trigg (1972) would have occurred. They suggest density peaks during early (mid May-24 June) and late (4 August-12 September) summer and a density depression in midsummer (25 June-3 August).

**Annotated List**

*Theridiidae*

*Robertus* sp. imm.  
*Theridion* sp. imm.  
*Theridion aurantium* Emerton. Mainly New England and Great Lakes area and adjoining areas in Canada; Newfoundland.

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**Figure 1.** Sex and age composition of spiders in each habitat.

**Figure 2.** Number of adult male and female spiders caught during the sample period, 13 June – 16 August 1971.

**Figure 3.** Total number of adult and immature spiders caught during the sample period, 13 June – 16 August 1971.
**Theridion sexpunctatum** Emerton. Widespread in Canada and the United States.

**Thymoites** sp. nr. **pallidus** Emerton.

**Erigonidae**

**Ceraticles fissiceps** Pickard-Cambridge. Common to the northeastern part of the United States and adjoining parts of Canada. Adults of both sexes found during all seasons. Lives in leaf litter, or on grasses and low bushes.

**Erigone** sp. undet. ♀.

**Erigonidae** sp. imm.

**Sciastes truncatus** Emerton. Eastern Canada and very northern parts of New England. A small leaf litter species.


**Linyphiidae**

**Agyneta** sp. undet. ♀.

**Bathyphantes** sp. imm.

**Bathyphantes pallidus** Banks. Alaska and Canada east to Labrador, northern United States. Often collected in large series.

**Bathyphantes pullatus** Pickard-Cambridge.

**Bathyphantes simillimus** Koch. Holarctic. Other Nearctic records are from New York and Quebec.

**Lepthyphantes alpinus** Emerton.

**Lepthyphantes complicatus** Emerton.

**Lepthyphantes** sp. nr. **flavipes** Blackwall

**Lepthyphantes intricus** Emerton.

**Linyphiidae** spp. imm.

**Meioneta** sp. undet. ♀.

**Oreometides** sp.

**Pityohyphantes** sp.

**Hahniiidae**

**Neoantistea** sp.

**Agelenidae**

**Agelenopsis utahana** Chamberlin and Ivie. Widespread in central North America.

**Cicurina brevis** Emerton. Southern Quebec and Ontario, eastern United States west to the Rocky Mountains.

**Cryphoeca montana** Emerton. Southern Ontario and Quebec, New England, west to Wisconsin. Lives in leaf litter and under stones in wooded areas.

**Lycosidae**

**Alopecosa aculeata** Clerck. Holarctic. Widespread boreal.

**Arctosa** sp. imm.

**Arctosa emertonii** Gertsch. Central and eastern North America. Found mainly in wooded areas and in clearings and pastures near woods.

**Lycosa frondicola** Emerton. Central and eastern North America. Widespread in wooded areas.

**Pardosa fuscula** Thorell. Boreal.


**Pardosa mackenziana** Keyserling. Widespread boreal. One female from this site was parasitized with a merithid worm.

**Pardosa milvina** Hentz. Widespread in central and eastern North America.

**Pardosa moesta** Banks. Southern boreal and mixed deciduous. Often found in clearings and plowed fields near woods.

**Pardosa xerampelina** Keyserling. Widespread North America. Often found along shores of rocky streams and ponds.

**Pirata** sp. imm., prob. **piratica** Clerck.

**Trochosa terricola** Thorell. Holarctic. Widespread boreal and mixed deciduous.

**Gnaphosidae**

**Drassodes neglectus** Keyserling. Widespread North America from southern boreal area south to Mexico.

**Haplodrassus signifer** Koch. Holarctic. Widespread in most of central and eastern North America.

**Zelotes** sp. imm.


**Clubionidae**

**Agroeca ornata** Banks. Widespread boreal, south into northern United States.

**Thomisidae**

**Misumena vatia** Clerck. Holarctic. Widespread. Commonly called the “Flower Spider” or “Golden Rod Spider”.

**Philodromidae**

**Ebo pepinensis** Gertsch.

**Philodromus** sp. imm.

**Xysticus elegans** Keyserling. Widespread North America. Boreal, south to Georgia and west to the Rocky Mountains.

**Salticidae**

**Pellenes americanus** Keyserling.

**Amaurobiidae**

**Amaurobius borealis** Emerton. Widespread boreal from northern British Columbia and Yukon Territory east to Labrador, south to Pennsylvania and west to Wisconsin and Minnesota. Common in leaf litter.

**Callioplus euopus** Bishop and Crosby. Widespread boreal from northern British Columbia to Newfoundland, south to New England. Common in leaf litter in mixed conifer-deciduous forests.

**Callioplus tibialis** Emerton. New England, Maritimes, Newfoundland Labrador, southern Ontario and Quebec. Rare.
Callobius bennetti Blackwall. Widespread eastern North America in broadleaf and mixed forests. Very commonly found.

Dictynidae

Dictyna alaskae Chamberlin and Ivie. Alaska south to Montana and east to Labrador.

*not captured at a designated trap site and not included in any calculations.

Acknowledgments

The authors wish to thank Peter Tropea and Sai Kung Lee for assisting in the collecting of spiders, and John Carry and Dan Gilbert for the forest inventory. Facilities at Lakehead University were utilized for the soil analysis. Thanks also are extended to the National Museums of Canada for sponsoring this project.

Literature Cited


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Vegetation and Flora of the Caribou Mountains, Alberta

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The mire complex and forests of the Caribou Mountains contain three forest community types dominated by Black Spruce: Picea mariana/feather moss, Picea mariana-feather moss-Cladina, and Picea mariana/Sphagnum-Cladina. These widespread forest types have strong affinities with vegetation types described from more northerly areas. Two other forest community types are recognized: Populus tremuloides-Picea glauca and Picea glauca-Betula papyrifera. Community types of the mire complex include: two flark community types, Menyanthes trifoliata and Carex limosa; two string community types, Betula glandulosa and Picea mariana/Rubus chamaemorus; three peat plateau community types; two very widespread Carex aquatilis community types; and a rare Eleocharis pauciflora community type. The known vascular flora presently consists of 195 species and the non-vascular flora consists of 22 lichen, 85 moss, and 4 liverwort species. Two vascular flora species are not known to occur elsewhere in Alberta. The vegetation and flora have northern boreal woodland affinities, suggesting a reclassification of the Caribou Mountains from an outlier of the Lower Foothills to Subarctic or Northern Transition.

Key Words: Caribou Mountains, Alberta, vegetation, flora, peat plateaux, patterned fens, boreal forest, peatlands.

The Caribou Mountains of north central Alberta (Figure 1) are isolated and little work has been done on their vegetation and flora. Raup (1933) visited the easternmost portion in the early 1930's and, stressing the importance of Pinus contorta, referred to the area as an outlier of the Cordilleran forest. He also described large areas as being densely covered with Black Spruce forests. Moss (1953 a, b) visited the southern part of the area in the early 1950's and described the large areas covered by muskabs and underlain by discontinuous permafrost. Rowe (1972) classified the Caribou Mountains as a northern outlier of the Lower Foothills Section of the Boreal Forest, presumably because of the reputedly widespread occurrence of Pinus contorta. In 1976 Horton et al. (1979) visited the plateau and reported on the habitats of the fourteen species of Sphagnum found there. As well, they described three wetland plant community types: treed-tundra, sedge thaw pockets, and shrub-bordered streams.

The present study is based on fieldwork conducted by the Alberta Ecological Survey on 19-21 August 1976 in the southern part of the plateau near Semo Lake and Foggy Tower and by the Natural Areas Program on 19-22 July 1979 in the northern part of the plateau around Horseshoe Lake and on the northern slope (Figure 1). The study was done to assist in the selection of candidate Ecological Reserves for the Alberta Government Natural Areas Program.

Study Area

The Caribou Mountains area in northern Alberta is a low saucer-shaped plateau that rises 600-700 m (1970-2300 ft.) above the surrounding lowlands. The highest elevations in northern Alberta are within the Caribou Mountains and reach a maximum of 1030 m (3380 ft.), in the western part of the plateau. The topography is gently rolling to rolling with some large areas of undulating to depressional relief (Lindsay et al. 1960). The plateau, including those areas above 770 m (2526 ft.), has a total area of about 1M ha with 87 000 ha within Wood Buffalo National Park. 160 000 ha or about 16% of the plateau are above 920 m (3020 ft.). Drainage is generally poor and numerous lakes occur. The four largest lakes, Margaret, Wentzel, Eva and Pitchimi cover about 16 000 ha. Drainage is to the Peace and Mackenzie Rivers. The slopes of the plateau are generally very gentle, with the steepest slopes occurring in a large area on the southern part and small sections on the northwestern and western part. The steepest slopes, on the northwest side, rise 310 m in 2 km. The area was glaciated by Laurentide Ice during the Wisconsin, but became ice-free around 9500BP (Ritchie 1976). The glacier advanced into the area from the Keewatin centre of glaciation to the northeast (Gravenor and Ellwood 1957). The Caribous formed an obstacle to the general flow of ice and this resulted in flutings on the northeastern slopes.

The bedrock geology consists of Cretaceous shales and sandstones, with some Tertiary gravels capping the high hills. These gravels protect the upland from erosion (Lindsay et al. 1960). Organic soils are widespread and often contain permafrost starting at

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depths of 30 to 75 cm from the surface (Lindsay and Odynsky 1965). Where mineral soils occur, they are principally Gray Luvisols, Dystic Brunisols and Cumulic Regosols developed on glacial till. There is no evidence of permafrost in the mineral soils.

The climate of the area is boreal, cold-temperate, continental with cold winters and short, cool summers. Meteorological data are scanty and incomplete for the area. There are two May to September meteorological stations on the plateau but these have data gaps. Ft. Vermilion is the closest year-round station, but being 50 km south of and 500 m below the plateau, is drier and warmer. Based on 30-year normals (1941-1970) Ft. Vermilion has a mean daily temperature of -1.4°C and a total annual precipitation of 360 mm with snowfall averaging 136 cm. For the four months growing season (May-August), the 1975 to 1977 means for Ft. Vermilion were 259 mm for total precipitation and 14.4°C for mean monthly temperature. Over the same period, Foggy Tower on the plateau recorded means of 318 mm for precipitation and 11.2°C for temperature.

Methods

A rapid reconnaissance technique was used to describe vegetation types in 1976. Investigators selected homogeneous stands, 0.5 ha or larger, from airphotos and ground examination. All species present in the stand were recorded and a cover class value assigned to each using an eight-point scale: R, rare; +, < 1%; 1, 1-5%; 2, 6-25%; 3, 26-50%; 4, 51-75%; 5, 76-95%; 6, 96-100% (Daubenmire 1959).

In 1979, this method was used for most stands. A systematic quantitative sampling technique was used on strings and flarks, where more detailed information was desired. A 50 m baseline was established along the centre of the long axis of the string or flark. The vegetation was sampled every 5 m along the baseline, using a 1 m² quadrat frame, for a total of 10 quadrats. Two transects were placed on each fen, one each on a string and a flark. A similar systematic sampling technique was used to characterize the transition between string and flark. A transect of continuous 1 m² quadrats, perpendicular to the long axis of a string, was started in a flark and placed across the string to the next flark. Transect length depended on the particular string-flark transition. Tree cores for stand age determination were obtained where possible at 20-30 cm heights. On peat plateau 3, temperatures at 10 and 50 cm depths were measured along a transect using a microvoltmeter.

Plant voucher specimens were collected and are deposited in the herbarium of the University of Alberta (ALTA). Nomenclature for vasculars follows Moss (1959) except for *Boschniakia rossica*, *Pinguicula villosa*, *Pedicularis sudetica* (Hulten 1968); lichens follow Hale and Culberson (1970); liverworts follow Stotler and Crandall-Stotler (1977); and bryophytes follow Crum (1976). Soil nomenclature and concepts follow those of the Canada Soil Survey Committee (1978).

Results and Discussion

Mire Complex

Patterned Fens

In the northwestern part of the Caribou Plateau are extensive peatlands of the patterned fen or stringmire type (Moore and Bellamy 1974) which cover approximately 960 ha in an area of 9300 ha. The largest of the fens is 175 ha. They occur on nearly level topography with long, simple slopes, and consist of alternating peat ridges or strings (from German "strang", Hein selman 1965) and water-filled depressions or flarks (from Swedish, Sjors 1963). The patterning is usually somewhat concentric. These mire complexes contain both rich and poor fen sections as indicated by species richness and indicator species (Slack et al. 1980). This type of patterned peatland is a general feature of the subarctic and is also common in the main boreal zone (Sjors 1963).

The width and relative relief of the strings and flarks varies both within and between fens. The average width of eight flarks measured in one fen was 20.6 m (range 4-30.4 m) and the width of eight strings was 4.9 m (range 2-9 m). Strings containing trees averaged 30 cm above water level while those without trees were generally not as high, but with a minimum height of 15 cm. Tree ages varied considerably (41-182 years) on the same and adjacent strings (Table 1) and no age-related patterns are discernible.

In the flarks of fen one, "rises" less than 15 cm above mean water level and of various lengths were frequent. These are not considered strings although they were usually parallel to the strings. Their vegetation resembles the flarks more than the strings, with *Andromeda polifolia* and *Sphagnum* spp. dominant. In fen one there were also hummocks with *Salix pedicellars, Andromeda polifolia, Oxyccocus microcarpus, Cladina rangiferina* and *Sphagnum* spp. which did not have a frozen layer (i.e. are not incipient peat plateaus). The developmental processes of these rises and mounds are unknown, but their possible relation to strings and peat plateaus is intriguing. In fen two, several strings had a frozen layer within 50 cm of the surface on July 20, 1979. Fen two also had the highest density of peat plateaus.

Flark Vegetation

*Menyanthes trifoliata* Community Type

*Menyanthes trifoliata* has high cover in all quadrats
Table 1. Tree ages on strings and peat plateaus within patterned fens

<table>
<thead>
<tr>
<th>Species</th>
<th>Tree hgt (m)</th>
<th>DBH (cm)</th>
<th>Age (yrs)</th>
<th>Origin</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Fen 1</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>String A</td>
<td>Picea mariana</td>
<td>6</td>
<td>12.4</td>
<td>73</td>
</tr>
<tr>
<td>Picea mariana</td>
<td>4.5</td>
<td>5.8</td>
<td>60</td>
<td>1919</td>
</tr>
<tr>
<td>Picea mariana</td>
<td>3</td>
<td>4.6</td>
<td>123</td>
<td>1856</td>
</tr>
<tr>
<td>String B</td>
<td>Larix laricina</td>
<td>2.6</td>
<td>2.7</td>
<td>41</td>
</tr>
<tr>
<td>Larix laricina</td>
<td>5</td>
<td>10.6</td>
<td>182</td>
<td>1797</td>
</tr>
<tr>
<td>Picea mariana</td>
<td>4</td>
<td>7</td>
<td>78</td>
<td>1901</td>
</tr>
<tr>
<td>Picea mariana</td>
<td>5.5</td>
<td>11.9</td>
<td>111</td>
<td>1868</td>
</tr>
<tr>
<td><strong>Fen 2</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>String A</td>
<td>Picea mariana</td>
<td>2.5</td>
<td>3</td>
<td>73</td>
</tr>
<tr>
<td>String B</td>
<td>Picea mariana</td>
<td>3</td>
<td>5.4</td>
<td>122</td>
</tr>
<tr>
<td>String C</td>
<td>Picea mariana</td>
<td>2.7</td>
<td>4</td>
<td>62</td>
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<tr>
<td><strong>Fen 3</strong></td>
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<td></td>
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<td></td>
</tr>
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<td>5.5</td>
<td>7.0</td>
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<tr>
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<td>Larix laricina</td>
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<td>10.1</td>
<td>66</td>
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<tr>
<td><strong>Peat Plateau</strong></td>
<td></td>
<td></td>
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<td></td>
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<tr>
<td>String A</td>
<td>Larix laricina</td>
<td>2.0</td>
<td>4</td>
<td>119</td>
</tr>
<tr>
<td>Picea mariana</td>
<td>1.7</td>
<td>5</td>
<td>102</td>
<td>1877</td>
</tr>
</tbody>
</table>

of this community type, averaging 20% (Table 2). Scorpidium scorpioides is the dominant bryophyte, forming continuous carpets with Drepanocladus revolvens and Meesia triqueta. Carex limosa and Juncus stygius also occur with high frequency. Eight vascular and three bryophyte species occur in the community type. It is very similar to the Scorpidium scorpioides-Drepanocladus revolvens-Carex limosa community type in rich fens of western Alberta (Slack et al. 1980).

**Carex limosa Community Type**

**Carex limosa** is the dominant vascular plant in this community type (Table 2). Sphagnum jenseni is the dominant bryophyte with lesser amounts of Cladopodiella fluitans. Drosera anglica occurs with high frequency but low cover. A total of four vascular and five bryophyte species occur in this community type. It is very similar to the Carex limosa association described from Swan Hills in central Alberta (Vitt et al. 1975).

**String Vegetation**

**Betula glandulosa Community Type**

A dense cover of Betula glandulosa (Table 2) characterizes this community type. Larix laricina, Menyanthes trifoliata, Picea mariana and Salix pedicellaris are also important. Dominant bryophytes include Sphagnum angustifolium, *S. warnstorffii* and Scorpidium scorpioides. Tomenhyphnum nitens, a rich-fen indicator (Vitt et al. 1975), is also present. Eighteen vascular and 13 bryophyte species occur in the community type. It is similar to the Tomenhyphnum nitens-Betula glandulifera-Larix laricina community type of western Alberta rich fens (Slack et al. 1980).

**Picea mariana**/Rubus chamaemorus Community Type

Strings of this community type appear to be raised higher above mean water level than those of the Betula glandulosa community type. Rubus chamaemorus and Chamaedaphne calyculata are dominant understory plants. These two species are also significant components of the similar Picea mariana-Ledum groenlandicum-Sphagnum magellanicum association in Swan Hills (Vitt et al. 1975). Important bryophytes include Sphagnum angustifolium, S. fuscum, *S. warnstorffii* and Pleurozium schreberi. Ten vascular and 19 bryophyte species occur in this community type.

**Direct Gradient Analysis of Ecotones**

In both strings and flarks, moisture is an influential factor in species presence and performance. A direct gradient analysis of flark-string-flark sequences from two fens (Figure 2 and 3) illustrates this influence.

In fen 1 (Figure 2), Picea mariana is restricted to the middle of the string. Three shrubs, Betula glandulosa, Andromeda polifolia and Salix pedicellars occur in the transition between string and flark. Menyanthes trifoliata is the most abundant vascular plant in the flarks, but its cover decreases on the strings. Carex limosa is most abundant in the flarks. Sphagnum angustifolium is the dominant string bryophyte, but is replaced by *S. warnstorffii* and Aulacomnium palustre in the transition zone and by Scorpidium scorpioides, Drepanocladus revolvens and Meesia triqueta in the flarks.

In fen 2 (Figure 3) a similar pattern prevails. Picea mariana is restricted to the middle of the string. Betula
<table>
<thead>
<tr>
<th>VASCULARS</th>
<th>Menyanthes trifoliata Community Type (fen 1)</th>
<th>Carex limosa Community Type (fen 2)</th>
<th>Betula glandulosa Community Type (fen 1)</th>
<th>Picea mariana Community Type (fen 2)</th>
<th>Peat plateaus #1</th>
<th>#2</th>
<th>#3</th>
<th>Carex aquatilis Community Type</th>
<th>Eleocharis pacaflora Community Type</th>
<th>Shrub transition zone</th>
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<tbody>
<tr>
<td>Andromeda polifolia</td>
<td>+</td>
<td>.</td>
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<td>.</td>
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<td>1</td>
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<td>.</td>
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<tr>
<td>Arctostaphylos rubra</td>
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<tr>
<td>Betula glandulosa</td>
<td>.</td>
<td>4</td>
<td>1</td>
<td>.</td>
<td>.</td>
<td>.</td>
<td>1</td>
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<tr>
<td>Calamagrostis canadensis</td>
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<td>.</td>
<td>1</td>
<td>.</td>
<td>1</td>
<td>1</td>
<td>2</td>
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<td>3</td>
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<tr>
<td>Carex aquatilis</td>
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<td>+</td>
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<tr>
<td>Carex diandra</td>
<td>+</td>
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<tr>
<td>Carex gynocrates</td>
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<tr>
<td>Carex interior</td>
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<td>+</td>
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<td>Carex rostrata</td>
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<tr>
<td>Carex tenuiforma</td>
<td>.</td>
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<td>.</td>
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<td>.</td>
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<tr>
<td>Chamaedaphne calyculata</td>
<td>.</td>
<td>.</td>
<td>2</td>
<td>.</td>
<td>+</td>
<td>.</td>
<td>.</td>
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<tr>
<td>Chrysosplenium iowense</td>
<td>.</td>
<td>.</td>
<td>.</td>
<td>.</td>
<td>+</td>
<td>.</td>
<td>.</td>
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<tr>
<td>Drosera anglica</td>
<td>+</td>
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continued
Table 2. Association table of species present in the mire complexes in the Caribou Mountains (concluded)

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<th>Vasculars</th>
<th>Menyanthes trifoliata Community Type (fen 1)</th>
<th>Carex limosa Community Type (fen 2)</th>
<th>Betula glandulosa Community Type (fen 1)</th>
<th>Picea mariana Community Type (fen 2)</th>
<th>Peat plateaus #1</th>
<th>#2</th>
<th>#3</th>
<th>Carex aquatilis community Type 1</th>
<th>Type 2</th>
<th>Eleocharis pauciflora Community transition zone Shrub Type</th>
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glandulosa is restricted to the transition zone, while Ledum groenlandicum and Chamaedaphne calyculata are more widely distributed. Carex limosa is restricted to the flarks. Cladina rangiferina, a lichen, has a narrow distribution on the string top. Sphagnum magellanicum and S. angustifolium have a wide distribution on the string. Vitt et al. (1975) found that Sphagnum angustifolium occurred on the string edges, while S. magellanicum occurred more in the center. Sphagnum jenseni and Cladopodiella fluitans occurred only in the flarks.

Peat Plateaus

The peat plateaus reported here are found in patterned fens in the northwest part of the Caribou Mountains. They have been previously reported from both the southern (Moss 1953) and northern parts (Lindsay et al. 1960) of the plateau. Peat plateau refers to a hummock of variable size with a frozen core rising out of a peatland (Brown 1968a). Peat plateaus vary in size from a few to hundreds of meters in diameter in the discontinuous permafrost zone (Zoltai and Tarnocai 1975) and are about 1 m high. Frozen peat landforms generally occur in the discontinuous permafrost zone of the Northern Hemisphere and the southern limit of permafrost is usually in raised peat landforms such as palsas and peat plateaus (Brown 1968a). In Alberta, permafrost peat landforms occur generally north of a line from Cold lake to Peace River (Lindsay and Odynsky 1965) and are common in northern Alberta (Reid 1977). The location of the Caribou Mountains peat plateaus in patterned fens is very similar to that described by Reid (1977).

Three peat plateaus which occur as islands in the flarks of stringmires were studied intensively. The plant cover of peat plateau 1 (Table 2) is dominated by Drepanocladus revolvens and Carex limosa. This community is very similar to the surrounding flark (Menyanthes trifoliata community type) except that Menyanthes trifoliata is absent on the peat plateau and Scorpidium scorpioides is greatly reduced in cover. Scorpidium scorpioides is less tolerant of the drier conditions of the peat plateau (Slack et al. 1980). This similarity to the flark may be because of the peat plateau's low relief, 15-20 cm higher than the surrounding flark. The peat plateau was 7 × 15 m; the maximum height was 20 cm; and a frozen layer on July 20, 1979 averaged 10 cm below ground surface. Although no depth to permafrost measurements were made later in the season at these specific sites, other researchers have found frozen layers in the fall (Lindsay et al. 1960 report frozen layers at 46 cm in September).

Peat plateau 2 (Table 2, Figure 4) is substantially different from the Menyanthes trifoliata community
Figure 2. Smoothed curves of height above water table and cover of the major vascular and bryophyte plant species along a transect through a flark-string-flark complex in fen 1. Top = height, middle = vasculars, bottom = bryophytes.
Figure 3. Smoothed curves of height above water table and cover of the major vascular and bryophyte plant species along a transect through a flark-string-flark complex in fen 2. Top = height, middle = vascular, bottom = bryophytes.
Other species occurring but not mapped:

Salix pedicellaris
Oxycoccus microcarpus
Menyanthes trifoliata
Carex limosa
C. interior

Figure 4. Species occurrence and contour map of peat plateau #2. Contour interval = 5 cm.
Figure 5. Species occurrence and contour map of peat plateau #3. Top = contours, bottom = species occurrence. Bryophytes solid lines; vasculars, broken lines

1. Sphagnum angustifolium
2. Sphagnum fuscum
3. Sphagnum russowii
4. Sphagnum warnstorfii
5. Aulacomium palustre
6. Dicranum undulatum
7. Drepanocladus uncinatus
8. Icmadophila ericetorum
9. Tomentypnum nitens
10. Tomentypnum falcifolium
11. Scorpipodium scorpioides
12. Drepanocladus revolvens
13. Mesia triqueta
14. Picea mariana
15. Betula glandulosa
16. Larix laricina

Other species occurring on peat plateau but not mapped:

- Ledum groenlandicum
- Salix pedicellaris
- Andromeda polifolia
- Oxycoccus microcarpus
- Carex aquatilis
- Rubus chamaemorus
- Smilacina trifolia
- Triglochin maritima
- Menyanthes trifoliata
- Pinguicula villosa
- Carex diandra
- Potentilla palustris
- Carex limosa
Figure 6. Height, temperature profiles and frozen layer depths of peat plateau #3 (measured 20 July 1979). Solid line is surface height above the water. Ice core refers to frozen core.
type which surrounds it. The dominant plant cover of the peat plateau consists of *Sphagnum warnstorfii*, *Andromeda polifolia*, and *Carex limosa*. *Cladina rangiferina* occurs in this peat plateau suggesting drier conditions than peat plateau 1. This peat plateau was 1.3 × 0.6 m; maximum height was 45 cm (Figure 4); and the frozen layer on 20 July 1979 averaged 20 cm below the summit of the peat plateau, although this varied greatly.

Peat plateau 3 (Table 2, Figure 5) has plant cover dominated by *Sphagnum angustifolium*, *Picea mariana*, *Ledum groenlandicum* and *Rubus chamaemorus*. As well, species richness is much greater with 26 species on peat plateau 3, 10 species on peat plateau 2, and 6 species on peat plateau 1. Peat plateau 3 was 10.5 × 5 m and the maximum height was 50 cm. Figure 6 shows height, temperature profiles at 10 and 50 cm depths and depths of the frozen layer along a transect across peat plateau 3. In general, the depth to the frozen layer was shallowest and temperatures were lowest on the highest portion. Two stunted trees were aged on peat plateau 3: a *Larix laricina* had an origin in 1867, while a *Picea mariana* started in 1877 (Table 1).

Various developmental stages of peat plateau development have been observed in northern Canada (Reid 1977; Zoltai 1972). Peat plateau 1 appears to be an incipient palsa since its relief is low and its vegetation differs only slightly from the surrounding flanks. Peat plateau 2 appears to be a well-developed, stable palsa. It is either increasing in size or remaining stable since there were no signs of desiccation cracks, vegetation demise, peat deflation, slumping or exposure of the frozen core. Peat plateau 3 is degrading as evidenced by the thaw pocket near the center-edge of the plateau (Figure 5) which has dead and dying *Picea mariana* and *Larix laricina* trees around it and tilted towards it. The reduction of tree cover perhaps initiated a change in the topography of the permafrost table (Brown 1968b) eventually forming the thaw-pocket.

**Carex aquatilis** fens

Fens dominated by *Carex aquatilis* occur commonly on the plateau usually adjacent to sluggish streams or shallow lakes. Two community types are distinguished: *Carex aquatilis-C. rostrata*, and *Carex aquatilis-C. pauciflora*. In the first, *Carex rostrata* is important along with *Salix pedicellaris* and *Potentilla palustris*. In the second, *Carex rostrata* is absent and *C. pauciflora*, *Eriophorum vaginatum* and *Andromeda polifolia* are important (Table 2). Similar communities dominated by *Carex aquatilis* are common across boreal (Viereck and Dyrness 1980, Moss 1953b, Jeglum et al. 1973) and Rocky Mountain (Achuff and Corns 1981) regions.

**Eleocharis pauciflora** Community Type

This community type appears to be rare and is described from the northwestern corner of the study area. It occurs in the transition between patterned fen and upland *Picea mariana* forests. *Eleocharis pauciflora* is dominant (Table 2) with lesser amounts of *Betula glandulosa*, *Sphagnum warnstorfii*, *Carex limosa* and *Andromeda polifolia*. The species richness and the occurrence of such indicators as *Sphagnum warnstorfii* and *Tomentypnum niten* (Vitt et al. 1975) suggest more minerotrophic conditions than those in the adjacent patterned fen.

**Forests**

*Picea mariana* Forests

Communities dominated by *Picea mariana* cover large areas of the Caribou Mountains in both upland and wetland sites. The three community types recognized here have strong affinities with vegetation types described from Alaska (Dyrness and Grigal 1979, Vie- reek 1975), Yukon Territory (Hettinger et al. 1973), and the western Northwest Territories (Reid 1977). Similarities are also apparent with *Picea mariana* stands described by La Roë (1967) from the western boreal forest.

*Picea mariana*/feather moss Community Type

The *Picea mariana*/feather moss community type is a closed forest occurring on moderately well to imperfectly drained mineral soils. The tree layer is 7-10 m tall and dominated by *Picea mariana* (Table 3). Diameter at breast height (dbh, 1.35 m) averages 10 cm. *Ledum groenlandicum* has the highest cover in the shrub layer. In the herb-dwarf shrub layer *Vaccinium vitis-idaea* is commonly dominant and associated with *Emetrum nigrum*, *Equisetum sylvaticum* and *Cornus canadensis*. Feather mosses (*Hylocomium splendens*, *Pleurozium schreberi*) usually dominate the bryoid layer. The soil often has a thick surficial organic layer but it is seldom thick enough to constitute an Organic soil.

This community type is very similar to the Black Spruce/feather moss vegetation unit of Viereek (1975) and Dyrness and Grigal (1979) in Alaskan boreal forests. In northern Alberta, a similar upland Black Spruce-feather moss forest has been described by Moss (1953a).

*Picea mariana*/feather moss — *Cladina* Community Type

The *Picea mariana*/feather moss — *Cladina* community type is an open forest occurring on well drained mineral soils. The sites are generally drier than the *Picea mariana*/feather moss community type. Only one stand was sampled (Table 3) although our field notes indicate a more widespread occurrence of this
TABLE 3. Association table of species present in the forests of the Caribou Mountains

<table>
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<tr>
<th>VASCULARS</th>
<th>Picea mariana/feathermoss</th>
<th>Picea mariana/Sphagnum-Cladina</th>
<th>Picea mariana/Cladina</th>
<th>1961 Burn</th>
<th>Populus tremuloides-Picea glauca</th>
<th>Picea glauca-Betula papyrifera</th>
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<td><em>Senecio indecorus</em></td>
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(continued)
Table 3. Association table of species present in the forests of the Caribou Mountains (continued)

<table>
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<tr>
<th>VASCULARS</th>
<th>Picea mariana/feathermoss</th>
<th>Picea mariana/feathermoss - Cladina</th>
<th>Picea mariana/Sphagnum - Cladina</th>
<th>1961 Burn</th>
<th>Populus tremuloides - Picea glauca - Betula papyrifera</th>
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<td>Viola orbiculata</td>
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<td>NON-VASCULARS</td>
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<td>Brachythecium salebrosum</td>
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<td>Cetraria pinastre</td>
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<td>Dicranum flagellare</td>
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<td>Dicranum fuscescens</td>
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<td>Dicranum polysetum</td>
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<td>Dicranum undulatum</td>
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<td>Distichium capillaceum</td>
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<td>Evertnia mesomorpha</td>
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<td>Hlycomium splendens</td>
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<tr>
<td>Hypnum pratense</td>
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<td>Hypogynnia physodes</td>
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<tr>
<td>Icelandophila ericetorum</td>
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<td>Marchantia polymorpha</td>
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<td>Mylia anomala</td>
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<tr>
<td>Parmelia sulcata</td>
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<tr>
<td>Peltigera aphthosa</td>
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<td>Peltigera canina</td>
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<td>Pleurozium schreiberi</td>
<td>2</td>
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<tr>
<td>Pohlia cruda</td>
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type in the Caribou Mountains. *Picea mariana*, with a height of about 8 m and an average dbh of 8 cm, dominates the scattered tree layer. *Ledum groenlandicum* is dominant in the shrub layer and *Vaccinium vitis-idaea* is most important in the herb-dwarf shrub layer. *Cladina* spp., especially *Cladina mitis*, have the highest cover in the bryoid layer with lesser amounts of feather moss (*Pleurozium schreberi*) and *Cetraria nivalis* occurring.

Similar Alaskan types are Black Spruce/feather-moss/*Cladonia* (Viereck 1975) and open Black Spruce/feather moss/*Cladonia* (Dyrness and Grigal 1979). This community type also falls within Moss’s (1953a) broader “black spruce-feather moss association”.

### *Picea mariana/Sphagnum - Cladina* Community Type

This is an open forest community type occurring on poorly drained, Organic and Organic Cryosol soils. Scattered *Picea mariana*, 4-6 m tall, dominate the tree layer (Table 3). *Ledum groenlandicum* and *L. palustre* have the highest cover in the shrub layer. *Rubus chamaemorus* and *Vaccinium vitis-idaea* are characteristic of the herb-dwarf shrub layer. The ground surface has a hummock and hollow pattern with *Sphagnum* spp. in the hollows and sides of the hummocks, and *Cladina* spp., especially *Cladina mitis* and *C. rangiferina*, on the drier hummock tops. Permafrost often occurs in this type at a depth of 35-45 cm.

This community type is very similar to the Black Spruce/*Sphagnum-Cladonia* type of Viereck (1975) and the open Black Spruce/*Sphagnum* type of Dyrness and Grigal (1979). Moss (1953a) described a somewhat broader “black spruce-peat moss association” from a number of sites in northern Alberta. Reid (1977) described a similar type as widespread in the Cameron Hills of extreme northwestern Alberta and also in the southwestern Northwest Territories. Horton et al. (1979) include this community type in “treed-tundra”.

Two stands of this community type were in an area which burned 15 years previously. The regenerating *Picea mariana* are about 2 m tall and of very low cover. *Ledum groenlandicum* dominates the shrub layer. The herb-dwarf shrub layer has a greater species richness than in the unburned stands with species such as *Epilobium angustifolium* and *Rubus strigosus* entering the community following disturbance by fire. *Sphagnum* spp. dominate the bryoid layer as in the unburned stands.

Nearly all the species present in the unburned stands are also present in the burned stands. The main effect of this apparently moderate intensity fire was not the elimination of the entire community. Rather,
the tree canopy was eliminated temporarily, new species entered the community, especially where the peat was burned, and the relative importances of the species were changed. Thus, postfire succession appears to involve re-establishment of a tree canopy, the introduction and later elimination of some species (e.g., Epilobium angustifolium), and a general shifting of relative species importances as time since fire increases. Most of the species of this community type appear to remain throughout the successional stages.

**Populus tremuloides - Picea glauca Community Type**

This community type occurs within forests of *Populus tremuloides - Picea glauca* closed forests, with *Picea mariana* frequently present, occur on the lower to upper slopes around the perimeter of the plateau. Important understory plants include *Elymus innovatus*, *Epilobium angustifolium*, *Cornus canadensis*, *Lycopodium* spp. and *Hylocomium splendens* (Table 3). This community type is similar to the *Viburnum edule*/*Hylocomium splendens* community type of other highland plateaus in northern Alberta (Achuff and La Roi 1977).

**Picea glauca - Betula papyrifera Community Type**

This community type occurs within forests of *Populus tremuloides - Picea glauca* or pure *Picea glauca* and is usually 1 ha in size. *Betula papyrifera* may reach heights of 10 m with 25 cm dbh and the one tree that was cored was 57 years old. *Picea glauca* may be quite large, up to 25 m tall and 40-50 cm dbh. *Alnus crispa* is prevalent in the understory. Other important understory plants are *Cornus canadensis*, *Viburnum edule*, *Hylocomium splendens*, *Pleurozium schreberi* and *Ptilium crista-castrensis* (Table 3). Moss (1953a) describes a similar type within his broader “white spruce” association from Lesser Slave Lake in central Alberta. In its mixedwood physiognomy, this community type is similar to the *Viburnum edule*/*Hylocomium splendens* community type which Achuff and La Roi (1977) described from northern Alberta.

**Other Vegetation**

There are numerous lakes and ponds in the Caribou Mountains, most of which are fairly shallow and rimmed by peatland. *Carex aquatilis* and *Carex rostrata* are common shoreline species. *Calamagrostis canadensis*, *Betula glandulosa*, *Potentilla palustris* and *Chamaedaphne calyculata* are also frequently found along the shoreline. *Potamogeton gramineus* and *Nuphar variegatum* are the most prevalent aquatic species.

Mesophytic shrub transition communities generally occur between the Black Spruce communities and the fens, or they occupy the area between upland sites and more aquatic habitats, such as lakes and streams. Important shrubs are *Salix pedicellaris*, *S. planifolia*, and *Betula glandulosa*. *Sphagnum teres*, *S. warnstorffii*, *S. squarrosum* and *Aulacomnium palustre* are the major bryophytes. *Rubus chamaemorus* and *Calamagrostis neglecta* frequently occur. (Table 2).

**Flora**


The non-vascular flora presently consists of 109 species of which there are 21 lichens, 84 bryophytes and 4 hepatics. Species-rich genera include *Sphagnum* with 15 species, *Cladonia* (9), *Dicranum* (7), *Drepanocladus* (4), *Pohlia* (4) and *Polytrichum* (4). Collections to date have only found this number of plant species. In comparison to other similar areas the Caribou Mountains have probably not been well collected (Bird et al. 1977, Bird et al. 1980 and 1981).

Two vascular species collected in the Caribou are not known to occur elsewhere in Alberta. *Boschniakia rossica*, a vascular plant parasitic on the roots of *Alnus crispa* and *Picea* spp. was found on the north slope of the Caribou Mountains (59°23'N, 115°45'W: Lee 1980). It frequently occurs in low and high subarctic regions in western North America, especially Alaska (Scoggan 1979). *Pinguicula villosa* occurs mainly in high arctic and both high and low subarctic regions (Scoggan 1979). In the Caribou Mountains it was found growing in *Sphagnum warnstorffii* on the sides of a degrading peat plateau in the flark of a patterned fen at about 59°29'N and 115°47'W.

*Pedicularis sudetica* was growing in a rich fen located at about 59°29'N and 115°47'W. It and two bryophyte species collected - *Pohlia bulbifera* and *Polytrichum gracile* have been reported only in one other location each in Alberta. (A list of the flora is available at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Canada K1A 0S2).

**Ecological Classification**

Rowe (1972) classified the Caribou Mountains as an outlier of the Lower Foothills (B19a) Section of the Boreal Forest Region. This was presumably based largely on the occurrence of *Pinus contorta* (Moss 1953a, Raup 1935) and Raup’s comment that the Caribou Mountains are “an outlier of northern Rocky Mountain or foothill forest” (Raup 1946). However, while the Caribou Mountains do contain
Pinus contorta, the area differs from the rest of the Lower Foothills Section, including outliers such as Swan Hills, in several significant ways. The overall vegetation composition is different in that *Picea mariana* is the predominant tree and *Picea mariana* forests are the most prevalent vegetation type. *Pinus contorta* usually occurs in mixed forests with *Picea mariana*, a situation quite different from the rest of the Lower Foothills. The general landscape pattern, with much of the area occupied by peatland with discontinuous permafrost and the presence of peat plateaus also differentiates the area. The absence of *Abies balsamea* and the presence of plants such as *Boschniakia rossica*, *Pedicularis sudetica* and *Pinguicula villosa* indicate affinities with more northern areas. The presence of birds such as Red-throated Loon, Gray-cheeked Thrush and Northern Phalarope and the absence of other birds typical of the Lower Foothills (e.g. Marsh Hawk, Black Capped Chickadee, Common Flicker) (Hohn and Burns 1975, 1976; Hohn and Marklevitz 1974; Hohn and Musell 1980) further distinguish the Caribou Mountains from other portions of the Lower Foothills and indicate more northern affinities.

In view of these differences the Caribou Mountains are better classified as Subarctic or, in Rowe's (1972) classification, as an outlier of the Northern Transition (B27) Section. Preliminary information indicates that the Cameron Hills in northwestern Alberta also should be included with the Caribou Mountains as Subarctic or Northwest Transition (Achuff and Wallis 1977).

Acknowledgments
Field work was assisted by A. Cairns, R. Hastings, D. J. Mussell and G. F. Tande. D. Horton and D. H. Vitt identified or verified bryophyte and lichen collections. J. G. Packer verified many vascular plant collections. W. J. Cody provided information on species ranges of *Boschniakia rossica*, *Pinguicula villosa* and *Pedicularis sudetica*. J. S. Campbell, A. J. Gould, D. G. Horton, G. P. Kershaw and D. H. Vitt reviewed portions of the manuscript.

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Literature Cited


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Parameters of Population and Seasonal Activity of Striped Skunks, *Mephitis mephitis*, in Alberta and Saskatchewan

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Due to differing habitat utilization, sex and age proportions of Striped Skunks (*Mephitis mephitis*) collected from 1972 to 1978 in Alberta and adjacent Saskatchewan varied seasonally. Patterns of weight gain and loss related to winter denning and reproduction. Young skunks did not attain adult weights their first year and experienced greater mortality than adults during winter denning. Weights of fall-captured skunks varied among years and in one year between north and south portions of the study area. Seasonal activity is discussed in relation to capture data. We suggest greater occurrences of rabies in November and December in Striped Skunks in western Canada than the United States results from greater mobility and mixing in fall in northern areas.


Early studies of the Striped Skunk, *Mephitis mephitis*, (Seton 1926; Hamilton 1936, 1937; Selko 1938a, 1938b, Allen 1939; Jones 1939) were related to fur market or natural history interests. Recognition of the role of Striped Skunks as predators of game and as rabies reservoir resulted in a number of additional studies (Upham 1967; Verts 1967; Bailey 1971; Houseknecht 1971; Rakowski 1972; Storm 1972). These studies examined specific or local skunk populations; comparatively few data are available on skunk populations on a regional basis.

In response to the spread of rabies in skunks across Saskatchewan (Hayles and Dryden 1970) Alberta Agriculture, Agriculture Canada (Animal Health Directorate), and the Alberta Fish and Wildlife Division undertook to limit the spread of the disease in Alberta. The primary instrument of this effort was a zone of skunk population reduction (control zone) within Alberta along the Saskatchewan boundary (Alsager 1973). Supporting activities were aimed at monitoring the occurrence of rabies (Gunson et al. 1978) and examining the biology, particularly movements of Striped Skunks (Bjorge 1977; Andersen 1981). Discussed here are population and seasonal activity parameters of skunks based on data collected as part of those supporting activities.

**Methods**

A total of 1926 skunks were collected during 1972-1978 in an area 575 km north from the international boundary by 300 km east to west. The easternmost 30 km of the collection area was in the province of Saskatchewan (Figure 1). The northern and western boundaries enclose the approximate limit of Striped Skunk abundance, although the species occurs well beyond this area (Soper 1964). Skunks were collected on a three-area basis; the 29 km-wide control zone, an approximately equal area in adjacent Saskatchewan, and a larger area west of the control zone in Alberta. However, habitat and climate factors (Government and University of Alberta 1969) indicated that analyses should include a north-south comparison. The 9th base-line (Figure 1) was used as the north-south division.

The northern area (hereafter referred to as Parkland) is predominately Aspen (*Populus tremuloides*) Parkland (Bird and Bird 1967); it has annual means of 40 cm of precipitation and 100 frost-free days/year (Government and University of Alberta 1969) and winters are characterized by snow accumulation. Cereal-grain production and mixed-farming are the predominate land use. The southern area (hereafter referred to as Prairie) is part of the Prairie Grassland Biome, although it has been extensively modified in some areas by irrigation. Outside of irrigated areas cereal-grain production and cattle ranching predominate. The southern area has annual means of 28 cm of precipitation and 120 frost-free days/year; winter snow accumulation is often minimal due to chinook winds.

Skunks were captured by trapping, snaring with poles, carbon monoxide gassing, shooting and night-lighting. Whenever possible skunks were taken at the time they were found. Capture with live-traps was greatest during the spring and summer. In September and October most skunks were taken by shooting during a night-lighting census in the population reduction zone and adjacent Saskatchewan (Gunson et al. 1978). During winter most skunks were taken at dens by gassing or shooting, although traps were set
out whenever there was evidence of skunk activity. Except those taken by night-lighting, almost all skunks were captured at buildings.

Body weights, sex, estimated age, collection method, and locality were recorded in the field, and reproductive organs and heads collected. In the laboratory canines were removed and histologically prepared for age determination (Rakowski 1972; Casey and Webster 1975). Ages were determined independently by two or more experienced personnel; when they occurred, differences in age determination were resolved by re-examination of the tooth sections. For purposes of analyses skunks were assumed to have been born on 1 May. Uteri were cleared according to Orsini (1962) and uterine scars counted. Ovaries were sectioned manually and corpora counted. Testes were weighed; smears were prepared and examined for sperm.

**Results and Discussion**

**Sex and Age**

Monthly rates of capture of females were 1.3 to 3.5 times greater than those of males (Figure 2). Females frequented areas around building sites (where most of our captures were made) more than males during summer (Andersen 1981) and females concentrated extensively at buildings during winter (Gunson and Bjorge 1979) in our collection area. Thus, uneven sex ratios were interpreted to be largely due to different habitat use by the sexes.

The juvenile proportion of females captured decreased from 64 to 38% from November through March (Figure 2). We considered these captures to be representative of the population as all females denned communally (Gunson and Bjorge 1979) and so were thought to be equally liable to capture. This decrease was essentially identical in both Parkland and Prairie. Adult male skunks occurred more frequently in communal dens than juvenile males (Gunson and Bjorge 1979), consequently the various ages of that sex were not equally subject to capture. However, the overall decrease in juveniles among males was similar to that of females. Juveniles evidently suffered greater mortality than adults during winter.

Juvenile males and females were captured equally often (110 males of 224 juveniles) from May through July while they were presumably still largely dependent upon their mothers. Juveniles of both sexes were captured proportionately less often as summer progressed (Figure 2); that may have been due to females having moved their litters to grain fields (and away from buildings) as reported by Andersen (1981), while adults continued to visit buildings. During summer juveniles made up a larger proportion of male captures than female captures (Figure 2). This was likely related to adult males having made limited use of buildings at that time; whereas, females and their litters were frequently found at buildings, as also found by Andersen (1981).

Juvenile females may have been more vulnerable to night-lighting than other sex and age groups (Table 1). As well, females predominated among road-killed juveniles found during night-lighting. Andersen (1981) found the longest fall movements to be by juvenile females; this greater activity may have resulted in their having been along roads more frequently. Eleven of 24 juveniles trapped during the fall were females (Table 1); suggesting that the night-lighted sample may not have been representative of populations. Adult sex ratios of night-lighted skunks in the Parkland and of those trapped during fall were near 1:1. Among those night-lighted and found as road-kills in the Prairie, females were somewhat more numerous.

Age data from skunks collected in the control zone suggested that the control program shortened life expectancy of skunks. For this reason skunks taken in the zone were excluded from age structure analyses.
Table 1. Numbers of Striped Skunks taken during 25 September through 15 October in Alberta and Saskatchewan: 1972-1978.

<table>
<thead>
<tr>
<th>Collection Method</th>
<th>Male</th>
<th>Female</th>
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<tbody>
<tr>
<td></td>
<td>Adult</td>
<td>Juvenile</td>
</tr>
<tr>
<td>Fall Nightlighted</td>
<td>15</td>
<td>23</td>
</tr>
<tr>
<td>Parkland</td>
<td>23</td>
<td>73</td>
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<tr>
<td>Prairie</td>
<td>7</td>
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<td>Trapped</td>
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Possible effects of the program on skunk populations are being examined elsewhere.

Only five percent of adult males and eight percent of adult females were older than three years (Figure 3). Among adults ages of females were greater than those of males in both the Prairie (P < 0.01) and Parkland (P < 0.05). Differences between ages of skunks for the Prairie and Parkland were not demonstrated. Differences in age of adults between years also were not demonstrated, although that such differences may occur is suggested by annual variation in recruitment found by Bjorge et al. (1981).

Body Weight

Body weight varied with sex, age, season (Table 2) and year. As reported by Verts (1967) males were heavier than females; as well weights of males were more variable. Mean weights of adult female skunks were greatest in the first half of October, immediately prior to winter denning. Those of adult males were greatest from late September through early November. During winter denning (November through March) skunks have been reported to eat...
little or no food (Verts 1967; Aleksiuuk and Steward 1977) and weight loss was relatively constant. We noted food, in winter, in stomachs of only a few skunks with ready access to garbage.

Lowest mean weights were recorded in late March; adult males lost proportionately more weight (54% of October weight) than females (44% of October weight) over winter denning. These losses were similar to those found by Sunquist (1974) and Bjorge (1977). Verts (1967), however, found the greatest loss to be among females. Reduced weight loss by females was consistent with the thermal advantages of communal denning of that sex (Mutch and Aleksiuuk 1978) and greater activity of males during the February-March breeding season (Selko 1938a, Allen and Shapton 1952; Ferris and Andrews 1966).

Adult males gained weight rapidly during summer; means were near greatest values by August (Table 2). Female weights increased in spring presumably with advancing pregnancy; and decreased during May-June, presumably with parturition, and then increased again prior to winter denning.

Mean weights of juveniles, particularly juvenile females, did not equal that of their adult counterparts during their first year (Table 2). Greater winter mortality of juvenile skunks compared to adults (Figure 2) could have been caused by their entering winter denning at lesser weights (and by extrapolation, in poorer condition) than adults. Mean weights of juveniles in spring were extremely low, suggesting that starvation may have occurred as has been observed by Sunquist (1974).
Table 2. Semi-monthly body weights (kg) [Mean, ± SD (N)] of Striped Skunks collected in Alberta and Saskatchewan; 1972-78.

<table>
<thead>
<tr>
<th>Period</th>
<th>Females</th>
<th></th>
<th>Males</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Juveniles</td>
<td>Adults</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Mean, ± SD (N)</td>
<td></td>
<td>Mean, ± SD (N)</td>
<td></td>
</tr>
<tr>
<td>May</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1-15</td>
<td>0.7 ± 0.1(6)</td>
<td>2.7 ± 0.6(27)</td>
<td>3.9 ± 1.0(14)</td>
<td></td>
</tr>
<tr>
<td>16-31</td>
<td>0.3 ± 0.1(30)</td>
<td>2.4 ± 0.6(31)</td>
<td>3.7 ± 0.9(18)</td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>0.5 ± 0.2(26)</td>
<td>2.1 ± 0.3(28)</td>
<td>3.8 ± 0.5(9)</td>
<td></td>
</tr>
<tr>
<td>1-15</td>
<td>0.7 ± 0.2(13)</td>
<td>2.3 ± 0.3(15)</td>
<td>4.4 ± 1.3(8)</td>
<td></td>
</tr>
<tr>
<td>16-30</td>
<td>1.1 ± 0.3(8)</td>
<td>2.8 ± 0.7(12)</td>
<td>4.9 ± 0.7(6)</td>
<td></td>
</tr>
<tr>
<td>July</td>
<td>1.6 ± 0.5(16)</td>
<td>3.4 ± 0.8(23)</td>
<td>5.0 ± 0.5(7)</td>
<td></td>
</tr>
<tr>
<td>1-15</td>
<td>2.4 ± 1.1(18)</td>
<td>3.6 ± 0.9(21)</td>
<td>6.0 ± 1.1(18)</td>
<td></td>
</tr>
<tr>
<td>16-31</td>
<td>2.4 ± 1.1(20)</td>
<td>3.6 ± 0.9(25)</td>
<td>5.4 ± 1.2(8)</td>
<td></td>
</tr>
<tr>
<td>August</td>
<td>2.9 ± 0.8(12)</td>
<td>3.7 ± 0.7(4)</td>
<td>5.7 ± 1.3(5)</td>
<td></td>
</tr>
<tr>
<td>September</td>
<td>2.9 ± 0.7(66)</td>
<td>3.9 ± 0.8(25)</td>
<td>6.2 ± 1.0(22)</td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>3.2 ± 0.7(58)</td>
<td>4.0 ± 0.6(32)</td>
<td>5.9 ± 1.0(19)</td>
<td></td>
</tr>
<tr>
<td>October</td>
<td>3.0 ± 0.4(5)</td>
<td>3.8 ± 0.6(5)</td>
<td>6.2 ± 0.5(3)</td>
<td></td>
</tr>
<tr>
<td>November</td>
<td>3.1 ± 0.5(10)</td>
<td>4.1 ± 0.6(6)</td>
<td>5.7 ± 0.5(6)</td>
<td></td>
</tr>
<tr>
<td>December</td>
<td>2.7 ± 0.6(44)</td>
<td>4.7 ± 1.5(18)</td>
<td>6.2 ± 1.1(4)</td>
<td></td>
</tr>
<tr>
<td>January</td>
<td>2.8 ± 0.6(45)</td>
<td>4.6 ± 2.4(3)</td>
<td>5.3 ± 1.0(11)</td>
<td></td>
</tr>
<tr>
<td>January</td>
<td>2.2 ± 0.4(8)</td>
<td>3.8 ± 1.1(9)</td>
<td>5.5 ± 1.1(13)</td>
<td></td>
</tr>
<tr>
<td>January</td>
<td>2.5 ± 0.3(4)</td>
<td>4.3 ± 0.6(3)</td>
<td>5.2 ± 1.1(3)</td>
<td></td>
</tr>
<tr>
<td>January</td>
<td>2.2 ± 0.6(12)</td>
<td>3.6 ± 0.5(5)</td>
<td>4.0 ± 0.7(3)</td>
<td></td>
</tr>
<tr>
<td>February</td>
<td>2.4 ± 0.5(35)</td>
<td>3.5 ± 0.8(20)</td>
<td>3.9 ± 0.5(6)</td>
<td></td>
</tr>
<tr>
<td>February</td>
<td>2.1 ± 0.3(26)</td>
<td>3.0 ± 0.5(19)</td>
<td>4.0 ± 1.2(21)</td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>1.9 ± 0.5(25)</td>
<td>2.5 ± 0.5(26)</td>
<td>3.5 ± 0.9(29)</td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>1.5 ± 0.5(11)</td>
<td>2.4 ± 0.5(36)</td>
<td>3.2 ± 0.7(20)</td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>2.1 ± 0.7(12)</td>
<td>2.2 ± 0.5(21)</td>
<td>2.9 ± 0.5(14)</td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>2.3 ± 1.1(4)</td>
<td>2.5 ± 0.7(30)</td>
<td>3.2 ± 0.8(18)</td>
<td></td>
</tr>
<tr>
<td>16-30</td>
<td>2.8 ± 0.3(4)</td>
<td>2.4 ± 0.6(23)</td>
<td>3.2 ± 0.9(5)</td>
<td></td>
</tr>
</tbody>
</table>

Unlike other capture methods, fall night-lighting was conducted on the same dates every year allowing comparison of weights among years for late September — early October. Differences between years occurred (Table 3), particularly among juvenile females. Variation of adult mean weights generally, though not always, paralleled those of juveniles. Means of weights of juveniles in the Parkland and Prairie were very similar except in 1977 when juvenile females were heavier (P < 0.01) in the Parkland. Parkland juvenile males may also have been heavier (P < 0.2) that year.

Greatest numbers of skunks observed in Saskatchewan by night-lighting were in 1975 (6.6/100 km) and 1976 (6.8/100 km) (Table 3). Trends in annual counts in the control zone in Alberta generally paralleled trends in Saskatchewan, but were presumed to have been effected by control. Both the 1975 and 1976 counts were preceded by years in which mean weights of juvenile females in fall were greater than average and weights of other cohorts were high (Table 3). This suggested that weights of skunks in fall affect survival and/or recruitment over the next year. In 1977 mean fall weights of juvenile females differed (P < 0.05) between Prairie and Parkland (Table 3); the number of skunks observed increased from 11 in 1977 to 18 in 1978 in the Parkland and decreased from 17 to 13 in the Prairie. Gunson (1979) has examined winter severity in the area of our night-lighting. Despite very mild weather during the winter 1976-77 the number of skunks observed in night-lighting in 1977 declined (Table 3), which suggested that the situation is more complex than outlined here.

Differences in mean weights of juvenile females collected during fall could not be related to variation in numbers of uterine scars or pregnancy rate the following year (see below). Bjorge et al. (1981) noted that mean litter size was 5.2 (9 litters) following a mild winter compared to 2.5 (6 litters) following a severe winter, and that females weighed less following the severe winter. However, uterine scar counts from their study area after parturition following the severe winter were not reduced in number. They suggested that differences in litter size were the result of intra-uterine mortality or death of neonates.

Bjorge et al. (1981) suggested that a long winter with severe conditions in November and March, the first and last month of winter denning, caused greater mortality and reduced recruitment in a skunk population. Entering winter denning at below average weights would seem likely to increase the impact of severe weather. In at least those years with sufficient data, below average fall weights were, broadly, carried over in early and mid-winter (Table 4). Late winter
monthly samples included smaller numbers of juveniles (see above) and some weights were thought to have been affected by access of the skunks to garbage; data for the period were equivocal.

The variation in juvenile weights in fall between years (Table 3) is probably due to the influence of summer weather on foraging time and food availability. Fall weights, and hence summer weather, are likely important in determining winter survival and spring recruitment in conjunction with the factors of winter temperature and duration of the denning period noted by Bjorge et al. (1981).

**Reproduction**

In the Prairie, field observations of births and young indicated that most skunks were born in mid and late May; parturition was first observed on 4 May. Back-dating estimates of the young indicated earliest date of birth at approximately 9 May in the Parkland; young were born as late as mid-June in both areas. Periods of parturition in our collection area were similar to, if a little later than, those described for skunks elsewhere (Verts 1967; Wade-Smith and Richmond 1978; Casey and Webster 1975). If parturition was delayed, juveniles would enter winter denning at even lower weights than adults resulting from the short period of growth and pre-winter fattening.

Of the adult females collected from 1 May to 31 January, 92% had embryos or uterine scars (Tables 5, 6). Pregnancy rates in the Parkland and Prairie were identical. Pregnancy rate was lower among yearlings (juveniles at time of breeding) and two-year skunks than older ones (Table 5, 6). Verts (1967) found that 96% of 75 females were parous in Illinois. Though slightly greater than our mean, that figure is within the range of variation we observed (Table 6). Slightly greater potential production of young may have occurred in the Prairie than the Parkland (Table 7).

Reported mean litter sizes of wild skunks have varied from 5.8 to 7.3 young (Seton 1926; Hamilton 1963; Verts 1967; Bailey 1971); similar to the number found in the present study. A possible difference, though small, in geographically adjacent samples described here was, therefore, unexpected.

Testes weights (Figure 4) and the presence of sperm in epididymal smears showed juvenile males to be reproductively active in their first year.

**Seasonal Behavior**

The proportion of skunks taken at buildings in traps (hereafter referred to as active skunks) as opposed to those taken during the day by gassing, shooting or snaring (inactive skunks) provided a crude insight into the use of buildings and general activity (Figure 5).

From November through March most females were
Table 4. Fall and early winter body weights [Mean ± SD(N)] of juvenile female Striped Skunks collected in Alberta and Saskatchewan.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>1974</td>
<td>3.8 ± 0.5(9)</td>
<td>2.9 ± 1.3(2)</td>
<td>2.9 ± 0.1(4)</td>
<td>2.9 ± 0.1(10)</td>
<td>2.7 ± 0.4(16)</td>
</tr>
<tr>
<td>1975</td>
<td>3.3 ± 0.6(28)</td>
<td>3.2</td>
<td>3.2 ± 1.0(10)</td>
<td>3.0 ± 0.6(9)</td>
<td></td>
</tr>
<tr>
<td>1976</td>
<td>2.8 ± 0.5(29)</td>
<td>2.4 ± 0.4(21)</td>
<td></td>
<td>2.3 ± 0.4(10)</td>
<td></td>
</tr>
</tbody>
</table>

Table 5. Age-specific pregnancy rates and mean numbers of corpora, embryos, and uterine scars in Striped Skunks collected in Alberta and Saskatchewan.

<table>
<thead>
<tr>
<th>Age</th>
<th>Corpora</th>
<th>Embryos</th>
<th>Uterine Scars</th>
<th>Pregnancy rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Juvenile (&lt; 1 yr)</td>
<td>6.0(18)</td>
<td>7.0(8)</td>
<td>-(0)</td>
<td>-(0)</td>
</tr>
<tr>
<td>Yearling (1-2 yr)</td>
<td>6.3(46)</td>
<td>6.8(38)</td>
<td>6.6(107)</td>
<td>90(125)</td>
</tr>
<tr>
<td>2</td>
<td>6.3(27)</td>
<td>6.8(23)</td>
<td>6.8(75)</td>
<td>90(86)</td>
</tr>
<tr>
<td>3-6</td>
<td>7.0(14)</td>
<td>6.9(10)</td>
<td>6.7(74)</td>
<td>100(75)</td>
</tr>
<tr>
<td>Unknown</td>
<td>6.2(11)</td>
<td>6.6(8)</td>
<td>6.6(18)</td>
<td>-(0)</td>
</tr>
<tr>
<td>All Ages</td>
<td>6.3(116)</td>
<td>6.8(87)</td>
<td>6.7(274)</td>
<td>92(278)</td>
</tr>
</tbody>
</table>

*Based only on skunks taken from 1 May to 31 January.

Table 6. Annual numbers of corpora, embryos and uterine scars and annual pregnancy rate of Striped Skunks in Alberta and Saskatchewan.

<table>
<thead>
<tr>
<th>Year</th>
<th>Corpora</th>
<th>Embryos</th>
<th>Uterine Scars</th>
<th>Pregnancy rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1972</td>
<td>5.0(6)</td>
<td>6.5(2)</td>
<td>5.7(3)</td>
<td>100(3)</td>
</tr>
<tr>
<td>1973</td>
<td>6.4(41)</td>
<td>6.9(31)</td>
<td>5.0(1)</td>
<td>71(5)</td>
</tr>
<tr>
<td>1974</td>
<td>6.9(19)</td>
<td>7.4(9)</td>
<td>6.7(53)</td>
<td>90(58)</td>
</tr>
<tr>
<td>1975</td>
<td>5.5(20)</td>
<td>6.5(25)</td>
<td>6.8(58)</td>
<td>88(68)</td>
</tr>
<tr>
<td>1976</td>
<td>6.5(15)</td>
<td>6.7(12)</td>
<td>6.8(55)</td>
<td>94(63)</td>
</tr>
<tr>
<td>1977</td>
<td>6.9(15)</td>
<td>7.5(7)</td>
<td>6.7(76)</td>
<td>97(71)</td>
</tr>
<tr>
<td>1978</td>
<td>-</td>
<td>5.0(1)</td>
<td>6.4(28)</td>
<td>100(18)</td>
</tr>
<tr>
<td>1972-78</td>
<td>6.3(116)</td>
<td>6.8(87)</td>
<td>6.7(274)</td>
<td>92(286)</td>
</tr>
</tbody>
</table>

*Of skunks taken from 1 May to 31 January the following year.
Table 7. Reproductive rates of Striped Skunks collected in Prairie and Parkland areas of Alberta and Saskatchewan, 1972-1978.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Year</th>
<th>Prairie</th>
<th>Parkland</th>
<th>Significance¹</th>
</tr>
</thead>
<tbody>
<tr>
<td>Uterine Scars</td>
<td>1972</td>
<td>5.0 ± 1.5 (1)</td>
<td>5.7 ± 1.5 (3)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1973</td>
<td>6.9 ± 1.4 (20)</td>
<td>6.5 ± 2.0 (33)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1974</td>
<td>6.9 ± 1.2 (26)</td>
<td>6.7 ± 1.4 (32)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1975</td>
<td>6.8 ± 1.6 (46)</td>
<td>6.7 ± 0.5 (9)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1976</td>
<td>7.0 ± 1.2 (21)</td>
<td>6.5 ± 1.5 (55)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1977</td>
<td>6.5 ± 2.0 (8)</td>
<td>6.3 ± 2.2 (6)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>1978</td>
<td>6.8 ± 1.5 (136)</td>
<td>6.6 ± 1.6 (138)</td>
<td>P &lt; 0.2</td>
</tr>
<tr>
<td>Embryos</td>
<td>1972-78</td>
<td>6.8 ± 1.3 (39)</td>
<td>6.6 ± 1.4 (48)</td>
<td>P &lt; 0.2</td>
</tr>
<tr>
<td>Corpora</td>
<td>1972-78</td>
<td>6.6 ± 1.5 (52)</td>
<td>6.1 ± 1.7 (64)</td>
<td>P &lt; 0.2</td>
</tr>
</tbody>
</table>

¹Student's t test

Figure 4. Mean monthly weights of testes of adult and juvenile Striped Skunks taken in Alberta and Saskatchewan 1972-78.
inactive (denned) as were most males from November through January (Figure 5). This behavior has been widely noted in the colder portions of the range of Striped Skunks (Allen 1939; Allen and Shapton 1942; Verts 1967; Sunquist 1974; Mutch and Aleksiuk 1977, Gunson and Bjorge 1979).

In late February the proportion of active males was high. Several workers (Selko 1938a, Allen and Shapton 1942; Ferris and Andrews 1966; Gunson and Bjorge 1979) have reported that males made extensive movements at that time, presumably as part of a search for females during the breeding season.

Communal dens broke up in early April (Gunson and Bjorge 1979) and the proportions of active and inactive female skunks remained constant from that month through July. Andersen (1981) found movements of parous females to be relatively restricted for a time prior to, and a considerable period after, parturition, to the area of the maternal den or litter. Continued use of maternal den sites made them easily located by collectors. As skunks were trapped when they could not be snared, active and inactive adult females taken during summer were not likely behaving differently.

The proportion of active males declined from March to a low in June (Figure 5); most male skunks taken in the latter month were juveniles (Figure 2). As reported by Andersen (1981) adult males did not utilize buildings extensively during summer.

The proportions of both sexes active during July through September increased markedly (Figure 5). Increasing trap success over those three months at
potential communal den sites (all under buildings) was found by Gunson and Bjorge (1979) as well. Adults may have begun pre-winter denning activities in August, but comparatively few juveniles were taken at buildings that month (Figure 2). That difference could have been related to the rapid weight gain of juveniles, whereas, adult mean weights in August were near the greatest values observed (Table 2) and that juveniles were actively dispersing (Bjorge et al. 1981). Feeding activity or dispersal, or both, of juveniles evidently did not involve a great deal of activity by juveniles at communal dens sites in August.

Due to night-lighting, limited effort was made to trap skunks in September and October, but skunks were readily trapped at buildings in those months as evidenced by the high active proportion (Figure 5). The juvenile proportions (66% of males and 68% of females) taken at buildings in those two months indicated that juveniles had become involved in pre-winter denning activity.

Co-incident with greatest mean body weights (except for juvenile males) in October (Table 2) the proportion of active skunks began to fall, indicating a lessening of activity. Juvenile males attained greatest mean weight in November; 1½ months after greatest mean weights occurred among other cohorts and 3½ months after adult males had first approached greatest pre-denning weight (Table 2). Those data suggested that juvenile males were likely actively foraging later than other cohorts. Such a tendency was not evident in our capture data although Sunquist (1974) and Andersen (1981) found that juveniles were more active than adults into November.

Conclusions

The range of the Striped Skunk is extensive, encompassing differing habitats and climates; differences in behaviour and population dynamics within the range of the species would be expected, and occur. For example winter denning in Alberta is 120 to 150 days in duration (Gunson and Bjorge 1979), 62 to 150 days in Minnesota (Sunquist 1974) and 62 to 87 days in Illinois (Verts 1967; Strom 1972). In more southern populations skunks remain active throughout the year (Cuyler 1924; Stout and Sonenshine 1974). That skunks do not usually feed during denning (Verts 1967; Aleksiuk and Steward 1977) would suggest that accommodation of winter denning would be a major factor in all aspects of skunk life-history at northern latitudes.

An expected effect of earlier and prolonged denning would be more rapid post natal growth to ensure storage of sufficient reserves of fat to last the winter (Case 1978). Late-born animals would be placed at a considerable disadvantage in preparing for winter denning and those born very early could encounter severe weather. A later, shortened period of parturition among northern skunks compared to those further south could therefore be expected, although as stated, was not obvious in our area.

Another behavior characteristic of northern skunks is the extensive utilization of buildings, though to a somewhat lesser extent in the Prairie (Andersen 1981) than the Parkland (Bjorge 1977). That is in marked contrast to results of studies further south (see Verts 1967; Houseknecht and Tester 1978) where skunks seldom utilize buildings.

Andersen (1981) found good winter denning sites, whether under buildings or naturally occurring, to be a limited resource on the Prairie. In his study area maternity dens were always near water bodies, which, in turn, usually had buildings nearby. Though adult males were rarely encountered near buildings in summer, buildings would appear to offer a significant new, though not necessarily superior, habitat in that biome. Extremely frequent use of buildings in the Parkland found by Bjorge (1977), and us, as reported here, indicate that buildings offer superior habitat to that occurring naturally in that biome despite the occurrence of numerous small bodies of water, groves of trees and fencerows, traditionally accepted as excellent habitat. A possible advantage of maternal denning under buildings may be that those sites are drier; dryness could also be a factor in winter den selection as may be the availability of space.

A third characteristic distinguishing northern skunk populations is extensive fall dispersal of juveniles. Bjorge et al. (1981) recorded a movement of 21.7 km and were able to relocate only 1 of 62 juveniles tagged prior to dispersal on a 130 km² study area. Andersen (1981) recorded a dispersal of 70.2 km. Most of his tagged juveniles disappeared from the study area as well; efforts to recover tagged individuals outside his study area suggested that most juveniles had moved > 10 km. Such long dispersals have not been reported elsewhere.

Long dispersals by skunks in Alberta and Saskatchewan could be related to the comparatively low densities of the populations as suggested by Bjorge et al. (1981). Low numbers and widely separated communal den sites would cause dispersing skunks to travel considerable distances to find dens. This could be particularly true of juvenile males as only one male actually spends the winter in the communal den and juveniles may undertake a search for a den without a resident male. Andersen (1981), however, found that longest movements were by females and our limited observations suggested that more skunks of both sexes visit den sites in the fall than would be likely to actually occupy the den. Additional observations of
the formation skunk communal dens and related movements of individual skunks are needed to examine this question.

A final distinguishing characteristic of northern skunk populations is the timing of occurrence of maximum numbers of rabid animals. Webster et al. (1974) and Gunson et al. (1978), found greatest numbers of rabid skunks to be diagnosed in early-winter and again in spring in Canada and that the former maximum tended not to occur in data from the United States.

The widely observed spring maximum in diagnoses of rabid skunks has been considered to be the result of the activity of males in the February-March breeding season and resultant intraspecific contact (see Gunson et al. 1978). The delay in positive diagnoses is the result of the incubation period of rabies and amplification by secondary contacts of infected animals (Webster et al. 1974). Webster et al. (1974) suggested that the occurrence of maximum numbers of independent animals in the fall could result in the early-winter maximum of rabies diagnoses observed in Canada; however, that argument would seem to apply equally to southern populations. The probability of greater population mixing in fall in northern populations resulting from extensive movements and selection processes in communal den formation was not known to them; and remains undemonstrated in central Canada. We propose that high levels of fall activity and associated pre-denning contact among skunks in northern areas is the primary factor causing large numbers of rabid skunks to be diagnosed in mid-winter in Canada. More precise observations of this fall activity and the possible effect of somewhat lowered body temperature of skunks during winter denning (Mutch and Aleksiuik 1977) on the incubation of rabies virus are worthy of additional research.

Acknowledgments

Funding for this research was primarily through H. Vance and the late G. R. Whenham of Alberta Agriculture (Animal Health Division); their outstanding and continued support of the program is gratefully acknowledged. P. Andersen, R. Bjorge and P. Rakowski contributed advice and reviewed drafts of this paper. P. Cole, Wm. Johnson, A. Norris, D. Pipella and Wm. Wynnyk provided valuable assistance in field and laboratory; other assistance was provided by D. Bedard, S. Bennett, H. Bowmans, J. Bradley, M. Caley, P. Dielman, Wm. Dorward, G. Fraser, L. Harder, J. Iversen, D. Kingsley, R. Masuda, D. Meyers and B. Prins. M. Boyd assisted in data analyses. The Saskatchewan Department of Tourism and Renewable Resources granted permission to collect skunks in that province.

Literature Cited


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Winter Habitat Use by Wapiti, *Cervus elaphus*, in Ontario Woodlands

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Habitat use by Wapiti (*Cervus elaphus*) surviving from western stock introduced in 1932 and 1933 was studied in the Burwash-French River area of Ontario. The Wapiti range was divided into four habitat zones that differed in physical features and amounts and distribution of ten habitat types. Wapiti occurred in three of the four zones and used all major habitat types in winter. Moose (*Alces alces*) used almost the same set of habitat types in winter although to different degrees and, it is hypothesized, in a more sedentary pattern compared to regular movement among several habitat types by Wapiti.

Key Words: Wapiti, *Cervus elaphus*, winter habitat, woodlands, Ontario.

Wapiti, or American Elk, (*Cervus elaphus*) are today confined mainly to western North America although in the recent past they ranged widely into eastern regions (Figure 1). Most reintroductions to eastern regions (where they disappeared between 1850 and 1900) have failed. In Michigan, Minnesota and Pennsylvania, small reintroduced populations occur sympatrically with high densities of White-tailed Deer (*Odocoileus virginianus*) but, in the Burwash-French River area of north-central Ontario, a small introduced Wapiti herd exists on a range that supports mainly Moose (*Alces alces*). Deer were abundant after widespread logging and wildfires at the turn of the century but have recently declined, possibly because of habitat succession and colder more snowy winters (Smith and Borczon 1977).

The Burwash-French River Wapiti population was started with western Wapiti from Buffalo National Park near Wainwright, Alberta (Ranta 1979). These imports were released in Ontario in 1932 and 1933. Most of the animals were held in pens at four locations and the progeny were subsequently released at several other locations in the province (Figure 1). Initially the Wapiti were under close supervision, with winter feeding programs and most herds increased. However, in 1949 an infection of cattle and sheep by the Large American Liver Fluke (*Fascioloides magna*) was discovered at Burwash Industrial Farm, one of the penned Wapiti release sites. Kingscote (1950) linked the infection to the Wapiti and recommended that all of the Wapiti herds that had been introduced into Ontario be eliminated. This recommendation was accepted and an extermination drive was initiated. Most Wapiti were still within pens but at almost all sites some animals had escaped, forming free-ranging populations. Professional hunters were employed originally but the practice was discontinued when Wapiti were included with White-tailed Deer for sport hunting purposes. The last combined Deer/Wapiti hunt was held during the fall of 1978.

Most Wapiti herds were successfully eliminated and present populations are known to exist only in the vicinity of the Chapleau Crown Game Preserve and near Burwash. Of the two populations, the Ontario Ministry of Natural Resources (OMNR) believes that the latter is considerably larger. No population estimates have been made but OMNR field staff believe fewer than 100 Wapiti are left in the vicinity of Burwash, from a herd once estimated to be 500 (Kingscote

![Figure 1. Release points and records of Wapiti in Ontario in 1950. Shaded area is the historic distribution of native Wapiti (Peterson 1966). Block shows location of study area.](image-url)
1950). The range of Wapiti at Burwash is currently about 1100 km² from north of the former Burwash Crown Game Preserve (until 1980) south to Georgian Bay (Figure 2).

According to Peterson (1966), this range is on the northern fringes of historic Wapiti range and the historic southern limits of Woodland Caribou (*Rangifer tarandus*) distribution. Caribou disappeared from the area in the early 1900's. Since then, Deer and now Moose have become the most abundant cervids. Management data suggest there are at least 130 Moose in the Burwash-French River Wapiti range (Van Wout, B. 1975, Aerial Moose surveys. Ontario Ministry of Natural Resources, Sudbury District. 20 pp.). Few deer are known to winter in the study area now.

The purpose of our study was to compare the use of specific vegetation types by Wapiti and Moose and to describe habitat types and habitat mosaics critical to the survival of Wapiti. We assumed winter to be the critical period for survival and concentrated our research in that season. We examined these questions primarily by identifying specific areas inhabited by Wapiti and Moose, investigating their food preferences and estimating the relative amounts of time spent by each species in particular habitat types. The only other study of Wapiti in similar eastern habitats was that of Moran (1973) in Michigan.

**Study Area**

The Burwash-French River Wapiti range is a rugged, hilly part of the Georgian Bay section of the Great Lakes-St. Lawrence Forest Region (Rowe 1972). The forests are patches of coniferous and deciduous habitat types. Soils are generally thin and stony except for some lowland clay deposits. Several barren hilltops are free of soil and rise 100 m above the valleys. Elevations in the study area vary between 30 m and 300 m asl.

Annual snowfall averages 200 to 240 cm and normally snow cover lasts from the end of November to the end of April. Snow accumulations often exceed 80 cm during the winter except near Georgian Bay where the water has a localized moderating effect and where barren areas remain windswept and snowfree.

**Materials and Methods**

Records of Wapiti sightings supplied by OMNR were used in locating field sampling surveys. A vegetation survey measured percent coverage by trees, shrubs, ferns and forbs in 185 sampled stands. Over twenty vegetation types based on dominant species (usually trees) were identified and mapped. Topographic maps and remotely sensed images were used together with plot data to draw vegetation boundar-

ies. These were aggregated into habitat types. The entire study area was then divided into four habitat zones, each with a characteristic recurring combination of habitat types.

Ungulate surveys flown by us and by OMNR during consecutive winters from 1974/75 to 1977/78 gave relative numbers of Wapiti and Moose in each habitat zone and their points of distribution (Figure 3). Surveys flown by us recorded the group size, sex and age (adult or juvenile) and the habitat type during the 1977/78 survey for Wapiti and Moose except during our March 1977 survey when the only data recorded for Moose were the number seen and their locations. For OMNR surveys for Wapiti and Moose, we deduced from vegetation maps the habitat types used only for Wapiti.

Snow, browse and pellet group survey locations were chosen with reference to: ungulate distribution, relative density (estimated from aerial surveys), habitat types represented and accessibility.

Snow depth, density and hardness were measured periodically at six stations in the vicinity of Burwash during the 1977/78 winter. Snow depths were measured with a metre stick and snow densities and hardness were measured using the methods described by Klein, Pierce and Gold (1950). Snow stations were located in areas and habitat types where Wapiti and/or Moose had been seen in previous winters.

Browse and pellet group surveys were conducted in the spring of 1978. Browsing was used as a measure of activity and pellet group distribution as a measure of time spent in a habitat (Telfer personal communication).

Pellet groups of Wapiti and Moose were counted in plots 20 m × 5 m at approximately 150 m intervals (modified after Van Etten and Bennett 1965). The first plot of a transect was chosen subjectively with subsequent plots along a compass bearing taken to ensure sampling of specific habitat types. The distribution of 345 pellet group plots was: North Burwash 112, South Burwash 73, French River 106 and Georgian Bay 54. Pellet groups counted were: 73 Wapiti and 10 Moose in North Burwash, 0 Wapiti and 26 Moose in South Burwash, 40 Wapiti and 26 Moose in French River, and 88 Wapiti and 0 Moose in Georgian Bay.

Browse surveys were done concurrently with pellet group counts. Plots 15 m long, 1 m wide and 3 m high down the centre of the pellet group plots were used. The number of stems of each woody browse species was recorded and any evidence of browsing on a stem was recorded as positive. Location, plot number and habitat type were recorded for each plot. The distribution of 291 browse plots was: North Burwash 100, South Burwash 73, French River 90, and Georgian Bay 25.
Figure 2. The Burwash-French River study area and arrangement of habitat zones. Shaded area identifies the old Burwash Crown Game Preserve.
Vascular plant names are according to Gleason and Cronquist (1963).

Results

Habitat Types and Habitat Zones

Ten habitat types of importance to Wapiti or Moose were defined in terms of vegetation and physical features. These were:

1. High Open Areas were either rocky hilltops with scattered, and often small, Red Maple (Acer rubrum) and/or White Birch (Betula papyrifera) or sparse stands of Red Oak (Quercus rubra) with or without White Pine (Pinus strobus) on high ground.

2. Cedar/Balsam/Spruce (Thuja occidentalis/Abies balsamea/Picea glauca and P. mariana) swamps were dominated by White Spruce (P. glauca) with a dense Balsam Fir understory and scattered clumps of White Cedar. White Birch, Red Maple, Beaked Hazelnut (Corylus cornuta), Maple-leaf Viburnum (Viburnum acerifolium) and Mountain Maple (Acer spicatum) were important deciduous inclusions.

3. Cedar Edge was a special case of Cedar/Balsam/Spruce found mainly along shorelines of the French River and Georgian Bay.

4. Jack Pine (Pinus banksiana) were often extensive on areas of shallow soil. Stands tended to be evenly aged. Occasionally large White Pine were co-dominant in some stands. Blueberries (Vaccinium angustifolium), Sweet Fern (Myrica asplenifolia) and Common Juniper (Juniperus communis) formed the main understory with scattered clumps of White Birch, Red Maple and Aspen (Populus tremuloides). In Georgian Bay stands were on rocky ridges, were more open, and had more sedges (Carex spp.) in the herb layer.

5. Mixed Coniferous included all other coniferous forests. These were of three types: White Pine and/or Red Pine (Pinus resinosa) with some Balsam Fir and White Spruce; White Pine and/or Red Pine co-dominant with White Spruce; and Eastern Hemlock (Tsuga canadensis).

6. Mixed Coniferous/Deciduous included all mixed forests. The most common were: i) Aspen, White Birch, and White Spruce with a dense and diverse shrub layer on damp sites with a thick humic layer. ii) Ash: both White (Fraxinus americana) and Black (F. nigra), Balsam Poplar (P. balsamifera) and White Spruce forests on sites similar to (i) but wetter. Shrubs and forbs were dense in the understory. iii) White Pine forests on well drained sites with a thick humic layer. Poplars, White Birch, Red Maple, Balsam Fir, Red Pine and White Spruce were subdominants.

7. All Deciduous were usually White Birch, Trembling Aspen and Red Maple and included all deciduous forests except those on High Open Areas. Other types included here were: Sugar Maple (A. saccharum), Black Ash and Silver Maple (A. saccharinum) along the Wanapitei and French rivers, and Bur Oak (Quercus macrocarpa) levees along the Wanapitei River.

8. Logged Cutovers were formerly dominated by conifers (principally White Pine) before logging. Depending on how recently they had been cut they were dominated either by herbaceous species or young Trembling Aspen, Red Maple or White Birch. Dense thickets of Speckled Alder, Beaked Hazelnut and raspberries also occurred in some of these areas.

9. Hydro Lines were dominated by herbaceous species and had few woody stems.

10. Open Meadows were found on formerly farmed areas (mainly near Burwash) and on Beaver (Castor canadensis) meadows. They were dominated by herbs and usually had a margin of woody species such as: Speckled Alder, Willows and White Spruce.

For a discussion of each vegetation type and a detailed vegetation map of the area see Ranta (1979).

The habitat zones shown in Figure 2 had characteristically different combinations of vegetation types and physical features. What follows is a general characterization of each habitat zone.

i) North Burwash

The most northerly habitat zone was also the most rugged. Hills and plateaus rose abruptly to 100 m above the valleys and had little topsoil. These High Open Areas were dominated by Red Oak or a scrubland of Red Maples and White Birch. The hillsides and better drained lowlands had more topsoil and supported a wide variety of deciduous, coniferous and mixed coniferous vegetation types. Poorly drained lowland areas supported dense Cedar, Balsam, Spruce swamps. Willow, Alder (Salix spp. and Alnus rugosa) swales and wet and dry beaver meadows were scattered in these lowlands. Except for the 4000 ha of field and pasture around the Burwash buildings, the area was a very heterogeneous mixture of habitat types where single stands were seldom greater than 50 ha in size.

ii) South Burwash

This was the central portion of the study area and was less rugged and without the pronounced habitat heterogeneity of North Burwash. Topsoil was generally continuous and there were few rocky ridges. The forests were mainly closed stands of mixed coniferous habitat types, often over 100 ha in size and dominated
Figure 3. Aerial Survey over Wapiti range 1974-1976 to 1977-78.

--- OMNR Wapiti survey, 1975-76. Flight lines east-west 1 km distant.

--- W. B. Ranta, March 1977. Flight lines north-south 1.6 km (1 m.) distant.

--- W. B. Ranta, 1977-78. Flight lines north-south 1 km distant.

Plot Surveys
- OMNR, 1974-75.
- OMNR, January 1976.
by large White Pines. Logged areas had regenerated in deciduous trees. Most of the numerous open areas were wet beaver meadows.

iii) French River

The northerly islands and land masses dissected by the lower French and Wanapitei Rivers comprised the French River habitat zone. Topography was low but the terrain was extremely rugged with great heterogeneity of habitat types. On suitable sites lush forests of mixed deciduous-coniferous habitats (often with towering White Pines), Cedar/Balsam/Spruce swamps, Ash-Maple lowlands, and Sugar Maple forests were found. Large hilltop areas of Red Oak and Red Oak, White Pine forests often formed a mosaic with ridges of Jack Pine and deciduous forests of White Birch, Red Maple and Aspens on the hillsides. Abandoned beaver ponds formed extensive networks of stabilized grass and sedge meadows. Many river backwaters were bordered by dense willows.

iv) Georgian Bay

This habitat zone was two areas of exposed bedrock that extended for several km inland from the shores of Georgian Bay and had extensive open forests of Jack Pine. Red Maple, White Birch and Trembling Aspens were small and scattered. Blueberries were also common. Lichens, principally Cladonia spp., grew in dense mats on the bedrock, while grasses and sedges (especially Deschampsia flexuosa) grew as tufts in crevices on rocky ridges. Lowland irregularities usually supported bog communities while White Cedar communities were spotted along lake and river shores. The landscape was broken by parallel north-easterly ridges seldom more than a few metres above adjacent troughs.

Aerial Surveys

Aerial surveys were designed to measure use of habitat types, not to estimate populations. Winter aerial surveys from 1974/75 to 1977/78 recorded 64 Wapiti in 26 groups and 327 Moose. Track aggregations also were recorded during the winter of 1977/78. Where animals or tracks were seen on ice, on meadows, in rare or small habitat types like willow or alder, the adjacent forest habitat type with ungulate activity was recorded.

Moose were seen in all wooded habitat types except Cedar Edge (Table 1) in all habitat zones but one although they were more common in some parts of the North Burwash and French River zones where Wapiti sightings were sparse. Wapiti were recorded only in specific habitat types, particularly Cedar/Balsam/Spruce which included Cedar Edges along Georgian Bay, Mixed Deciduous/Coniferous forests, Jack Pine ridges, and High Open Areas.

Snow Characteristics

Snowfall during the 1977/78 winter totalled 256.4 cm at the Sudbury District weather office 40 km north of the study area. The weather office reported that January had a maximum snow depth on the ground of 72.0 cm, which exceeded all monthly records for the previous ten years. Mean maximum and minimum temperatures were colder than normal for the months of December through April. Snow covered the ground in the study area from early December to late April. Snowfalls were heavy and snow accumulated quickly until mid-January. Figure 4 shows examples of deep, intermediate and shallow snow depths developed in High Open Areas, Cedar/Balsam/Spruce, and on frozen waterways, respectively. Other habitats that developed deep snow cover were: Open Meadows and All Deciduous. In addition to Cedar/Balsam/Spruce, Mixed Coniferous, Mixed Coniferous/Deciduous and Jack Pine habitats also developed intermediate snow depth.

However, snow depths as shown in Figure 4 do not reveal the great variation in depth within each habitat. For example, although High Open Areas had the greatest snow depths (up to 100 cm), ridges in these areas remained windswept and had little or no snow throughout the winter. As late as 20 March, such ridges had less than 30 cm of snow and were traversed by Wapiti. Extensive trails through rocky barrens and mixed deciduous cover in High Open Areas north of the Burwash complex indicated that movement was not difficult even though snow depths in some places along the route were 70 to 90 cm. Similar observations were made in High Open Areas in the Georgian Bay zone. In all these instances, Wapiti spent little time in the windswept areas and tracks always led back to heavy coniferous cover. In these conifer swamps, maximum snow depth was inversely related to canopy closure so that snow depth was very patchy. This variability was greatest in habitats dominated by cedar. Snow cover was least on rivers and lakes where it never exceeded 50 cm. Tracks indicated that Wapiti commonly travelled on waterways, often for several kilometres.

Snow density and hardness also were measured but the data do not distinguish among habitat types. This was caused in part by variation in both density and hardness caused by ice layers, ice clumps fallen from the vegetation and similar irregularities in coniferous and mixed habitats. Lesser variability may have been generated by the method of measuring hardness horizontally in the wall of the snow pits.

Habitat Utilization

The frequencies of browsing of various species differed significantly from the availabilities of those species as browse in each habitat zone (Table 2).
Table I. Use of habitat types by Wapiti and Moose seen during winter aerial surveys (Wapiti: 1974-5 to 1977-8; Moose: 1977-8)

<table>
<thead>
<tr>
<th></th>
<th>Mixed Coniferous</th>
<th>Mixed Deciduous/Coniferous</th>
<th>Cedar/Balsam/Spruce and Cedar Edge</th>
<th>High Open Areas</th>
<th>Jack Pine</th>
<th>All Deciduous</th>
<th>Logged Cutover</th>
<th>Totals</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Wapiti</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of groups</td>
<td>4</td>
<td>6</td>
<td>11</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td>26</td>
</tr>
<tr>
<td>No. of animals</td>
<td>10</td>
<td>15</td>
<td>26</td>
<td>13</td>
<td></td>
<td></td>
<td></td>
<td>64</td>
</tr>
<tr>
<td><strong>Moose</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>No. of groups</td>
<td>15</td>
<td>8</td>
<td>4</td>
<td>9</td>
<td>4</td>
<td>3</td>
<td>1</td>
<td>44</td>
</tr>
<tr>
<td>No. of animals</td>
<td>30</td>
<td>18</td>
<td>9</td>
<td>15</td>
<td>10</td>
<td>8</td>
<td>1</td>
<td>91</td>
</tr>
</tbody>
</table>

Figure 4. Maximum snow depths* in the Burwash-French River Wapiti range, winter 1977-78.

High Open Areas
Cedar/Balsam/Spruce
Frozen Waterways
Table 2. Percentage of stems of browsed species that were browsed and total available stems in all browse plots in each habitat zone.

<table>
<thead>
<tr>
<th></th>
<th>North Burwash</th>
<th>South Burwash*</th>
<th>French River</th>
<th>Georgian Bay**</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>percent stems browsed</td>
<td>total stems available</td>
<td>percent stems browsed</td>
<td>total stems available</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>10.8</td>
<td>194</td>
<td>16.2</td>
<td>247</td>
</tr>
<tr>
<td>Salix spp.</td>
<td>30.2</td>
<td>116</td>
<td>43.3</td>
<td>30</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>5.5</td>
<td>73</td>
<td>30.6</td>
<td>144</td>
</tr>
<tr>
<td>Betula papyrifera</td>
<td>1.4</td>
<td>141</td>
<td>44.4</td>
<td>45</td>
</tr>
<tr>
<td>Quercus rubra</td>
<td>0.8</td>
<td>124</td>
<td>14.3</td>
<td>14</td>
</tr>
<tr>
<td>Viburnum acerifolium</td>
<td>57.5</td>
<td>87</td>
<td>28.6</td>
<td>7</td>
</tr>
<tr>
<td>Corylus cornuta</td>
<td>6.3</td>
<td>693</td>
<td>5.1</td>
<td>612</td>
</tr>
<tr>
<td>Thuja occidentalis</td>
<td>12.9</td>
<td>46</td>
<td>0</td>
<td>7</td>
</tr>
<tr>
<td>Abies balsamea</td>
<td>2.0</td>
<td>153</td>
<td>12.2</td>
<td>49</td>
</tr>
<tr>
<td>Cornus rugosa</td>
<td>12.0</td>
<td>25</td>
<td>71.4</td>
<td>7</td>
</tr>
<tr>
<td>Acer spicatum</td>
<td>27.1</td>
<td>59</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Viburnum cassinoides</td>
<td>—</td>
<td>—</td>
<td>4.4</td>
<td>23</td>
</tr>
<tr>
<td>Populus grandidentata</td>
<td>0</td>
<td>16</td>
<td>100</td>
<td>2</td>
</tr>
<tr>
<td>Prunus pennsylvanica</td>
<td>0</td>
<td>1</td>
<td>18.2</td>
<td>11</td>
</tr>
<tr>
<td>Spiraea latifolia</td>
<td>—</td>
<td>—</td>
<td>40.0</td>
<td>5</td>
</tr>
<tr>
<td>Spiraea alba</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Myrica Gale</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Amelanchier spp.</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Sambucus pubens</td>
<td>60.0</td>
<td>5</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Alnus rugosa</td>
<td>2.6</td>
<td>38</td>
<td>0</td>
<td>80</td>
</tr>
<tr>
<td>Sorbus americana</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Tsuga canadensis</td>
<td>0</td>
<td>16</td>
<td>100</td>
<td>1</td>
</tr>
<tr>
<td>Juniperus communis</td>
<td>—</td>
<td>—</td>
<td>0</td>
<td>15</td>
</tr>
</tbody>
</table>

*Moose browsing only  
**Wapiti browsing only (see text)

Census and pellet group data from the Georgian Bay zone showed no evidence of Moose. Similarly, browsing in South Burwash is known to be done only by Moose. Cause of browsing in the other two zones can only be inferred from pellet group data (see later).

Red Maple and willows were generally available and were preferred browse in all habitat zones. Maple-leaf Viburnum was less generally available but clearly preferred. Round-leaf Dogwood (Cornus rugosa) provided little because of low availability despite preference shown for it. Trembling Aspen, White Birch and Red Oak provided moderate amounts of browse although both availability and preference were quite variable. Beaked Hazelnut was highly available in most zones but utilized little. Although usually browsing by Wapiti could not be distinguished from Moose browsing, some direct field observations and differences between zones suggested that most browsing of White Cedar was by Wapiti and most browsing of Balsam Fir was by Moose.

The Georgian Bay habitat zone had some unique feeding patterns. It was the only habitat zone where heavy grazing was evident (principally Deschampsia flexuosa). This grazing may occur due to the wind-swept and snowfree nature of the Georgian Bay zone. Consequently, in this zone food intake was not totally dependent on browse availability.

The number of browsed stems per browse survey plot (45 m²) is used to index browsing intensity in the habitat types in each habitat zone (Table 3). Open Meadows had an outstanding index of browsing on willow in one (North Burwash) of three habitat zones where Wapiti overwintered. However this value was based on only three browse plots. In the other two, Open Meadows either were a minor source of browse (French River) or included no Open Meadows (Georgian Bay). The other outstanding index of browsing was for Cedar Edge in the Georgian Bay zone. Again, although Cedar Edge clearly was heavily browsed, the extent was limited and difficult to sample and the index was based on only two plots. As sources of browse, other habitats can be considered to have: prime, intermediate, or low importance (see Table 3 for exact index values). Cedar/Balsam/Spruce was of prime importance for browsing in two of the three habitat zones where Wapiti overwintered (North Burwash and French River). In the third (Georgian Bay) where Cedar/Balsam/Spruce was unavailable,
Table 3. Number of browsed stems per 45 m² browse plot for each habitat type in each habitat zone. (Data from Spring 1978).

<table>
<thead>
<tr>
<th>Habitat type</th>
<th>North Burwash</th>
<th>South Burwash</th>
<th>French River</th>
<th>Georgian Bay</th>
</tr>
</thead>
<tbody>
<tr>
<td>High Open Areas</td>
<td>0.58</td>
<td>n.s.*</td>
<td>2.87</td>
<td>5.00</td>
</tr>
<tr>
<td>Cedar/Balsam/Spruce</td>
<td>5.17</td>
<td>0.67</td>
<td>3.54</td>
<td>n.a.**</td>
</tr>
<tr>
<td>Cedar Edge</td>
<td>n.s.</td>
<td>n.a.</td>
<td>n.a.</td>
<td>12.50</td>
</tr>
<tr>
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<td>n.a.</td>
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<td>0.39</td>
<td>n.a.**</td>
</tr>
</tbody>
</table>

*not sampled
**habitat type did not occur in zone
***included with Jack Pine

Cedar Edge may have substituted to some degree. In the Georgian Bay zone, Mixed Coniferous and High Open Areas were prime sources of browse. In French River, although Mixed Coniferous and High Open Areas had lower browse index values, they still were important as browse sources. The index values are lower simply because browsing is divided among more habitat types. In French River, Mixed Coniferous/Deciduous was also a major source of browse.

In North Burwash, Mixed Coniferous/Deciduous was lower in importance as a browse source compared to Cedar/Balsam/Spruce but still a vital browse source. Jack Pine habitat was intermediate in importance for browse in French River and Georgian Bay, but was unimportant in North Burwash.

Only four habitats were important sources of browse in the Georgian Bay zone and were nearly equal in importance.

Both High Open Areas and All Deciduous were of low importance as browse sources in North Burwash and All Deciduous was in this category in French River.

The data on browse plots in South Burwash were gathered because Wapiti had not been recorded overwintering there and so the browsing would be assignable primarily to Moose. However, as Table 3 shows, the habitats providing browse in South Burwash were so different from the other zones, mainly because of Logged Cutover availability, that South Burwash data do not help interpret the contribution of Moose to browse indexes in the other zones where both Moose and Wapiti were present.

The number of pellet groups per pellet plot is used to represent time spent in each habitat type in each habitat zone (Table 4). With few exceptions, data from the pellet group plots suggest a pattern of use similar to that seen in the browse survey. In North Burwash and French River habitat zones, Cedar/Balsam/Spruce was the habitat type used most often and Cedar Edge was used heavily in Georgian Bay habitat zone. When Open Meadow and Jack Pine habitat types were present in a habitat zone, they were also favored. For Jack Pine this was true even though stand characteristics changed substantially from French River to Georgian Bay. Wapiti spent more time in Jack Pine than can be explained simply by browsing. They were probably using this habitat as loafing shelter. The few woody stems along Hydro Lines were not browsed at all, but Hydro Lines had the third highest pellet group index in North Burwash. Field observations indicated that Wapiti were grazing on Deschampsia flexuosa on these Hydro Lines in early winter before snow accumulated. Moose on the other hand never frequented Hydro Lines. Although Mixed Coniferous and High Open Areas were important as browsing areas in French River and Georgian Bay, pellet group counts indicate that Wapiti did little more than browse there.

Discussion

Aerial surveys found Wapiti in only a few habitat types in winter while Moose were found in all major wooded habitats. However, pellet group counts showed that Wapiti used the majority of habitat types available in each habitat zone. Counts of browsed stems could not distinguish between browsing done by Wapiti and that done by Moose. Pellet group data from the Georgian Bay zone showed no evidence of Moose, so browsing in these same plots can be assumed to be done by Wapiti, although direct correspondence between pellet groups and stems browsed cannot be assumed. Browsing in South Burwash is known, conversely, to be done only by Moose. In the other two zones where both species were pre-
sent, Wapiti used the majority of habitat types for browsing also. However, the level of activity as indicated by pellet groups could differ strongly from the amount of browsing in that habitat type. For example, Jack Pine in the French River zone was not a prime source of browse but was highly used by Wapiti. The Jack Pine habitat had many openings in the canopy in French River and Wapiti probably were using this habitat type both for basking and for protection from wind. Field observations suggested that the coniferous components of habitats provided shelter and loafing areas but that most habitats dominated by conifers also provided important deciduous browse species for Wapiti.

Data on habitat use and on browsing show that Wapiti use several habitat types. Field observations indicate that Wapiti move among these several habitat types in satisfying their complete set of winter requirements. Movements along waterways and windswept ridges were most frequent and often began and ended in conifer swamps. Moose also used most of the same habitat types as Wapiti but with different browse preferences and with no evidence of moving among the habitats to satisfy their needs.

From these observations we suggest that the major elements underlying the winter habitat relationships of Wapiti in the Burwash-French River area are: their browse preferences, their utilization of an array of habitat types for browsing and other functions, and their need to move among these habitat patches.

Acknowledgments

Field research was funded by the University Research Support Fund of the Canadian Wildlife Service; Carleton University, Ottawa, and by the Ontario Federation of Anglers and Hunters. Don Flook and Charles Dauphiné, Jr., CWS, and M.B. Fenton, Carleton University, were generous with time and advice. Results of the research were used as partial requirements for a Master of Science degree by W.B. Ranta.

Literature Cited


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Table 4. Number of pellet groups per pellet plot for each habitat type in each habitat zone for Wapiti and Moose. (Data from Spring 1978)

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>North Burwash</th>
<th>South Burwash</th>
<th>French River</th>
<th>Georgian Bay</th>
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<tbody>
<tr>
<td></td>
<td>Wapiti</td>
<td>Moose</td>
<td>Wapiti</td>
<td>Moose</td>
</tr>
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</tr>
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<td>n.a.</td>
</tr>
</tbody>
</table>

*not sampled  
**habitat type did not occur in zone  
***included with Jack Pine

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A radio-telemetry study of a resident population of Fisher and an invading population of Marten was conducted from August 1978 to August 1980, in the boreal forest of southeastern Manitoba. Two juvenile, female Fisher had winter ranges of 15.0 and 20.5 km², while other juvenile females and males dispersed from the study area after their release. One juvenile, male Marten had a range of 9.6 km² in early winter, while another wandered at random in late fall and early winter, but had a range of 8.1 km² by the following spring. A juvenile, female Marten had seasonal ranges varying from 6.0 to 8.4 km². A fire that swept through the study area in May 1980 perhaps caused one male Marten to disperse 61 km, while a female Marten did not alter her range during the two months that radio contact was maintained.


A radio-telemetry study by Kelly (1977) in New Hampshire showed that Fisher (*Martes pennanti*) there had a mean home range of 19.2 km², with the largest range being 39.6 km². Leonard (1980) recorded ranges of similar size for radio-tagged Fisher in Manitoba. Radio-telemetry studies have established that Marten often have ranges from 2 to 20 km² (Mech and Rogers 1977, Davis 1978, Campbell 1979, Steventon and Major 1982).

A radio-telemetry and tracking study of Fisher and Marten was conducted at Taiga Biological Station (51° 05’N, 95° 20’W) from August, 1978 to August, 1980 in order to determine the range size and the length of the daily movements of the two species. The Fisher population in the study area was a resident one, whereas the Marten population was an invading one. No Marten were known to be present in the study area until 1978. The sudden influx of Marten appeared to be part of the widespread expansion of Marten range in Ontario and northeastern Minnesota (Mech and Rogers 1977). My study was also unique in that I radio-collared only juvenile Marten. Other authors deliberately collared only adults (Campbell 1979; Steventon and Major 1982), or did not age their study animals (Mech and Rogers 1977, Davis 1978).

**Study Area and Methods**

The 324 km² study area is part of the low boreal land region (Woo et al. 1977). The dominant features are bedrock knolls and ridges of up to 30 m in height, with bogs and fens in between. The mean January temperature varies from −22.8 to −19.8°C and the mean July temperatures varies from +18 to +19.5°C. Annual precipitation ranges from 410 to 535 mm, with 250 to 355 mm of this falling as rain between 1 May and 30 September.


The movements of Fisher and Marten were determined by radio-telemetry. Animals were captured and were anesthetized with 15 to 20 mg of ketamine hydrochloride per kg body weight and with 2.5 mg of acepromazine maleate per animal. Similar dosages were used by Kelly (1977) to anesthetize Fisher and by Hash and Hornocker (1980) to anesthetize Wolverine. The first premolar, lower right, was extracted from some animals for age determination. The ages of others were determined by the degree of development of their sagittal crests based on skull palpation (Marshall 1951).

Fisher and Marten were fitted with radio-collars (AVM Instrument Company, Champaign, Illinois) that weighed 70-115 gm and 13-15 gm, respectively. The animals were fed and kept in captivity 24 hours before release. They were then located by triangulation once a day when possible and occasionally twice a day. An AVM portable receiver and a four-element yagi antenna were used. Home range estimates were based on the minimum area method (Mohr 1947). The outermost locations of an animal were connected and the enclosed areas measured.

Winters were divided into three periods based on snow cover. The first period was from the time of the
first snowfall (13 November in 1978; 1 November in 1979) to when the snow thickness began to restrict the movements of Fisher and Marten. This thickness I arbitrarily chose as 20 cm, and it happened to be reached on 26 November of both winters. The second period encompassed the mid-winter months of soft, thick snow cover when the vertical hardness was less than 100 gm/cm\(^2\) in all habitats except rivers and lakes, and was often less than 10 gm/cm\(^2\). The third period began when a vertical hardness of greater than 100 gm/cm\(^2\) was reached in all habitats. The change to crust conditions was quite abrupt in both winters and occurred in all habitats at about the same time (21 March in 1979; 23 March in 1980). I undertook a trailing study of the two species at the same time as this study (Raine 1981, 1982). Fisher were found to be restricted by the soft, thick snow cover that was present during mid-winter. Fewer tracks were observed at this time, and Fisher travelled on Snowshoe Hare trails and on their own trails to a greater extent than in either the early winter period of thin snow cover or the late winter period of crust conditions. Fisher were also found to walk through the snow cover and leave a body drag in mid-winter.

Marten did not appear to be hindered by soft snow cover to the degree that Fisher were. Marten tracks were encountered with equal frequency throughout the winter and they never left a body drag in the snow cover. They did travel on hare trails and on their own trails to a greater extent in the mid-winter, but never as much as did Fisher.

**Results and Discussion**

*Fisher Range*

The two male (weights of 4.5, 3.4 kg) and four female (\(x\) weight \(=\) 2.4 kg) Fisher live-trapped were all juveniles. One male and two females moved out of radio reception range within 4 to 10 days of their release, and all three were later killed by trappers 9.5 to 18.0 km away. Kelly (1977) and Leonard (1980) both found that juvenile Fisher moved greater distances than adults. One juvenile in Leonard's study was killed by a trapper 60 km from its release site.

Two female Fisher (F3, F5) were found to have mid-winter ranges of 20.5 (45 locations in 64 days) and 15.0 km\(^2\) (25 locations in 24 days) (Figure 2). These results compare favourably with the results of Kelly (1977) and Leonard (1980). F3 and F5, however, were only radio-tracked for short periods, and it is not known whether the animals travelled out of radio reception range or the collars ceased to function.

F4, a male, exhibited unusual behaviour before he was captured. I followed his trail back from his capture site for 3.6 km. He had travelled on top of ski and other trails for 69\% of this distance, and had followed every twist and turn of these trails. Other Fisher trailed during the same mid-winter period had spent only 2\% of their time on such trails and they generally only followed ski trails which were parallel to their path. F4 was also unusually docile in the trap and was light in weight (3.4 kg)

Sixteen days after his release, he was found dead in a cave. During this time his minimum range was 12.0 km\(^2\) (31 locations) (Figure 2) and he travelled on ski and animal trails for 58\% of the 3.7 km that I trailed him. I found no scats while trailing him, and when dead he weighed only 2.7 kg. Although the trauma of being captured and collared could certainly have had an effect on F4's health, his behaviour before his capture indicated that the soft snow cover of mid-winter had a greater restrictive effect on his movements than on the movements of other Fisher. Perhaps this was the cause of this death. In any case, his range size cannot be considered as typical of juvenile, male Fisher.

*Marten Range*

The Marten population was quite low in the study area, as the capture rate was only 0.4 Marten per 100 trap nights. Other authors have caught 2.8 (Koehler and Hornocker 1977), 3.8 (Soutiere 1979), 6.8 (Campbell 1979), 7.0 (Miller et al. 1955) and 13.1 (Hawley and Newby 1957) Marten per 100 trap nights.

Of the six male (\(x\) weight \(=\) 1.2 kg) and four female (\(x\) weight \(=\) 0.7 kg) Marten that were live-trapped, all but two were juveniles. One male was 1.5 years old and one female was 4 years old.

Two juvenile males (M3, M4) and one juvenile female (M9) were radio-collared. M3 was first caught in October 1979. During the 14 days before the first snow fall of the year, he had a minimum range of 6.7 km\(^2\) (24 locations) (Figure 3,A) and during the 26 days of the thin snow cover period he had a range of 5.5 km\(^2\) (n = 18) (Figure 3,B). During 30 days of the mid-winter period of soft snow cover before radio contact was lost, he had a range of 4.7 km\(^2\) (n = 14) (Figure 3,C). Forty-two days later, 7 February 1980, M3 was recaptured 5.3 km northeast of his last radio location (Figure 3,D). His collar no longer functioned and it was removed, but he was released without being recollared. He was next recaptured 4.2 km to the southeast, recollared, and released on 8 April. During the next 10 days of crust conditions, M3 had a minimum range of 2.1 km\(^2\) (n = 9) (Figure 2,E) and after the snow melted, his range was 8.1 km\(^2\) (31 days, n = 26) (Figure 3,F).

Thus M3 appeared to shift his range constantly during the fall and early winter of 1979. Due to the paucity of track observations in this area, it was most likely that there were no other Marten near M3 at this
Figure 1. Trap distribution in the study area, each square represents from 1-5 traps. Trap locations were not permanent; the areas trapped most continuously were those close to the station. Map insert shows the location of the study area in Manitoba.
Figure 2. Mid-winter ranges of female Fisher F3 (o) and F5 (●) and of male Fisher F4 (▲) as determined by radio-telemetry.
time. The size of each of his ranges did not appear to change in accordance with the change in snow cover conditions. However, the sample size in each of the periods was small. M3 may have established a permanent home range by the spring, as his range was fairly stationary during the 41 days of the crust and snow free periods that radio contact was maintained. Unfortunately, a forest fire that began 20 May swept through the study area and radio contact was lost from this date to 3 June. Most of the bogs were not burnt, but the ridges were burnt severely. M3 survived the fire and I located him four times in as many days before radio contact was lost. He was in unburnt bogs for each of these locations. On 2 November 1980 he was killed by a trapper 61 km to the east. His total minimum range, excluding the location of his death, was 42.4 km² (n = 95, 223 days). It cannot be said whether M3 dispersed 61 km because of the fire or because he had not yet established residency.

The second juvenile male, M4, was caught and released with a collar shortly after M3’s first release (20 October 1979). During the 11 days before the first snow-fall, he had a range of 3.0 km² (n = 18) to the east of M3’s range. During the thin snow cover period he was located 21 times in 25 days, and had a range of 9.6 km² before radio contact was lost on 26 November. M4 was recaptured within his previous range 22 days later, but he died during anesthesia. During the time that M3 and M4 were radio-tracked concurrently, there was little overlap in their ranges.

The temporary ranges of these juvenile males were similar in size to the ranges of males of unknown age.
in Minnesota (10.5 to 19.9 km²; Mech and Rogers 1977) and adult males in Maine (5.0 to 10.0 km²; Steventon and Major 1982).

Another juvenile male Marten (M6) was not radio-collared but was live-trapped 19 times in a 103 day period during mid-winter 1979/80 and had an estimated minimum range of 5.3 km² that was approximately centered upon Taiga Biological Station. He was first captured on 6 December. By this time M4 was dead and M3 had a temporary range several kilometers to the west of where he had been previously. Based on live-capture data, the range of M6 remained relatively stationary through the winter, while M3's range expanded to the north and then to the east and south. Thus M3 appeared to avoid M6's range.

The third Marten radio-tagged (M9, a juvenile female) was released on 7 April 1980. Her minimum range during the remainder of the crust period (12 days, n = 15) was 8.4 km² (Figure 4). After the snow melted but before the fire her range was 6.6 km² (31 days, n = 34). She also survived the fire. Once it was safe to walk in the burn she was located nearly every day until radio contact was lost on 3 August 1980 (minimum range = 6.0 km²; 64 days; n = 80). Her total range was 12.5 km² (118 days, n = 129). Thus M9 had the most stable range of the Marten radio-collared in this study. Her range was larger during the crust period than during the snow free period of spring. Snow crusts make travelling easy for Marten, and they hinder Marten from hunting in subnivean spaces (Raine 1981). Thus Marten may have to travel farther to find food when there is a crust.

After the burn I approached M9 closely enough to be certain of what habitat she was in nine times. On every occasion she was in unburnt bogs, except twice when I accidentally approached too closely and treed her. On these two occasions, she climbed live spruce trees that bordered unburnt bogs. As determined by a habitat map of the study area, made from aerial photographs, bogs composed 32.9% of M9's home range during the snow free period prior to the burn, and 35.2% after the burn.

The range size of the juvenile, female M9 was comparable in size to the range of a female of unknown age in Minnesota (4.3 km²; Mech and Rogers 1977) and to two females of unknown age that were introduced into Wisconsin (7.7 and 8.2 km²; Davis 1978). Steventon and Major (1982), however, found that an adult, female Marten in Maine had a range of only 2.0 to 2.5 km².

Fisher Twenty-four Hour Movements

The two radio-collared female Fisher (F3 and F5) moved a mean distance of 1.1 km (n = 32) and 2.5 km (n = 18), respectively, between successive daily locations in mid-winter. Although these means are significantly different (1-way ANOVA: F(1,40) = 14.61 P < 0.001), the small sample size obscures the meaning. Their home ranges did not appear to differ in habitat composition, and therefore productivity, and the snow conditions between winters were comparable. Kelly (1977) found that female Fisher in New Hampshire moved a mean distance of 1.5 km (n = 99) between successive daily locations.

Marten Twenty-four Hour Movements

The means of the 24-hour movements of Marten M3 did not differ significantly between the winter periods and the no snow periods (F(4,48) = 1.68; P < 0.25). There is a trend, however, as M3 moved less during the thin snow cover and mid-winter periods (1.0 km, n = 10, 1.1 km, n = 6) than during the fall period of no snow (1.4 km, n = 12), the crust period (1.5 km, n = 7) and the spring period of no snow (1.8 km, n = 18). M4 also appeared to decrease his activity from the fall period of no snow (1.5 km, n = 8) to the thin snow cover period (0.8 km, n = 14) (F(1,20) = 4.83, P < 0.05). M9 decreased her daily activity from the crust period (2.1 km, n = 9) to the snow free period of spring (1.5 km, n = 29) and after the burn (1.3 km, n = 60) (F(2,95) = 4.63, P < 0.025). Thus there is some evidence that Marten travel less in the thin snow cover and mid-winter periods, and travel more in the crust period, than in the periods of no snow cover.

Acknowledgments

I would like to express my gratitude to Dr. W.O. Pruitt, Jr., for the advice and encouragement that he gave to me during this study. W. Heck helped with the illustrations and M. Strickland sectioned the Fisher and Marten teeth. This study was funded by the Manitoba Government Department of Natural Resources, the University of Manitoba Northern Studies Committee, the Taiga Biological Station Research Trust, and a University of Manitoba Fellowship.

Literature Cited


Figure 4. Ranges of M9 as determined by radio-telemetry, 1979.


Raine, R. M. 1982. Winter habitat use and responses to snow cover of fisher (Martes pennanti) and Marten (Martes americana) and southwestern Manitoba. Canadian Journal of Zoology. In press.


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Marten, *Martes americana*, Movements and Habitat Use in Algonquin Provincial Park, Ontario

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The behaviour of five male Marten, *Martes americana*, was studied between 1973 and 1975 using radio-telemetry. They spent proportionately more time in predominantly coniferous habitats than in hardwood habitats. The maximum foraging area was 3.53 km². Individuals often moved rapidly about their foraging area; the fastest recorded speed was 7.2 km/h. Marten move from one foraging area to another for reasons other than food supply and do not always return. The Marten were tracked simultaneously on several occasions and each moved quite differently. Marten seem to show mutual avoidance and their foraging areas do not usually overlap.

Key Words: Marten, *Martes americana*, Algonquin Park, movements, habitat use, radio-telemetry.

The North American Marten, *Martes americana*, is a commercially important fur species which occurs in forested areas of northern North America. It is a predator of small mammals, particularly voles, *Microtus* and *Clethrionomys*. The biology and food habits of Martens have been studied in the Northwest (Newby 1951; Jonkel 1959; Weckwerth and Hawley 1962), in Central Alaska (Lensink et al. 1955), and in Ontario (De Vos 1951; 1952; Francis and Stephenson 1972). These studies have all used trapping or snow tracking to determine the presence, abundance, and activity of animals. Little is known of the movements and patterns of habitat use of this rather secretive predator. We have used radio-telemetry to determine movement patterns of Martens in Algonquin Park, Ontario.

The study area, described previously by Francis and Stephenson (1972), is situated immediately north of Highway 60 in central Algonquin Park. This part of the Park is hilly and the study area is characterized by granite and granite-gneiss ridges (364-516 metres above sea level) with many steep-sided valleys.

**Materials and Methods**

The study was initiated in the fall of 1973 and was concluded in the summer of 1975. We visited the study area for three days once a month, every month, for a one-week interval in December, and more or less continuously from May to August of 1974.

The Marten were captured in Tomahawk live traps which were set in the major forest types present in the study area: coniferous (more than 75 percent conifers), coniferous-hardwood (51-75 percent conifers), hardwood-conifers (26-50 percent conifers), and hardwood (less than 25 percent conifers). The bait was a mixture of fish oil and raspberry jam as described by Francis and Stephenson (1972).

Trapped Marten were brought back to the laboratory, anaesthetized with ether, and then weighed, sexed and marked. Each Marten was tagged with either a coloured plastic identification collar or a marked radio-transmitter on a collar. The identification collars were made from a whitish, slightly flexible plastic with bands of different coloured adhesive tape. The collars were closed with easily removable copper rivets to facilitate changing. They did not appear to affect the animal in any way and did not cause any skin damage (one individual which carried a succession of collars and transmitters throughout the study maintained his weight and did not suffer any obvious neck or fur damage). Marten were returned to the trap site and released as soon as they had recovered from anaesthetic, or if they were brought back to the laboratory late in the day, the following morning.

The transmitters (Daytron Electronics) were attached to a collar which also acted as a loop antenna. Small whip antennae were tested but did not last long on these animals, and we found that chafing occurred with stiff brass collars, even when a machine belting liner was used, and so a flexible collar was preferred. A wire braid covered in plastic was used successfully, but a better material was "photoised chjel-clad" No. GTAA608 produced by Sheldahl Inc. Department G. Highway 3, Northfield, Minnesota 55057. This material is light, easy to cut and, when covered with a protective plastic casing, is very strong. The total weight of radio collar was 25 grams. The transmitters have a maximum range of about 2.8 km under optimum conditions.
Sixteen Marten were trapped in the study area and were fitted with identification collars; three were females. Two problems, transmitter failure and the animal moving away, reduced the quantity of information we collected, and the data presented are based on five males. Accuracy of plotting radio locations was tested against transmitters at known locations; such locations were correct to within 50 metres. Initially, hand-held three element yagi antennae were used for tracking, but because of the irregular topography we installed three permanent towers on high points approximately 1.5 km apart. Each receiving tower consisted of a 15-metre telescopic tower on a ball bearing race. Three antennae were mounted on each tower. They were an eight element, two metre yagi (Model 28, Hygain, RR 3 Lincoln, Nebraska, 68505) for tracking; an omnidirectional antenna (HWA-202-4, Heathkit, 1480 Dundas Highway E., Mississauga, Ontario L4X 2R7) for picking up a signal during diel rhythm studies; and a communications antenna (Trik Stik, Cush Craft, 621 Hayward St., Manchester, New Hampshire 03103) for maintaining continuous contact between observers. AVM Model CA12 receivers (AVM Instrument Co., 810 Dennison Drive, Champaign, Illinois, 61820) operating in the 150 MHz range were used throughout the study. Constant communication between towers was maintained with three watt transeivers (Realistic Model TRC-99C, Radio Shack, Fort Worth, Texas 76107). Portable, collapsible, three element yagi antennae were also used; these were manufactured in the Electronics Shop at York University.

Because of the speed at which Marten move it was found necessary to man all three towers simultaneously to keep track of one or more individuals. It was sometimes necessary for observers to leave the towers and use the three element yagis to check on the exact location of an animal which was picked up by only one tower.

The location of a Marten was plotted every five or ten minutes on a map of the study area divided up into 45-metre squares. Often there were large gaps in the radio-contact, when the animal went underground or was so sheltered that no radio-signals were received. In such cases, the time of last contact was recorded as five minutes, and no further time at that location was recorded even if the signal was picked up later at exactly the same coordinates. The total time an animal spent in each square was determined and this “spatial-use” map was superimposed upon a forest-type map modified from Francis and Stephenson (1972).

Results and Discussion

The proportion of time which radio-tagged marten spent in the four different forest habitats is shown in Table 1, and an example of habitat utilization by Male 10 is shown in Figure 1. The chi-square values for the differences between actual time spent in a habitat and expected time spent in a habitat were calculated for each habitat, and the figures are given at the right of the table. All the values are significant; \( P < .01 \), indicating that the animals did not utilize the forest types randomly but spent more time in the forest types containing more than 50 percent conifers. The combined data for the five Marten suggest that this Marten population is consistent in its preference for predominantly coniferous habitats. Francis and Stephenson (1972) found that the common prey species of Marten during the summer months were the Meadow Vole, Microtus pennsylvanicus, and the Boreal Redback Vole, Clethrionomys gapperi, and that these species occur in the wetter coniferous areas near creek edges.

Daily Activity and Foraging Areas

The foraging area of each animal during the study periods is shown in Figure 2. The term “foraging area” is used to denote the area in which the animals spent their time during the period of radio-tracking. It may be less than the home range, as defined by Jewell (1966), in that the period of observation was too short to determine whether the foraging area represented the animal’s home range; in several cases, part of the animal’s home range extended beyond the range of the receiving towers. By connecting the outermost points of each animal’s movements, we estimate its foraging area, which takes the form of a convex polygon. Convex polygons are not accurate in indicating the actual spatial use of a foraging area, particularly when the general home range is as heterogeneous as this study area, and when the animal shows marked preferences for particular habitats as demonstrated in the analysis of habitat usage (Figure 1 and Table 1). Figure 3 shows the actual use of the foraging area for male 10; the distances and rates of movement for all animals are summarized in Table 2. Male 10 had two main centres of activity; from 23 June until 16 July he occupied a wet coniferous area on the north side of Crosby Pond, and thereafter he moved about 1 km to an area west of Kathlyn Lake. On 21 July he shifted to the north side of Kathlyn and appeared to leave the study area 23 July. In spite of regular monitoring for the following week no further signals were received, nor was he ever retrapped. The mean speed of the animal was 0.36 km/h, the maximum speed obtained on any day was 7.2 km/h for a 30 minute period, and the maximum distance covered in any one day was 7.64 km in 10.5 h (on 16 July). There are no previous published records of the rates of movement of Marten.

The foraging areas are relatively distinct except for
Figure 1. Habitat use by Marten 10.

Table 1. Time spent by five Marten in the four forest types. The percentage of forest types is derived from Francis and Stephenson (1972).

<table>
<thead>
<tr>
<th>Animal No.</th>
<th>Total time animal observed (min.)</th>
<th>Conifer habitat (19%)</th>
<th>Conifer/ Hardwood habitat (26%)</th>
<th>Hardwood/ Conifer habitat (17%)</th>
<th>Hardwood habitat (38%)</th>
<th>X²</th>
<th>Significance Level</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>170</td>
<td>12</td>
<td>59</td>
<td>6</td>
<td>24</td>
<td>96.6</td>
<td>&lt; 0.005</td>
</tr>
<tr>
<td>10</td>
<td>1480</td>
<td>14</td>
<td>39</td>
<td>15</td>
<td>32</td>
<td>142.0</td>
<td>&lt; 0.005</td>
</tr>
<tr>
<td>11</td>
<td>165</td>
<td>42</td>
<td>27</td>
<td>0</td>
<td>30</td>
<td>79.0</td>
<td>&lt; 0.005</td>
</tr>
<tr>
<td>12</td>
<td>575</td>
<td>41</td>
<td>20</td>
<td>5</td>
<td>34</td>
<td>201.0</td>
<td>&lt; 0.005</td>
</tr>
<tr>
<td>13</td>
<td>100</td>
<td>15</td>
<td>35</td>
<td>25</td>
<td>25</td>
<td>12.0</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Total</td>
<td>2490</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>X²</td>
<td></td>
<td>220.8</td>
<td>183.9</td>
<td>94.7</td>
<td>32.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Significance Level</td>
<td></td>
<td>&lt; 0.005</td>
<td>&lt; 0.005</td>
<td>&lt; 0.005</td>
<td>&lt; 0.005</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 2. The foraging areas of five male Marten, 9 from 4 June to 20 December; 10, 23 June to 23 July; 11, 13 July to 15 July; 12, 30 July to 8 November; and 13, 31 July to 8 August.
Figure 3. Total activity of Marten male 10. This represents 115 hours of activity between 23 June and 23 July.

Table 2. Activity of five Marten over varying periods of time. The shortest distance between successive location points was drawn and the total distance travelled represents the minimum distance the animal must have travelled in the time taken. The foraging area is derived from Figure 4.

<table>
<thead>
<tr>
<th>Marten No.</th>
<th>Dates of Radio-Tracking</th>
<th>Minimum Distance Moved (km)</th>
<th>Time Taken (hours)</th>
<th>Average Speed (km/h)</th>
<th>Foraging Area (sq. km)</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>4 June-20 December</td>
<td>5.47</td>
<td>10.25</td>
<td>0.53</td>
<td>0.70</td>
</tr>
<tr>
<td>10</td>
<td>23 June-23 July</td>
<td>40.12</td>
<td>115</td>
<td>0.36</td>
<td>3.53</td>
</tr>
<tr>
<td>11</td>
<td>13 July-15 July</td>
<td>4.2</td>
<td>16</td>
<td>0.26</td>
<td>0.59</td>
</tr>
<tr>
<td>12</td>
<td>30 July-8 November</td>
<td>7.57</td>
<td>44.4</td>
<td>0.61</td>
<td>2.39</td>
</tr>
<tr>
<td>13</td>
<td>31 July-8 August</td>
<td>7.38</td>
<td>20.4</td>
<td>0.35</td>
<td>1.11</td>
</tr>
</tbody>
</table>
the apparently almost complete overlap of males 10 and 12 (Figure 2). However, since male 10 moved out of the study area on 23 July, and since male 12 was not caught in the area until 30 July, there was, in fact, no actual overlap between these individuals. These results agree with the findings of Francis and Stephenson (1972) and Hawley and Newby (1957) who, using trapping and retrapping techniques, found little overlap between individuals. The cause of male 10's disappearance is not known, but because he was tracked moving out of his foraging area and was replaced by male 12, we suggest that he was leaving his foraging area voluntarily. It is of course possible that he died, but male 1 also left the study area after we tracked him for six months and he came back a year later. Since Marten tend to avoid each other, as do foxes (Preston 1975) and weasels (Simms 1979), we cannot believe that male 12 forced male 10 out, nor could the disappearance of male 10 be related to a shortage of food, since there was enough to support male 12 through the winter.

Because males 9, 11, and 13 were monitored for relatively few days, and their range of activity probably extended beyond the range of the radio receiving antennae, foraging areas depicted in Figure 2 are probably minimal. However the figures for male 10 and 12 probably represent reasonable values of foraging areas for this species, and they approximate the mean home range of 3.57 km² calculated for five males by the trapping retrapping method in a study by Francis and Stephenson (1972). Whether the foraging areas of males 10 and 12 represent their home ranges in unknown, though from the evidence of males 1 and 10 it may well be that these areas represent only a small part of their home range, and that previous studies represent a gross under-estimation of the Marten's home range.

One of the problems with radio-telemetry of carnivores under these field conditions is the difficulty of following animals over their entire ranges. For instance, it appears that male 1, who was trapped several times, and followed for short periods in the fall and winter of 1973-74 in the central region of the study area, came back in the early winter of 1974-75 to the area east of Kathryn Lake. In spite of periods of relatively heavy trapping during the summer of 1974, he was not caught in the study area, so we must assume that he left his original foraging area for a year and then came back. This, together with the fact that male 10, who was in good condition, was moving his foraging area during the summer, suggests that adult male Marten may move from one foraging area to another during the year and may not, in fact, have a permanent home range as defined by Jewell (1966) or territory as proposed by Lockie (1966). It is possible that individuals may maintain a relatively fixed foraging area for a period of time and then shift to a completely new area. It is also conceivable that "territorial" adult males move their foraging areas from one area to another, as opposed to "transient" males (Lockie 1966), who are more mobile and are not able to set up a semi-permanent "home" foraging area. It would be necessary to perform further studies to see if this is indeed the case.

Simultaneous Marten Movements

For several days two Marten were tracked simultaneously to determine if individuals in the same area and with the same weather conditions interact and whether they behave similarly.

Figure 4 illustrates the movements of males 10 and 11 on 14 July. Both animals were located early in the day (0945) and followed until the receiving stations closed down in the evening (2100). Male 11 remained near the west end of Kathryn Lake during the morning, for some time resting near a known den site, and then moved into the coniferous area on top of the hill immediately west of the lake. Here he moved around, presumably foraging and at 2035, as he was moving west, he possibly picked up the scent of male 10 who had just headed north through the area. Male 11 then turned back into the hardwood and returned to the coniferous forest at 2055.

Both animals were tracked the following day and found to utilize similar areas. However, male 11 did not start moving until 1745. Male 10 was already on the move at 0910, laid up from 1230 to 1420, and then continued moving until 1800. Another marten, without a collar, was seen near the Kathryn tower at 1215. Male 10 was moving most of the day, but rested for a two hour period in the early afternoon and the unmarked Marten was mobile at midday.

From 31 July to 2 August, males 12 and 13 were tracked (Figure 5). They were quite different in their activity levels. On 31 July, male 13 remained in a small area south of Sasajewun Lake and moved approximately 0.31 km, while male 12 circled a large part of his foraging area and travelled at least 4.8 km. On 1 August, male 12 moved from Crosby Pond northwards toward Broadwing Pond and then westward towards Kathryn Lake. This individual concentrated his activities in coniferous areas and moved rapidly between such areas. Male 13 moved very little compared with male 12. On 2 August he moved about in the vicinity of Davies Swamp, and at 1055 was quite far west of the swamp. Meanwhile, male 12 did not start moving until 1040 and then moved southwards, stopping to hunt near one coniferous area and then moving to the southern part of his foraging area, where contact was lost. At this point he was fairly
close to the location that male 13 reached in the morning, though there was no temporal overlap of their foraging ranges. During the day's activities both animals moved approximately the same distance: male 12, 2.23 km and male 13, 2.31 km. From the evidence of monitoring several individuals on the same day, it appears that Marten may behave quite differently under the same environmental conditions.

Conclusions
This study confirms previous work demonstrating the preference of Marten for coniferous forest types. In a heterogeneous habitat, where a choice of forest types are available, Marten spend most of their time in forest types containing more than 50 percent conifers. The size and shape of the home range of Marten is presumably different in a heterogeneous habitat than in a homogeneous one. Traditionally home ranges are illustrated as convex polygons and this may well be adequate in homogeneous areas, but where a species such as Marten show distinct habitat preference within a heterogeneous home-range the convex polygon may not be truly representative. In this case, activity maps showing where the major areas of activity are located is probably a better representation of the animals's home range.

From the evidence obtained by monitoring several individuals on the same day, it appears that Marten may behave quite differently under the same environmental conditions.

The use of radio-telemetry in basic studies of home range of small carnivores confirms data acquired by trapping techniques. It does, however, provide more accurate information as to how the animals may interact within a given area. Over a month or so, there appear to be overlapping home ranges but this study shows that Martens have dynamic home ranges which may be moveable. With trapping-retrapping tech-
Figure 5. Simultaneous Marten movements. Male 12 (foraging area in centre) and Male 13 (foraging area at bottom right) for three successive days, 31 July to 2 August.

niques this change in home range is not picked up so quickly. Also, from the analysis of two adjacent Marten home ranges, it is apparent that they do not overlap temporally and a mutual avoidance appears to be practised. A similar situation was shown by King (1975) for weasels. Because some Marten appear to be conditioned to traps and to use them as a source of food, the use of trapping for home-range studies may be of limited value.

The movements of an individual Marten are probably related to its hunting success, and this may explain the differences between the different Marten in this study. Some individuals may patrol and mark their foraging areas with scats when the population density of Marten is high, though this might not be necessary under low population densities. Until further work is done on the behaviour of Marten under different population densities, considering both females and males and the effect of transients upon the resident Martens, these questions cannot be answered. Radio-telemetry is a useful technique in studying Marten in the wild, particularly for habitat utilization in heterogeneous habitats and for behavioural studies. For basic work on home ranges, however, it is probably best to use trapping and retrapping, since the results seem to be similar.

Acknowledgments
This research was made possible by a National Research Council Grant A9623 and grants from the Faculty of Science and the Faculty of Environmental Studies, York University. Assistance was also provided by the Ontario Ministry of Natural Resources without which this work would not have been possible. Thanks are due to the many people who helped, particularly to M. Crombie, S. Mihok, S. Pitch, and G. Rother. We would also like to thank those people who helped with the manuscript, particularly Dr. C. S. Churcher, Dr. P. R. Grant and Dr. T. S. Parsons.
Literature Cited


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Intensive capture efforts for an interior Brown Bear, *Ursus arctos*, population in southcentral Alaska permitted calculation of a minimum density estimate of one bear/61 km\(^2\) based on the total number of captured and observed bears. Petersen Index (mark-recapture) estimates on the same data, corrected for biases, yielded an estimate considered more accurate of one bear/41 km\(^2\). Females with newborn cubs were identified as having lower probabilities of capture than other bears. Brown Bear biomass in the study area was estimated at 262 kg/200 km\(^2\).

Key Words: Brown Bear, Grizzly Bear, *Ursus arctos*, density, biomass, Petersen Index.

Accurate bear density estimates have been difficult for wildlife managers and researchers to obtain. Direct counts are seldom possible because of low observability and generally low densities; indirect estimates based on scats or tracks are seldom attempted because of the infrequent and highly variable distribution of these signs in both time and space. Reliable density estimates have been derived primarily from intensive marking and radio-tracking studies wherein essentially all bears in a well-defined area have been captured and monitored over a period of years as was done for Black Bear, *Ursus americanus*, by Rogers (1977). Many other reported bear densities, especially for Brown Bear, represent little more than a guess on the number of bears, divided by the area of some unit of management significance. Although such estimates have value in some circumstances, the lack of definite procedures make replicate studies difficult and density comparisons between areas questionable.

This paper reports a Brown Bear density estimate in a portion of interior Alaska where no previous bear density estimates have been made. The opportunity to investigate Brown Bear population densities in this region arose as a result of an effort by the Alaska Department of Fish and Game (ADF&G) to experimentally reduce Brown Bear numbers, by transplant, in order to evaluate the response of Moose, *Alces alces*, calves to relief from Brown Bear predation (Ballard et al. 1980; 1981). The study was conducted in an area where Brown Bear home ranges and movements had been previously documented (Ballard et al. 1982). The design of the study permitted a bear density estimate through use of a standard population estimation technique (the Petersen Index).

Potential sources of bias and assumptions implicit in the Petersen Index estimate have been widely reported (e.g., Seber 1973). Although all of the potential sources of bias could not be adequately tested or adjusted, we believe that our procedures provided a bear density estimate that is realistic, is based on objective numerical procedures, and is replicable in other areas or at other times to provide directly comparable estimates. At least in relatively open areas with moderate to high Brown Bear densities, this method may provide density estimates quickly and inexpensively relative to attempts to capture and radio-collar all individuals.

Study Area and Methods

The bear removal area encompassed 3,436 km\(^2\) centered on the head waters of the Susitna River in southcentral Alaska (Figure 1). The study area was bordered on the north by the Alaska Range, on the east by the Clearwater Mountains, and on the southwest by the Talkeetna Mountains. Between these mountains is a broad, flat plateau known as Monahan Flats (approximately 830 m mean elevation) crossed in several places by the braided, glacial tributaries of the upper Susitna River.

Vegetation on the study area is predominantly shrubs dominated by Dwarf Birch (*Betula nana*) and willow (*Salix* spp.) Local areas of spruce (*Picea glauca* and *P. mariana*) are found along river courses and areas of poor drainage. Vegetation at the higher elevations is open tussock grasslands. The Brown Bear habitat in the study area was considered above average relative to other areas of interior Alaska where bears have little or no access to salmon (*Oncorhynchus* spp.) Doubtless, areas of equivalent vegetation where salmon are also available can support higher Brown Bear densities. Portions of interior Alaska where spruce forests predominate and Black Bears are
also resident, probably support lower Brown Bear densities. The study area is accessible to hunters using highway vehicles, boats and aircraft.

Bears were located by two fixed-wing aircraft (Piper Super Cub PA-18), each with a pilot and observer. Once located, bears were darted from a helicopter (Bell 206B) and removed from the area as described by Miller and Ballard (1982). Fates of transplanted bears were described elsewhere (Miller and Ballard 1982).

Ages of adult bears were estimated based on sections of the first premolar using methods described by Mundy and Fuller (1964); ages of cubs and yearlings were estimated by size and tooth replacement. Weights were obtained using a hand-held spring scale with a capacity of 91 kg or with a spring scale with a capacity of 680 kg.

Forty-seven bears were captured from 22 May to 7 June 1979. Additional efforts on 21-22 June resulted in the capture of one additional bear and the recapture of one returned bear. All observed bears were captured, except for one unmarked individual. Previous radio-tracking studies (Ballard et al. 1982 and unpublished data) indicated that bears denned in the mountainous terrain on the periphery of the study area, exited these dens between 9 April and 12 May, and then moved to the lowland habitats in the center of the study area. Because these observations suggested that most bears should occur in the central portion of the experimental area during the capture period and because search efforts were most efficient in this portion because of the relatively flat terrain, search efforts were concentrated in the central portion of the study area although the mountainous terrain on the periphery was also searched.

Some bears were located at Moose kill sites, including kills of radio-collared Moose calves equipped with mortality-sensor radio collars (Ballard et al. 1979; 1980; 1981). Of the bears captured the preceding year (1978), only two retained functioning radio collars; both of these animals were radio-tracked and recaptured on the first day of the removal effort.

Twelve Brown Bears marked in 1978 inhabited the 1979 study area; these served as the basis for adjusted Petersen Index estimates of population size. Mark-recapture calculations were made separately for each sex and included all bears older than 3.0 y in 1979. This age restriction was used because no yearlings were marked in 1978, so no marked 2.5 y-old bears could have been present in 1979. The probability of
capture of 2.5 y-old bears in 1978 was assumed equivalent to that of 3.5 y-old bears in 1979, therefore it was not necessary to correct for recruitment into the 1979 sample of bears 3.0 y or older. Search areas were essentially the same in 1978 and 1979.

The Chi-square test statistic was used to compare subpopulations on the basis of sex ratio. The equation used in Petersen estimate calculations was (Ricker 1975):

\[
\hat{N} = \frac{(M + 1)(C + 1)}{(R + 1)}
\]

In this equation: \( M \) = number marked in 1978, \( C \) = number captured in 1979, and \( R \) = number of recaptured bears in 1979.

Results and Discussion

The number of captures/day ranged from 0 to 8 (0-4 for adult bears). Daily capture rates for the 17-day continuous removal effort were highest in the first 6 days (4.5 bears/day), lowest in the middle 5 days (0.8 bears/day), and intermediate in the last 6 days (2.7 bears/day). This pattern of capture probably resulted from normal seasonal movements of Brown Bears from high elevation den sites on the periphery of the study area to the relatively flat central portion where search efforts were concentrated.

The possibility that this pattern of capture resulted from immigration into the study area was rejected on the basis of analyses of sex and age composition as related to time or location of capture. For this purpose a periphery zone was defined as the area within one average home range radius inside of the search area, 15.7 km for males and 11.5 km for females (Miller and Ballard 1982).

Groupings of consecutive time periods (six 3-day intervals, three 6-day intervals, and two 9-day intervals) \( P > 0.30 \). The sex ratio in the center of the area throughout the capture period was skewed in favor of males (8:7); this was not different from the sex ratio in peripheral areas during the last half of the removal period (3:2 in favor of males) \( P > 0.2 \).

A similar lack of evidence for immigration existed in age ratio data. The seven males captured in the last half of the capture period were younger (\( \bar{x} = 5.8 \) y) than the 12 males captured in the first half (\( \bar{x} = 7.6 \) y), however, excluding one exceptionally old bear (21.5 y) no differences in mean male ages were apparent (5.8 y and 6.2 y, respectively). No differences were apparent in the mean age of eight females captured early (\( \bar{x} = 7.1 \) y) relative to seven captured later (\( \bar{x} = 7.6 \) y).

Significant immigration was also considered unlikely because the surrounding mountains on three sides of the study area would have limited the ability of bears living in adjacent areas to perceive the relative vacuum of bears being created in the study area during the bear removal period. Moose calves were available in equivalent densities in adjacent drainages so there was no reason to suspect that bears living in these drainages would be seasonally attracted to the study area in order to prey on Moose calves.

These analyses provide no reason to reject the assumption that the bear population in the study area was "closed" (Seber 1973) with respect to immigration or emigration. Rigorous examination of this assumption would be less necessary under experimental designs where captured bears were not being removed from the population.

Minimum Population Estimate

The number of bears actually captured was 48. In addition, eight bears were known to have been missed in the removal effort (two of unknown sex which were observed in June and July, two others observed in August, and four marked bears from 1978 which were not recaptured in 1979, two males and two females). These bears were individually identified on the basis of pelage, size, and the absence of ear flags or other marks. Therefore, the study area population contained a minimum of 56 bears. This number appeared to be a reasonable minimum estimate, as some bears which were missed in the capture effort were doubtless also missed during subsequent monitoring flights. Furthermore, the rate at which bears were being captured in the last days of the removal effort clearly indicated that not all bears had been captured.

Mark-Recapture Population Estimates

Seven male bears were captured and marked in the study area in spring 1978 (Ballard et al. 1982). Of these, all were recaptured in spring 1979 except for two, both 3.5 y-old in 1978. Both of these bears were likely in the study areas in 1979, as each was verified in or near the experimental area in 1980. One had a functioning radio collar in 1978 and was relocated 15 times in the center of the removal area that year. On this basis it was concluded that both of the previously marked males not found in 1979 were present. One of the 1978 captured males still had a functioning radio collar in 1979. This bear was, correspondingly, easily tracked and captured in 1979 and therefore was excluded from Petersen Index calculations as capture-prone.

Five female bears were captured and marked in the study area in spring 1978 (Ballard et al. 1982); three of these were recaptured in spring 1979. One of the recaptured females still had a functioning radio collar and was excluded from Petersen estimate calculations. The two females not recaptured in 1979 were 10.5 and 4.5 y-old in 1978, both were in estrus when
captured in 1978 and therefore likely had newborn cubs in 1979. Both had functioning radio collars in 1978 and were well-documented study area residents in that year. Therefore, they were assumed present during the 1979 intensive capture effort. The younger of the two missed females was subsequently shot in the study area in the fall of 1982.

Excluding the bears with functioning radio-collars described above, adjusted mark-recapture calculations (Ricker 1975) were made for each sex using the total number of bears aged 3.0 years or older captured in 1979 (16 males and 14 females) and the recaptures of bears marked in 1978 (4 of 6 males and 2 of 4 females). This process yielded population estimates of 24 males and 25 females older than 3.0 years (Table 1). By lumping sexes, Petersen Index calculations independently provided an estimate of 49 bears older than 3.0 years (Table 1). Because of the low numbers of marked individuals, the numerical confidence intervals (Ricker 1975) for these estimates were large (Table 1).

**Corrections to Mark-Recapture Estimates**

The mark-recapture estimates were based on the assumption that the probabilities of capture were equal and remained constant through both 1978 and 1979 capture efforts. This assumption may be incorrect for females, as there were indications that females with newborn cubs had lower capture probabilities. Only two females with newborn cubs were located during capture efforts conducted during 1978, 1979, and 1980 in the study area and adjacent areas. One of these females was capture-prone in 1979 because of her functioning radio collar. The other, from a nearby study area, was captured with three newborn cubs in 1978. The following evidence indicates lower probabilities of capture of females with newborn cubs compared to other bears using the capture techniques employed in this study:

1. In both 1978 and 1979 only one female with newborn cubs was encountered, although females with yearlings were relatively numerous in 1978 (1 with cubs: 5 with yearlings,) 1979 (1:7), and 1980 (0:2). This suggests that the low capture rates of females with newborn cubs were not likely due to low reproductive rates.

2. The two females marked in the study area in 1978 that were not recaptured in 1979 both likely had cubs in 1979. Both were in estrus when originally captured in 1978 and were subsequently seen either copulating with or in the company of another bear in that year.

Females with newborn cubs have been reported to remain in the vicinity of their den sites longer than other bears (Glenn and Miller 1980; Craighead and Craighead 1972). On the Alaska Peninsula, females with newborn cubs were seldom captured in the spring because they tended to remain in mountainous terrain and near protective cover (Glenn and Miller 1980). The 1978 female accompanied by three newborn cubs, in an adjacent study area, tended to remain in thickly vegetated habitats and, consequently, was less frequently observed than other radio-collared bears (Ballard et al. 1982).

In recognition of this apparent capture bias, the Petersen recapture estimate was adjusted upwards for the female segment to correct for the escape of females with newborn cubs. A conservative adjustment was derived by assuming that the number of females with newborn cubs was equal to the number of captured females with yearlings (7). This adjustment increased the female estimate to 33 bears older than 3.0 y (Table 2), but is still probably conservative because it is unlikely that all females with yearlings were captured. Probable females with newborn cubs were used both in the Petersen estimate and in the correction to this estimate.

Sex ratio of captured bears older than 3.0 y was 113

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**Table 1. A summary of Brown Bear population and density estimates, upper Susitna River, Alaska.**

<table>
<thead>
<tr>
<th>BEAR POPULATION</th>
<th>No. of captures</th>
<th>Captured plus known missed bears</th>
<th>Uncorrected Petersen estimate (95% CI)</th>
<th>&quot;Corrected&quot; Petersen estimate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Males (3.0 y+)</td>
<td>17*</td>
<td>21**</td>
<td>24 (9-96)</td>
<td>24</td>
</tr>
<tr>
<td>Females (3.0 y+)</td>
<td>15*</td>
<td>19**</td>
<td>25 (8-280)</td>
<td>33</td>
</tr>
<tr>
<td>Both Sexes (3.0 y+)</td>
<td>32</td>
<td>40</td>
<td>49 (23-136)</td>
<td>57</td>
</tr>
<tr>
<td>Offspring (0.5-2.5 y)</td>
<td>16</td>
<td>16</td>
<td>—</td>
<td>26</td>
</tr>
<tr>
<td>All Bears</td>
<td>48</td>
<td>56</td>
<td>—</td>
<td>83</td>
</tr>
<tr>
<td>BEAR DENSITY (km²/bear)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Both Sexes (3.0 y+)</td>
<td>107</td>
<td>86</td>
<td>70</td>
<td>60</td>
</tr>
<tr>
<td>All Bears</td>
<td>72</td>
<td>61</td>
<td>—</td>
<td>41</td>
</tr>
</tbody>
</table>

* Includes one capture-prone bear that was excluded from mark-recapture calculations.
** The four adult bears of unknown sex not captured were assigned as two males and two females.
males: 100 females. In exploited bear populations hunters tend to selectively harvest males because: (1) males range greater distances, (2) females accompanied by offspring are legally protected, and (3) hunters tend to select large bears. With this hunter bias towards males, a population with a sex ratio skewed towards females would be expected (Bunnell and Tait 1981). Harvest data from Alaska’s Game Management Unit 13, which includes the study area, indicate that males represented 52% of the kill of bears older than 3.0 y in the period 1970-1979. The “corrected” mark-recapture estimate has a sex ratio (bears older than 3.0 y) of 73 males:100 females, this sex ratio more closely corresponds with the model proposed by Bunnell and Tait (1981) than does the observed sex ratio of captured bears.

Estimates of number of newborn cubs required similar adjustments. Seven females accompanied by 12 yearlings were captured in 1979 yielding an average litter size of 1.7 yearlings/females with yearlings. The assumption that there were at least as many newborn cubs as yearlings captured, provided a conservative correction for newborn cubs (Table 1). This was conservative because a high rate of cub mortality likely occurs (Glenn et al. 1976) and because all females with yearlings were probably not captured.

With these adjustments to the female and cub classes, the “corrected” Petersen Index population estimate was 83 bears; of these, 57 were bears 3.0 y or older (Table 1).

Population Density Estimates

To arrive at density estimates using the above population estimates, the area occupied by the removed bears must be determined. Some of the bears captured had portions of their 1978 home ranges outside of the search area, suggesting that the total area from which bears were removed was larger than the area searched. However, it appeared reasonable to assume that for each such bear captured, another bear which was only partially resident in the search area was not captured. Assuming that bears with home ranges that are not completely included within the search area have a probability (P) of being captured (where [P] is equivalent to the proportion of their home ranges which is within the search area) and a probability of being missed of (1-P), it is reasonable to use just the search data area in making density estimates. Making this assumption, and using the search area (3436 km²) combined with the above estimates of the bear population gave bear density estimates (Table 1) for each of the above population estimates.

The accuracy of the “corrected” mark-recapture density estimate was supported by 1978 home-range data in the study area (Ballard et al. 1982). The total area occupied by seven bears (older than 3.0 y) was 1560 km² (overlaps counted only once). A simple proportional extrapolation to the experimental area yielded an estimate of 15 bears aged 3.0 y or older. This figure must be corrected for the presence of unmarked bears. Of the 32 adult bears caught in 1979, only 8 (25%) were marked. If it is assumed that the above estimate of 15 bears represents the same proportion of the total population, then by simple extrapolation the population of bears older than 3.0 y would be 60. This figure is only slightly larger than the “corrected” Petersen Index estimate (Table 1) and adds credence to this estimate.

The “corrected” Petersen Index density estimate was compared to Brown Bear density estimates elsewhere in North America (Table 2). The estimated density fell about where subjectively expected, lower than in portions of Alaska where Brown Bears have access to salmon, lower than in more southern areas with more productive habitats, but higher than in the Alaskan Brooks Range (Table 2).

### Table 2. Reported brown bear densities in North America.

<table>
<thead>
<tr>
<th>km²/bear</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.6</td>
<td>Kodiak Island, AK</td>
<td>Troyer and Hensel 1964</td>
</tr>
<tr>
<td>16</td>
<td>Alaska Peninsula, AK</td>
<td>Unpublished data (Glenn, personal communication)*</td>
</tr>
<tr>
<td>21</td>
<td>Glacier National Park, Montana</td>
<td>Martinka 1974</td>
</tr>
<tr>
<td>28**</td>
<td>Glacier National Park, B.C.</td>
<td>Mundy and Flook 1973</td>
</tr>
<tr>
<td>23-27</td>
<td>SW Yukon Territory</td>
<td>Pearson 1975</td>
</tr>
<tr>
<td>41</td>
<td>Upper Susitna River, AK</td>
<td>This study</td>
</tr>
<tr>
<td>288(42-780)***</td>
<td>Western Brooks Range, AK</td>
<td>Reynolds 1980</td>
</tr>
<tr>
<td>148-260****</td>
<td>Eastern Brooks Range, AK</td>
<td>Reynolds 1976</td>
</tr>
</tbody>
</table>

*Data refer to a 1800 mi² intensively studied area of the central Alaska Peninsula.

**Estimated density, minimum was 1/18 km².

***1/288 km² is mean density for the whole of the National Petroleum Reserve, Alaska, the range represents values for different habitat types in this reserve where the highest density occurred in an intensively studied experimental area (Reynolds, personal communication).

****Highest density (1/148 km²) was in an intensively studied area of relatively high quality habitat, region-wide density was estimated at 1/260 km².
...bines density estimates with information on the size of individuals in the population. This parameter has been infrequently reported in the bear literature although, commonly, data are available to calculate biomass.

Measured weights were available from 88 Brown Bears captured from 1978-1980 in the study area and adjacent areas (Table 3). All bears were captured in the spring (April-June). For each sex, the density estimate lumped bears 3.0 y or older. Therefore, it was necessary to calculate average weights in the same age categories (Table 3). Similarly, sexes were lumped in the calculation of average weights of cubs, yearlings, and 2 y-old bears (Table 3).

Combining these weights with the "corrected" mark-recapture density estimate (Table 2) yielded a Brown Bear biomass estimate of 262 kg/100 km² (1,500 lbs/100 mi²).

Acknowledgments

Financial support for this study was provided by the Game Division, Alaska Department of Fish and Game (ADF&G). Comparison data reported for 1978 was supported by Alaska Federal Aid in Wildlife Restorations Project W-17-R while 1980 studies were financed by the Alaska Power Authority.

We gratefully acknowledge the assistance of many employees of the Game Division (ADF&G) in capturing and transplanting Brown Bears, data reduction and tooth sectioning. K. Schneider, D. McNight, C. Schwartz and C. Gardner (all ADF&G) and D. E. N. Tait reviewed earlier drafts of the manuscript and offered constructive comments.

We especially acknowledge the participation of T. Spraker (ADF&G) who assisted in the bear transplant, and provided technical assistance and advice throughout the project.

Much of the success of the bear capturing phase of this project was due to the skills and cooperative attitudes of our spotter plane pilots: Ken Bunch, Al Lee, and Rick Haldorf, and to the skill and cooperative attitude of our helicopter pilot, Vern Lofstedt.

---

### Table 3. Measured weights (kg) of spring-captured Brown Bears by sex and age, southcentral Alaska.

<table>
<thead>
<tr>
<th>Age (Years)</th>
<th>Males</th>
<th></th>
<th>Females</th>
<th></th>
<th>Both Sexes</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>n</td>
<td>x</td>
<td>S.D.</td>
<td>Range</td>
<td>n</td>
</tr>
<tr>
<td>0.5</td>
<td>3</td>
<td>35.0</td>
<td>—</td>
<td>—</td>
<td>1</td>
</tr>
<tr>
<td>1.5</td>
<td>10</td>
<td>38.2</td>
<td>14.4</td>
<td>21-63</td>
<td>4</td>
</tr>
<tr>
<td>2.5</td>
<td>6</td>
<td>89.9</td>
<td>30.0</td>
<td>61-140</td>
<td>3</td>
</tr>
<tr>
<td>3.5</td>
<td>5</td>
<td>113.3</td>
<td>19.3</td>
<td>93-139</td>
<td>4</td>
</tr>
<tr>
<td>4.5</td>
<td>7</td>
<td>133.4</td>
<td>25.7</td>
<td>100-181</td>
<td>5</td>
</tr>
<tr>
<td>5.5</td>
<td>3</td>
<td>181.3</td>
<td>61.1</td>
<td>115-236</td>
<td>4</td>
</tr>
<tr>
<td>6.0+</td>
<td>16</td>
<td>255.9</td>
<td>20.4</td>
<td>217-289</td>
<td>12</td>
</tr>
<tr>
<td>3.0+</td>
<td>31</td>
<td>198.0</td>
<td>68.0</td>
<td>93-289</td>
<td>25</td>
</tr>
</tbody>
</table>

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### Literature Cited


*Available from Alaska Department of Fish and Game, Division of Game, P.O. Box 3-2000, Juneau, Alaska 99802.

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Accepted 30 June 1982

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This study was designed to provide a preliminary investigation of the responses of shrew (*Sorex* spp.) populations to logging and burning of coastal forest habitats, Douglas-fir (*Pseudotsuga menziesii*) seeding, and removal of the presumed competitor, the Deer Mouse (*Peromyscus maniculatus*). Shrews were trapped in three habitats at Maple Ridge, British Columbia, from May 1975 to November 1978. The average density of shrews was consistently higher in the forest (4.3/ha) compared with the burned (2.0/ha) and unburned areas (2.4 and 3.0/ha). Shrew density was lowest in the year after burning. Douglas-fir seeding produced generally little change in shrew abundance although a slight positive response was recorded at low seed densities on a cutover area. Shrews did not respond consistently to removal of Deer Mouse and vole co-inhabitants. Therefore, presumed competition between these species probably did not lower the response of shrews to Douglas-fir seed. Shrews should not be a major concern to reforestation as seed predators in the coastal coniferous forests of southern British Columbia.

Key Words: logging, shrew populations, *Sorex* spp., coastal forest, competition, direct seeding, Douglas-fir, *Pseudotsuga menziesii*.

Interactions between Soricidae (Shrews, *Sorex* spp.) and forestry practices are of interest to both ecologists and foresters involved in regeneration of cutover and burned habitats. The effects of clearcutting practices and natural or artificially induced fires on shrew populations have been studied by several authors. Such information not only enhances the knowledge of the taxa under investigation but adds to the understanding of succession and niche occupancy following environmental disturbance. It is also significant for predicting the success of future attempts at regeneration of a disrupted area.

*Sorex* spp. prefer a wide range of habitats from old fields to moist coniferous forests (Banfield 1974). Kirkland (1978) reported that the response of *Sorex* spp. to clearcutting was not significant or at most, species-specific and inconsistent. Other studies indicated an initial increase in the abundance of *Sorex* spp. on clearcuts (Gashwiler 1959; Harris 1968; Hooven 1973; Kirkland 1977). However, shrews were also reported to prefer virgin timber and were adversely affected by clearcutting (Gashwiler 1970; Black and Hooven 1974; Hooven and Black 1976). Wild fires and burning of clearcuts which increase the available seed supply, appear to result in a consistent initial reduction in shrew populations (Cook 1959; Ahlgren 1966; Hooven 1969; Sims and Buckner 1973; Black and Hooven 1974; Lovejoy 1975; Bunnell and Eastman 1976).

Shrews, normally considered to be insectivorous, will eat vegetable matter including Douglas-fir (*Pseudotsuga menziesii*) seed (Moore 1942; Kangur 1954), Sitka Spruce (*Picea sitchensis*) seed (Kangur 1954), and pine (*Pinus* spp.) seeds (Fitch 1954), particularly during the winter and spring when insect populations are less accessible or scarce. Kangur (1954) concluded that control measures were necessary for both Deer Mice (*Peromyscus maniculatus*) and shrews in regeneration with direct seeding. Sullivan (1979a) has reported the numerical and functional responses of the Deer Mouse to Douglas-fir seeding. However, little information is available on the quantitative responses of shrews to Douglas-fir seed and their presumed interaction with Deer Mice. Moore (1942) first suggested that Deer Mice may affect the abundance of shrews in areas of co-habitation.

This paper compares shrew (*Cineres; S. cinereus*, Dusky; *S. obscurus*, and Wandering; *S. vagrans*) populations in burned and unburned cutover areas with that in an uncut forest stand. In addition, the responses of shrews to Douglas-fir seeding and removal of *P. maniculatus* are examined.

**Study Areas**

Field installations were set up in forest and clearcut habitats at the University of British Columbia Research Forest, Maple Ridge, B.C. The forest habitat in the southeast corner of the Research Forest
The Shrew composition
The logged on burnt.
checkerboard time
Therefore, our March 1932 1925.
Alder areas.
Hemlock
Natural tree of the southwest.
The slash-1 study areas were on clearcut blocks in the southern part of the Research Forest. The Burn was logged in the autumn of 1973 followed by slash burning in August 1974. The slash burn was uniform in some areas but patchy in others. The main cover was burnt or dead slash with growth of Bracken (Pteridium aquilinum), Fireweed (Epilobium angus-
tifolium), and several other less abundant success-

tional herbs. One control and three experimental grids were located on this block. Slash-1 was on a similar area also logged in the autumn of 1973 but not burnt. Cover included slash and a similar species composition to that of the burnt area. There was more Red Alder (Alnus rubra), Black Raspberry (Rubus leu
codermis), and Salmonberry (Rubus spectabilis) on the slash area. Slash 2 was in the central part of the Research Forest east of Loon Lake. This area was logged in the spring of 1976. Ground cover vegetation was very sparse amid the slash and the terrain was relatively flat. Two grids (one control and one experimental) were located on each of the Slash-1 and Slash-2 areas.

Materials and Methods
Shrew populations
The Forest, Burn, and Slash-1 grids were trapped every two weeks with Longworth live-traps from May to September 1975, April to November 1976, and March to November 1977. The Slash-1 study area was trapped from April to November 1977. The Forest, Burn, Slash-1 and Slash-2 control grids were also trapped from March to November 1978. On each 1-ha checkerboard grid, forty-nine trap stations were located at 15.2-m intervals. One live-trap was placed within a 2-m radius of each station. Traps were baited with peanut butter, Purina lab chow, and coarse brown cotton was supplied as bedding. Traps were set on day 1, checked on days 2 and 3, and then locked open between trapping periods.

All shrews captured were recorded as to trap loca-
tion and whether they were dead or alive. Because of our overnight trapping technique there was a high (approximately 50%) mortality rate for shrews. Therefore, minimum number captured was calculated assuming that, if a live animal caught on the first check was recaptured on the second check, then it was only counted once for that period. Other species cap-
tured included: P. maniculatus, Oregon Vole Micro-
tus oregoni, Boreal Redback Vole Clethrionomys gapperi, and Townsend’s Chipmunk Eutamias townsendii.

Douglas-fir seed
Before each experiment, seed was weighed and packaged according to the amount desired for each of 36 (231 m²) plots on a grid (area of grid = 8317.44 m²). The allotted seed was then spread by hand as uni-
formly as possible over the area of the grid.

Changes in shrew density were determined by sub-
tracting the minimum number of shrews caught two weeks after seed application from the minimum number of shrews caught the trapping period imme-
diately before seeding.

Removal experiments
On two Forest grids (experiments A and B, June 1975) and one Slash-1 grid (experiment C, August 1975), all mice (M. oregoni and P. maniculatus) as well as shrews were removed just prior to a Douglas-

tier seed application. This was done to determine if there is any competition between Sorex spp. and the mouse and vole species. On the same unburned clear-
cut an extended period of removal (every two weeks) occurred from August to October 1977 (experiment D) and March to mid-April 1978 (experiment E). Douglas-fir seeding took place on 24 August 1977 and 20 March 1978 on this grid. Another grid on the same clearcut acted as a control.

Results
Population Density
The population densities of Sorex spp. caught at each two-week interval are plotted for the control (Forest) grid, the two slash grids (Slash-1 and -2), and the burned clearcut grid (Burn) (Figure 1). In all areas the number caught was variable from one trapping period to another, but in most cases the populations were able to recover or maintain their densities over the winter.

Shrew populations in this study did not appear to have an obvious multi-annual cycle. On the Forest grid, peaks in density occurred in August 1975, April 1976, October 1977, and July 1978 which suggests the existence of a definitive annual cycle.

Over the periods that each area was trapped, the average density of shrews was consistently higher in the forest when compared with any of the three exper-
imental areas. The density of shrews one and two years (Slash-1 and -2 respectively) after clearcutting without subsequent burning, most closely approached that of an untreated forest grid (Table 1). The most drastic reduction in shrew densities occurred on an area that had been burned the year previous to trap-
Sorex spp.

Figure 1. Population densities of shrews (Sorex spp.) on the Forest, Slash-1, Burn, and Slash-2 study areas from 1975 to 1978
Table 1. Average number of Sorex spp. captured on a Forest grid, Slash clearcut grids of two ages and a Burned clearcut grid during 1975 to 1978. Number of weeks sampled in parentheses.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Forest</td>
<td>3.77 (13)</td>
<td>3.35 (20)</td>
<td>4.57 (21)</td>
<td>4.80 (15)</td>
<td>4.30 (39)</td>
</tr>
<tr>
<td>Slash-1</td>
<td>3.11 (9)</td>
<td>1.62 (13)</td>
<td>2.77 (13)</td>
<td>2.40 (20)</td>
<td>2.42 (36)</td>
</tr>
<tr>
<td>Burn</td>
<td>0.92 (12)</td>
<td>2.32 (19)</td>
<td>2.55 (20)</td>
<td>1.94 (18)</td>
<td>2.00 (69)</td>
</tr>
<tr>
<td>Slash-2</td>
<td>—</td>
<td>—</td>
<td>3.88 (17)</td>
<td>2.22 (18)</td>
<td>3.00 (35)</td>
</tr>
</tbody>
</table>

ping (Burn). By the second year after burning, shrew densities had returned to levels comparable to unburned areas that had been clearcut two or more years previously.

**Douglas Fir seeding**

The changes in minimum number of shrews captured on the forest grids as a result of Douglas Fir seeding are presented in Figure 2. From these data it is apparent that the range in shrew density change on the seeded areas was, if anything, less than that of the control.

Alternatively, Figure 3 indicates that shrews may show a positive response to low densities of Douglas-fir seed on clearcuts. The change in number of shrews on the control grids ranged from 0 to 2 while the grids seeded with up to 400,000 seeds/ha had values above 0. There appeared to be no consistent difference in the
response of shrews to seedings on burned versus unburned clearcuts.

Removal experiments
To determine the potential competitive effect of Deer Mice on shrews, all mice (and voles) were removed from some seeded grids. In these experiments the density of shrews increased in two of the three trials (A and B), while the density of shrews on seeded and unseeded controls decreased (Table 2). The extended removal of mice, voles, and shrews on the unburned clearcuts in 1977 (experiment D-August to October) and 1978 (experiment E-March to mid-April) indicated that the shrews were rather unaffected by the procedure and if anything, their densities were reduced. In the spring 1978 experiment, the density of shrews decreased after seeding even though the numbers of shrews in both controls were increasing at this time. The most noticeable difference resulting from the extended removal experiments is the overwinter recovery and early spring densities on the removal grid when compared with the control.

Discussion
Population Density
The variable nature of the shrew densities observed on our trapping grids may result from two factors. Firstly, the majority of shrews caught either did not survive the overnight trapping or were removed alive from the areas. Thus, the number of shrews caught in subsequent trapping periods would be dependent upon immigrants from other areas with a higher density of shrews than the depopulated grids. If there was little advantage for the shrews to move from their present residence, such as good food supply or established home territories for breeding, the vacated study

<table>
<thead>
<tr>
<th>Experiment</th>
<th>Seeding rate</th>
<th>Date applied</th>
<th>Pre-seeding</th>
<th>Post-seeding</th>
<th>Pre-seeding</th>
<th>Post-seeding</th>
<th>Pre-seeding</th>
<th>Post-seeding</th>
</tr>
</thead>
<tbody>
<tr>
<td>A</td>
<td>0.81</td>
<td>June 19</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>6</td>
</tr>
<tr>
<td>B</td>
<td>0.81</td>
<td>June 19</td>
<td>2</td>
<td>0</td>
<td>2</td>
<td>1</td>
<td>6</td>
<td>7</td>
</tr>
<tr>
<td>C</td>
<td>3.24</td>
<td>Aug. 15</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>D</td>
<td>0.81</td>
<td>Aug. 24</td>
<td>6</td>
<td>1</td>
<td>7</td>
<td>4</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>E</td>
<td>0.41</td>
<td>Mar. 20</td>
<td>1</td>
<td>8</td>
<td>0</td>
<td>1</td>
<td>5</td>
<td>1</td>
</tr>
</tbody>
</table>

Table 2. Density of Sorex spp. before and after experimental seeding with Douglas-fir seed on control and removal grids in 1975 (A, B and C), 1977 (D), and 1978 (E). Seeding rate is in kg/ha.
areas may not be repopulated at as great a rate as might occur later in the summer or fall when populations are normally higher.

Secondly, the regimented monitoring procedure used in this study leaves to chance the weather conditions occurring on the trapping nights. Trappability of shrews is greatly affected by their activity which itself is influenced by weather conditions (Doucet and Bider 1974; Vickery and Bider 1978). However, trapping conditions were identical for all grids and experiments, thereby providing relative indices of shrew numbers in this study.

As determined by Krull (1970), and verified in this study, Sorex spp. do not appear to have a multi-annual cycle. However, as for most small mammals, Sorex spp. densities appear to have an annual late summer to early fall peak in numbers (Buckner 1966, 1969, Gashwiler 1970; Gentry et al. 1971). This annual cycle was suggested in our study on the Forest grid. With the exception of April 1976, the peak densities of each year occurred in the mid- to late summer and early fall. During 1976 the density of shrews steadily declined from April 1976 until the next spring. This trend was also evident on the unburned clearcut (Slash-1) in 1976 which suggests that some factor characteristic of that year may have affected the shrew populations.

In our study we found Sorex spp. to prefer the forest over logged areas, whether burned or not. The average numbers of shrews caught on Slash -1 and -2 indicate that an initial response to clearcutting is an increase in the number of shrews for the first one or two years, followed by a more consistent pattern of density below that of an uncut forest. After the initial response, the density of shrews on both cut blocks and the burned area were all at comparable levels.

Several studies have reported an initial increase in the abundance of shrews on clearcuts (Gashwiler 1959, Harris 1968; Hooven 1973; Kirkland 1977). Alternatively, Tevis (1956) found that logging caused a decrease in the numbers of Sorex spp. Hooven and Black (1976) found S. vagrans to prefer an untreated control to an unburned clearcut. Gashwiler (1970) also concluded that virgin timber was better than clearcut as habitat for S. vagrans. The differential responses by Sorex spp. to clearcutting may depend upon the locality and characteristics of the clearcut and pre-harvested forest. Since shrews are secondary consumers, they should not be directly affected by changing plant communities as are herbivores. They are more likely to be affected by shifts in the abundance and community composition of their invertebrate prey, as well as by changes in the physical environment such as dessication and temperature extremes (Pruitt 1959; Getz 1961).

Comparisons of the preference of Sorex spp. for burned and unburned clearcuts also tend to be equivocal. Although numbers of S. vagrans and S. rowbridgii were originally decreased after burning, their recovery indicated a preference for such areas (Hooven 1969; Black and Hooven 1974). S. cinereus, though low and variable, appeared to be higher on burned areas (Krefting and Ahlgren 1974) Other studies indicated a preference for unburned areas by S. cinereus (Sims and Buckner 1973) and four species of Sorex spp. including S. vagrans (Hooven and Black 1976). The initial decrease in density may result from burrow destruction and the fact that the fire removes the litter or duff layer in which shrew invertebrate prey live (Bunnell and Eastman 1976). The subsequent increase in density may be a result of the fact that insects apparently thrive on burned-over areas.

Our results agree with the observations that shrew densities decrease initially after a fire but recover by the second year to levels comparable with unburned areas.

Douglas-fir seeding

Results from the forest seeding experiments imply that shrews in their natural habitat are unaffected by seed density and thus cannot be considered major predators of Douglas-fir seed. However, on clearcuts the shrews showed a positive response to low densities of Douglas-fir seed. This may be a result of decreased invertebrate prey on such areas so that shrews must switch to a more available food. Shrews are more important predators on pine and Douglas-fir seed when insects are scarce, such as in the winter and spring (Fitch 1954; Kangur 1954). Moore (1940) found that S. vagrans had a special preference for Douglas-fir with 13 of 17 shrews containing this species of seed in their stomachs. In addition, this author believes that the high shrew population may account for the relative scarcity of Douglas-fir in the stand studied.

We conclude from this study that shrew densities would have to be considerably greater than 12/ha to result in significant seed predation. In our study area the major predator on the seed supply was the Deer Mouse (see Sullivan 1979b).

Removal experiments

Moore (1942) states that Deer Mice will consume dead shrews and may thus inhibit populations of shrews from entering areas where mouse populations are high. However, from our studies, P. maniculatus and M. oregoni did not appear to have a consistent effect on densities of shrews. The increased overwinter and spring immigration onto the removal area (experiments D and E; Table 2) was more likely a result of factors other than the density of mice and voles as no removals were occurring during this time.
Conclusions

Presumed competition from Deer Mice was apparently not responsible for suppressing shrew activity and possibly seed predation. Thus, the results of this study suggest that in the areas examined, *Sorex* spp. should not be a major concern for reforestation. Their densities are low (up to 12 animals/ha) when compared with other seed eaters such as *Peromyscus* (15-35 animals/ha), and they show little or no population response to seeding with Douglas-fir.

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We thank J. Walters and his staff at the University of B.C. Research Forest. For help with the field work, we thank R. Boonstra, C. Fleming, D. Jahnke, W. Kaiser, D. Lancaster, L. Nordstrom, and E. Watts. We are grateful for the financial assistance of the B.C. ministry of Forests.

Literature Cited


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Arctic Fox, *Alopex lagopus*, Predation on Nesting Common Eiders, *Somateria mollissima*, at Icy Cape, Alaska

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Arctic Foxes, *Alopex lagopus*, preyed on Common Eiders, *Somateria mollissima*, nesting on a barrier island at Icy Cape, Alaska. Small clutches and late nesting in the Common Eiders possibly resulted from predation early in the season. Foxes had access to one barrier island via an estuarine mudflat and presumably swam to reach the adjacent island containing an eider colony. A single fox destroyed the colony, cached an estimated 500 eggs, and killed at least one female eider. Glaucous Gull, (*Larus hyperboreus*) nests were also destroyed by foxes, but Arctic Tern (*Sterna paradisaea*) nests survived. Man-made causeways connecting the mainland to a barrier island could provide easier summer access to barrier island systems for foxes and thus pose a threat to Common Eider nesting colonies along the Chukchi and Beaufort Sea coasts.

Key Words: Common Eider, *Somateria mollissima*, Arctic Fox, *Alopex lagopus*, predation, barrier island, causeways.

Arctic Foxes (*Alopex lagopus*) are predators on ground nesting birds in most northern areas. Along the northern Chukchi and Beaufort Sea coasts, most Common Eiders (*Somateria mollissima*) nest in colonies on barrier islands (Schamel 1977; Divoky 1978). Although Arctic Foxes visit barrier islands during the winter and may be stranded during ice break-up, most islands are free of foxes during the summer. However, year-round access may be provided where man-made causeways connect isolated islands to the mainland. Such causeways may pose threats to colonies of nesting birds on barrier island systems. At Icy Cape, Alaska, a barrier island is connected to the mainland by a periodically exposed mudflat. This paper reports our observations of Common Eider nesting biology and Arctic Fox predation on nearby barrier islands in 1980, when foxes reached one island early and late in the nesting season.

**Study Area**

Icy Cape (70° 20' N, 161° 52' W) is on the northwest coast of Alaska on the Chukchi Sea (Figure 1). Several Common Eider colonies occur there; the two largest known colonies along the northern coast of Alaska, on Amaulik and Tern Island (Divoky 1978), were studied. These flat gravel islands (98.6 ha and 23.5 ha, respectively) separate Kasegaluk Lagoon from the Chukchi Sea. Sparse vegetation grows only in areas that are rarely submerged by storm-tides. Major plant species include *Elymus arenarius*, *Puccinellia langanee*, *Carex subspathacea*, and *Honckenya peploides*. Tidal fluctuation is only 10-15 cm.

For most of the year, Kasegaluk Lagoon is frozen and barrier islands are connected to the mainland by ice. Following breakup in May or June most barrier islands are separated from the mainland by 2-8 km of shallow lagoon (0.3-4.0 m deep). Cape Island (Figure 1), however, is connected to the mainland in summer by a broad mudflat and Arctic Foxes have access except during southerly winds when the mudflat is inundated by lagoon waters.

The summer of 1980 was exceptionally cold; Kasegaluk Lagoon remained partially frozen until 21 June, and Chukchi Sea ice was packed against the barrier islands into the first week of July. Summer temperatures at Point Barrow, 200 km northeast, were the coldest in 30 years (Myers and Pitelka 1979).

In addition to Arctic Foxes, potential predators of eider eggs included Brown Bears (*Ursus arctos*), Parasitic Jaegers (*Stercorarius parasiticus*), and Glaucous Gulls (*Larus hyperboreus*). Several bird species used the barrier islands for feeding and resting, but the only other nesting species were Arctic Tern (*Sterna paradisaea*), Brant (*Branta bernicla*) and Oldsquaw (*Clangula hyemalis*); all nested at lower densities than eiders.

**Methods**

During a study of bird use of the Icy Cape area from 20 May to 23 September 1980, we observed Common Eider nesting and Arctic Fox activities. Until boat travel was possible, we observed eider activity on Amaulik Island through a 20-40 X spotting scope from a camp on the mainland. We visited Amaulik Island on 28 June, 11, 16, 20, 23, 25, and 31 July, and 4, 12, and 24 August; we visited Tern Island on 16, 23, 25, and 31 July. Nests were marked with a numbered stake 0.5 m from each bowl. We kept records of all beach nests on the southern half of Amaulik Island and all nests in a 9.5 ha plot that encompassed about
half of the main nesting colony there. We marked and kept records for all beach nests on the north end of Tern Island and all those in a 0.5 ha plot encompassing about half its main colony. We recorded presence of down, and number of eggs, young, or eggshells on each visit. After checking a nest, we covered the eggs with down. We also kept records of all fox sightings, noting date, time, location, and activity.

Results and Discussion
Common Eider flocks were first seen migrating past Icy Cape on 25 May. Eider pairs were first observed on 4 June in melt water ponds on the mainland and in overflow water on the lagoon. We first observed eiders walking on Amaulik Island on 11 June, coincident with the development of an open lead in the lagoon. Schamel (1977) also noted that Common Eiders did not walk on the nesting island until the ice sheet connecting it to the mainland was broken; he suggested that eiders avoid most fox predation by delaying nesting. At Icy Cape, however, foxes were able to reach Amaulik Island after the lagoon ice sheet melted. We observed a fox being mobbed by Arctic Terns on Amaulik Island on 19 June. On 28 June, fox tracks were found in the sand along the beach; they appeared to be two-three days old. Foxes may have reached Amaulik Island from Cape Island via the Chukchi Sea ice, which remained packed against the barrier islands until early July, or by swimming the pass between the islands (about 150 m).

Table 1 summarizes the information on nesting chronology, clutch size, and nesting success in the two colonies. Nesting at Tern Island was slightly earlier than on Amaulik Island. Clutches hatched 23-31 July on Tern Island, so egg-laying occurred between 23 June and 2 July. This calculation is based on a 26-day incubation period (Schamel 1977) and we assumed that incubation began after the third or fourth egg was laid (Belopol'skii 1957).

On Amaulik Island, we examined 151 nest bowls on 28 June; 17 contained a single egg, and 46 contained down but no eggs. Eiders do not line their nests with down until after laying the first egg and sometimes not until the clutch is complete (Cooch 1965), so those 46
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<table>
<thead>
<tr>
<th></th>
<th>Amaulik Island</th>
<th>Tern Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of nest bowls on island</td>
<td>479</td>
<td>est. 200</td>
</tr>
<tr>
<td>Monitored nests in plot on beach</td>
<td>244 (84)¹</td>
<td>109 (68)</td>
</tr>
<tr>
<td>Nesting density plot (bowls/ha)</td>
<td>40 (18)</td>
<td>17 (16)</td>
</tr>
<tr>
<td>Nesting density island (bowls/ha)</td>
<td>4.9</td>
<td>Unknown</td>
</tr>
<tr>
<td>Estimated laying dates</td>
<td>27 June-12 July</td>
<td>23 June-2 July</td>
</tr>
<tr>
<td>Clutch size mean (eggs/nest)</td>
<td>2.9</td>
<td>3.6²</td>
</tr>
<tr>
<td>s</td>
<td>1.18</td>
<td>1.41</td>
</tr>
<tr>
<td>n</td>
<td>92</td>
<td>77</td>
</tr>
<tr>
<td>range</td>
<td>1-6</td>
<td>1-7</td>
</tr>
<tr>
<td>Nesting success chicks/nest/bowl</td>
<td>0</td>
<td>1.3</td>
</tr>
<tr>
<td>average brood size</td>
<td>3.79 (1.50)</td>
<td></td>
</tr>
</tbody>
</table>

¹Number of nest bowls containing eggs in parentheses.
²Clutches of more than seven were assumed to be dump nests and were excluded from calculations of mean clutch size.

The nesting season, all nests on Amaulik Island were destroyed by an Arctic Fox, which presumably reached the island by swimming Icy Cape Pass (Figure 1).

We observed a fox on Amaulik Island near Icy Cape Pass at 0100, 23 July. When we approached within 300 m of the eider colony at 0300 we saw the fox in the midst of the nesting area. About 100 female eiders were gathered in a small lake at the edge of the colony, but most nests we could see through binoculars were occupied by incubating birds. Two pairs of Arctic Terns and several Glaucous Gulls mobbed the fox. The fox occasionally jumped or ducked when a gull or tern swooped low over its back, but it continued trotting around the colony. The fox ran up each Elymus-covered sand mound looking for nests. Most incubating birds flew or scrambled away when the fox approached within 2 m of their nests. At each nest, the fox took one egg in its mouth, trotted 10-20 m away, dug a hole with its forepaws, dropped the egg in and covered it by moving sand with its muzzle. Often the fox dug more than one hole before burying an egg. The fox buried each egg in a different place, but consistently chose sites on the southwest side of clumps of Honckenya peploides. It did not scent-mark any of the spots, which suggests that Arctic Foxes do not mark sites which contain food. Red Foxes (Vulpes vulpes) also do not mark food caches (Arehart-Freichel 1977). We were able to locate only two buried eggs later and each was covered by about 4 cm of sand.

One female eider did not flush until the fox was within 0.5 m of her nest, and was captured. When the eider flushed, the fox leaped in the air and caught the bird by its tail. After a few seconds of struggling, the fox released the eider’s tail and bit her neck. The fox ate the eider’s head, left the carcass, and returned to flushing eiders and burying eggs. We saw the fox unsuccessfully attempt to catch two other eiders that flushed closely.

At 0600 we returned to camp because of deteriorating weather. During 3 h of observation, we saw the fox bury about 30 eggs, but it never ate one. We were unable to return for 36 h (25 July). The colony then was virtually deserted by eiders, although 50 females were on the beach. We checked all nests on the island and only two contained eggs. Down remained in some nest bowls, but had blown away from many others. The two surviving nests were isolated on the far side of the lake adjacent to the colony. Because all other isolated beach nests were destroyed, it seems likely that the fox did not visit the far side of the lake. There were no eggshells to indicate avian predation and we believe that the fox destroyed the entire eider colony. Based on the percentage of active nests and mean clutch size in our plot, we estimated the fox buried 498 ± 42 (95% C.I.) eggs, (assuming it did not eat any of
the eggs). Also, six of seven Glaucous Gull nests were empty (15 eggs); the surviving gull nest was on the same stretch of beach as the surviving eider nests. In contrast, the three Arctic Tern nests on the island survived, though they were in the midst of the eider colony.

Although we walked around the entire island on all visits, including four visits after the predation occurred, we only saw a fox or fox-sign on 28 June and 23 July. Divoky (1978) suggested that foxes were living on some barrier islands, but if a fox had been living on Amaulik Island eider nests would certainly have been destroyed before 23 July. Hence, we conclude that the fox swam to the island.

We have found only one published account of swimming by Arctic Foxes. Childs (1969) reported that a fox swam across a river after he startled it from a gravel bar where it was sleeping. We first observed foxes swimming on 10 June in a saltmarsh pond adjacent to the lagoon. This fox swam a distance of about 3 m, then got out and rolled in the snow. On 12 June we saw two different foxes swimming large meltwater ponds on the lagoon ice as each crossed to the barrier islands. On 28 June, we observed a fox swim about 100 m from the mainland into the lagoon and return. The barrier island is about 1.5 km from the mainland. Foxes often waded through water 10-20 cm deep and walked across the wide mudflats connecting the mainland and Cape Island. Foxes were observed crossing the mudflats almost daily during May and June. After reaching Cape Island via the mudflats, a fox would have to swim about 100-150 m across Icy Cape Pass to reach Amaulik Island.

Beetz (1916) and Gudmundsson (1932) hypothesized that the foul-smelling excreta of incubating eiders is an adaptation to deter fox predation. Eiders eject this excreta over their eggs when frightened from their nests. This excreta is unpalatable to rats and ferrets (Swenson 1968) and possibly deters crows (Corvus corone) from preying on eider nests (McDougall and Milne 1978). The fox preying on eider nests on Amaulik Island showed no aversion to the fouled eggs, unless in not eating them immediately. We observed a fox on the mainland preying on eggs covered with excrement. The fox picked up one egg, but laid it down about 1 m from the nest. The fox then rubbed its nose on the ground and trotted around the area sniffing. It then returned to the nest, carried away and buried the remaining eggs. Despite its initial reaction, the fox returned to the first egg, carried it away and buried it.

Colonial Common Eiders evidently require nest sites that are inaccessible to foxes. Fox predation on island nesting colonies may be rare. The Icy Cape area is unusual because foxes are able to reach a barrier island in the summer via an exposed mudflat. Although we believe a fox swam more than 100 m to reach the eider colony, it seems unlikely that a fox would swim 1-2 km of lagoon to reach a barrier island, as would be necessary in most areas. Also, due to a late break-up in 1980, foxes were able to reach the barrier island across the ice late into June after eiders began egg-laying and thus may have learned of the potential food source on the island. Small mammal populations appeared to be low in the area, which may have forced foxes to exploit alternative foods. Eberhardt (1976) found that the main prey of Arctic Foxes on the north slope were Brown Lemmings (Lemmus sibiricus) and Collared Lemmings (Dicrostonyx torquatus) and birds and bird eggs were of secondary importance in the summer. More observations are needed to determine whether fox predation on eider colonies at Icy Cape occurs regularly.

Oil and gas developers have proposed building highways between the mainland and various barrier islands along the arctic coast. Such roads would provide foxes with year-round access to barrier island systems (cf. Errington 1961). Our observations indicate that foxes with summer access to one barrier island may swim to reach nearby islands where they prey on bird nests. Such highways could pose a serious threat to Common Eider nesting colonies on barrier islands.

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Literature Cited


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Population Consequences of Winter Forage Resources for Moose, 
*Alces alces*, in Southwestern Québec

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As a part of a global study on the population dynamics of Moose (*Alces alces*), winter habitat use by this herbivore was studied in three 530 km² blocks with low hunting pressure and high Moose density (0.26-0.39 Moose km⁻²), and in three other 530 km² blocks with high hunting pressure and low density (0.06-0.12 Moose km⁻²). Habitat selection in January and March was not obvious in either set of blocks. Group size in January and extent of yard areas in March were both larger at the higher Moose densities. In 18 late winter-yards surveyed in May and early June (three per block), weight of browsed twigs, stem breakage, pellet-group abundance, and preferred plant species did not differ with Moose density. Percentage of browse removed was higher in yards with higher Moose densities, but this seemed attributable to a sampling problem, fewer plots being in the less-used margins of these yards. There was no indication that winter forage was a limiting factor even at high density.

Key Words: Moose, *Alces alces*, Balsam Fir, winter habitat, winter forage, Québec.

Dans le cadre d’une étude globale sur la dynamique des populations d’Orignaux (*Alces alces*), l’utilisation de l’habitat hivernal par cet herbivore a été étudiée dans trois aires de 530 km² supportant une pression de chasse faible et une densité d’Orignal élevée (0.26-0.39 Original km⁻²) et dans trois autres aires de même dimension connaissant une pression de chasse plus grande et des densités plus faibles (0.06-0.12 Original km⁻²). La sélection d’habitat n’était pas évidente ni en janvier ni en mars pour les deux groupes d’aires. Pour 18 ravages d’Orignaux échantillonnés en mai et au début de juin (trois par aire), le poids de ramilles broutées, de tiges, l’abondance des fumées et les espèces végétales préférées étaient pareilles dans les deux groupes d’aires. Le pourcentage de nourriture broutée était plus élevé dans les ravages situés là où l’Original était plus dense, mais cette différence semble plutôt attribuable à un échantillonnage moindre de la périphérie des ravages dans le groupe d’aires à densité élevée. Il n’y avait aucune indication que la nourriture d’hiver était un facteur limitant, même à forte densité d’orignaux.

Mots Clés: Original, *Alces alces*, habitat hivernal, nourriture d’hiver, Québec.

Aerial surveys of Moose (*Alces alces*) from a helicopter (Crête and St-Hilaire 1979) indicated densities were more than twice as great on three 535 km² blocks within a game reserve and a park than in three adjacent blocks within hunting zones (Crête et al. 1981a). A significant inverse relationship was found within the six blocks between Moose density and hunting pressure (Crête et al. 1981a). On the other hand there was no relationship found between either summer or winter browse production and density (Crête and Jordan 1982). Two possible factors limiting Moose populations at higher density (i.e. at lower hunting pressure) were examined, predation and forage availability. Computer simulations suggested that predation could regulate Moose numbers when hunting was either absent or light and when an alternate source of food was available to the Wolves (*Canis lupus*) such as from garbage dumps (Crête et al. 1981b). This paper examines the possibility that availability of winter forage might be a factor limiting Moose in southwestern Québec.

In testing the hypothesis of winter-forage limitation, we used the following two alternative scenarios. (1) If the classical vegetational and winter-distribution symptoms associated with winter malnutrition are found, then, since this alone only suggests malnutrition is operative, we will next examine physiological parameters in the herd. (2) If classical vegetation impacts are not found, then it will be assumed that winter malnutrition is not likely as an operative factor, and that population growth is limited by another factor.

On the Kenai peninsula, Alaska, major calf mortality due to depleted range was recently observed during severe winters (Bailey 1978). At Isle Royale, Michigan, winter starvation was observed during three declines of the Moose population since 1930 (Peterson 1977). For White-tailed Deer (*Odocoileus virginianus borealis*) in Québec, Crête (1976) suggested that winter mortality was related to forage quality; starvation commonly occurs at the northern limit of the deer range in North America during harsh winters (Runge and Wobeser 1975; Potvin et al. 1978). Moreover, depleted winter range indirectly affects population
The dynamics of Moose and deer by increasing neonatal mortality (Kucera 1976; Peterson 1977; Verme 1977) and by slowing development to adult size (Peterson 1977).

If winter forage was limiting a Moose population, one should observe: (1) high utilization of preferred habitat types and common utilization of marginal ones; (2) high utilization of available browse, particularly of the most preferred species; (3) frequent browsing of generally unused plant species; (4) changes in plant composition induced by Moose browsing; and (5) lower digestibility of browse consumed.

Study Area and Methods
The study was conducted within six 530-km² blocks arranged as three pairs (Figure 1). One of each pair was in a lightly hunted (permit only) reserve and the other was nearby in an open or heavily hunted zone. Two blocks were within La Vérendrye Reserve and one within Mont Tremblant Park. The heavily hunted or "H" blocks sustained 3.9–12.8 hunter days/km² each year while the lightly hunted "L" blocks sustained 0.1 hunter day/km². Block pairs were further designated according to the year in which its Moose had been surveyed by winter aerial counts, 1977, 1978 and 1979 = 77, 78 and 79. Climate, physiography and vegetation of the region were described previously (Crête et al. 1981a). Habitat was partitioned into five forest types according to Crête (1977): mixed stands containing shade-tolerant hardwoods (Ht) with closed (C ≥ 50% crown) or open (C < 50% crown) canopy (i.e., HtC, HtO); mixed stands containing shade-intolerant hardwoods (H,) with closed or open canopy (H,C, H,O), and the remaining stands (R) comprising generally pure stands of conifers. Strata were delimited on 1:20 000 forest maps from examination of

Figure 1. The study area, showing blocks of high (H) and low (L) hunting pressure; numbers indicate the year of aerial survey. F2, F3, F4, J1, J2, and H represent hunting zones.
aerial photographs. These particular forest types had been found to be well related to winter densities of both Moose in the study area (Crête 1977) and Whitetailed Deer nearby (Huot 1974).

Two blocks were surveyed each winter during three consecutive years, one in the reserve or the park, and the other in its paired hunting zone. Moose density for each forest type was determined in January when Moose are easiest to see from the air by aerial census with a helicopter (Crête and St-Hilaire 1979). Moose locations were made on 1:50 000 topographic maps and later transferred on 1:20 000 forest maps. Group size was determined for each location. In mid-March when Moose movements decrease due to thicker and harder snow cover (Desmeules 1965), the two blocks were flown again by a crew in a fixed-wing single-engine Beaver for locating late winter Moose yards in the manner described by Crête and St-Hilaire (1979). Late winter yards are defined as the area occupied by Moose at the end of this season; they were delineated by networks of tracks in the snow as observed from the aircraft. Location of Moose late-winter yards was also transcribed on 1:20 000 forest maps. Only 50 and 80% respectively of blocks L-78 and L-79 were censused because of limited flight time.

From the mid-March aerial survey, three late winter yards per block were randomly selected and examined the following spring between early May and mid-June to estimate the percentage of browse removed by Moose, the proportion of broken stems and the abundance of pellet groups. Yards in the two blocks examined during the same year were located in identical forest types.

Vegetation measurements were recorded in 5-m² circular plots, spaced 50 m apart, systematically covering the yard along equidistant transect lines. Unbrowsed twigs longer than 5 cm, plus those browsed by Moose and by Snowshoe Hare (Lepus americanus), were counted by species on all stems originating within the plot (height = 0.5-3.0 m). Stem breakage by Moose was also recorded by species. Plant species on which Moose generally do not feed were not tallied i.e. Speckled Alder (Aethus rugosus), Tamarack (Larix laricina), Spruce (Picea spp.) and Raspberry (Rubus spp.). Diameter at the point of browsing by Moose (DPB) was measured by caliper to 0.1 mm on the first two stems of each species encountered in each plot (maximum 20 DPB measurements per species per plot). Weight of browse removed by Moose was estimated by means of regression curves relating DPB and twig dry weight as developed by Telfer (1969). Linear regressions (data transformed to natural logarithm) were calculated for the three species expected to be most abundant, Balsam Fir (Abies balsamea), Mountain Maple (Acer spicatum) and Beaked Hazelnut (Corlyus cornuta) by randomly clipping and weighing 100 twigs of each per block in the following November. Diameters of clipped twigs covered the range of DPB measured in spring. Twigs were oven dried at 70°C for at least 72 h. Mean twig weight for the other browsed species was estimated through Telfer’s (1969) equations. Since no regression was available for Mountain Ash (Sorbus americana), Yellow Birch (Betula alleghaniensis) and Shadbush (Amelanchier spp.), weight of browsed twigs was estimated for the same yard by the average weight of Trembling Aspen (Populus tremuloides), White Birch (Betula papyrifera) and Pin Cherry (Prunus pensylvanica). Distal diameters of 100 randomly selected unbrowsed twigs were also measured at three sites per block during the following November; these measurements were limited to Balsam Fir, Mountain Maple and Beaked Hazelnut. Weight of unbrowsed twigs was then estimated from distal diameters by means of the linear regressions computed for DPB. The average weight for those three species together in the six blocks (0.7 g) was used as the best estimate for unbrowsed twigs of the remaining species.

Due to the clustered distribution of many parameters measured in this study (vegetation, browsing and pellet-groups) and to the small sample size (three yards per block, six blocks) nonparametric tests were selected for the statistical analysis. Statistical comparisons were generally made between blocks with high and low hunting pressure, i.e. with lower and higher Moose density. We used the sign test (two-tailed), the Mann-Whitney U test (two-tailed), the Spearman rank correlation coefficient (two-tailed), and the chi-square test (Siegel 1956).

Results and Discussion
Pattern of habitat use in January

Desmeules (1965), Bergerud and Manuel (1969), Lynch (1975) and Joyal et al. (1978) showed that Moose are easier to see from the air in early winter when they use more open stands than at the end of the season. The preference for open stands is probably in response to the more luxuriant shrub layers there; many authors (Brassard et al. 1974: Ahlen 1975: Peek et al. 1976: Crête 1977) have shown a relationship between browse availability and winter distribution of Moose. In the present study, the results (Table 1) failed to illustrate a preference by Moose for open stands. In both highly and lightly hunted blocks, density in open stands (H2O and H2C) was only slightly higher than in closed stands (H2C and H2C) and this difference was not statistically significant (P>0.1). The failure to show habitat preference can be explained by the Spruce Budworm (Choristoneura fumiferana) epidemic that affected the study area.
Table 1. Moose per km² found by aerial survey in January with a helicopter according to the six blocks studied and to the forest types, southwestern Quebec, 1977-1979. H-block = area with high hunting pressure; L-block = area with low hunting pressure; Ht = tolerant hardwoods; Hi = intolerant hardwoods; C = closed canopy i.e. ≥ 50% closure; O = open canopy; R = remaining stands.

<table>
<thead>
<tr>
<th>Forest type</th>
<th>1977</th>
<th>1978</th>
<th>1979</th>
<th>Average</th>
</tr>
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<tbody>
<tr>
<td></td>
<td>H-block</td>
<td>L-block</td>
<td>H-block</td>
<td>L-block</td>
</tr>
<tr>
<td>Ht</td>
<td>0.13(14)*</td>
<td>0.29(21)</td>
<td>0.15(23)</td>
<td>0.27(13)</td>
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<tr>
<td>Hi</td>
<td>0.22(9)</td>
<td>0.16(1)</td>
<td>0.10(8)</td>
<td>1.90(6)</td>
</tr>
<tr>
<td>Ht</td>
<td>0.12(20)</td>
<td>0.22(49)</td>
<td>0.05(8)</td>
<td>0.29(42)</td>
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<tr>
<td>Hi</td>
<td>0.10(12)</td>
<td>0.45(64)</td>
<td>0.06(3)</td>
<td>0.42(4)</td>
</tr>
<tr>
<td>R</td>
<td>0.29(7)</td>
<td>0.22(5)</td>
<td>0.04(1)</td>
<td>0.21(3)</td>
</tr>
<tr>
<td>Entire block</td>
<td>0.12</td>
<td>0.26</td>
<td>0.11</td>
<td>0.27</td>
</tr>
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</table>

*Number of moose counted.
*bIncluding water bodies.

(approximately 1970-1977) and by the scale of our study. The stratification of the habitat was based on aerial photographs taken before the Spruce Budworm outbreak: often canopy classified as closed had been opened by heavy conifer mortality. However, habitat reclassification was impossible because recent aerial photographs were not available. On the other hand, Moose habitat selection is made at Moose scale and studies using photointerpretation may be deceptive (compare Poliquin et al. 1977 and Proulx 1978).

Mean group size and proportion of groups above the mode (two Moose/group) were always higher in L-blocks than in H-blocks (Table 2). The Spearman rank correlation coefficient indicated a significant (p < 0.02) relationship between proportion of large groups and Moose density, but none between group size and density. Peek et al (1974) also observed this relationship when comparing Alaska, Montana, and Minnesota Moose populations. In our study, it is not clear if larger groups in L-blocks resulted from lower hunter disturbance of postrouting groups (Peek et al. 1974; Rounds 1978), or from greater facilities for an animal to find conspecifics belonging to social categories inclined to aggregate.

Pattern of habitat use in March

Desmeules (1965) showed that Moose moved progressively from open to closed stands during winter as snow cover thickness increased. Table 3 indicates such a trend. In general, percentages of forest type used as late winter yards were higher for stands with closed canopy in both H- and L-blocks. Forest type Ht was clearly selected by Moose in the L-blocks, as it probably represented the best habitat available in late winter (Crête 1977). Had the areas classified as "closed", been

Table 2. Mean group size of Moose counted from a helicopter in January and percentage of aggregations larger than two in heavily hunted (H) and lightly hunted (L) blocks, southwestern Quebec, 1977-1979.

<table>
<thead>
<tr>
<th>Block</th>
<th>Mean (standard error; n)</th>
<th>% groups over 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>H-77</td>
<td>1.86 (0.15; 35)</td>
<td>17</td>
</tr>
<tr>
<td>L-77</td>
<td>2.17 (0.18; 65)</td>
<td>28</td>
</tr>
<tr>
<td>H-78</td>
<td>1.68 (0.13; 31)</td>
<td>13</td>
</tr>
<tr>
<td>L-78</td>
<td>2.41 (0.27; 32)</td>
<td>34</td>
</tr>
<tr>
<td>H-79</td>
<td>2.11 (0.41; 19)</td>
<td>16</td>
</tr>
<tr>
<td>L-79</td>
<td>2.48 (0.33; 75)</td>
<td>35</td>
</tr>
</tbody>
</table>

Table 3. Percentage of forest types used as winter yards by Moose in mid-March in southwestern Québec, 1977-1979 according to the six blocks studied and to the forest types. H-block = area with high hunting pressure; L-block = area with low hunting pressure; Ht = tolerant hardwoods; Hi = intolerant hardwoods; C = closed canopy i.e. ≥ 50% closure; O = open canopy; R = remaining stands.

<table>
<thead>
<tr>
<th>Year</th>
<th>H-block</th>
<th>L-block</th>
<th>H-block</th>
<th>L-block</th>
<th>H-block</th>
<th>L-block</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>1977</td>
<td>0.29(21)</td>
<td>0.16(1)</td>
<td>0.10(8)</td>
<td>1.90(6)</td>
<td>0.15(13)</td>
<td>0.30(15)</td>
<td>0.20</td>
</tr>
<tr>
<td>1978</td>
<td>0.12(49)</td>
<td>0.22(5)</td>
<td>0.06(3)</td>
<td>0.42(4)</td>
<td>0.00(0)</td>
<td>0.37(19)</td>
<td>0.23</td>
</tr>
<tr>
<td>1979</td>
<td>0.29(7)</td>
<td>0.22(5)</td>
<td>0.04(1)</td>
<td>0.21(3)</td>
<td>0.06(2)</td>
<td>0.47(16)</td>
<td>0.22</td>
</tr>
</tbody>
</table>

*Area surveyed in km²
actual closed canopies rather than canopies recently opened by Budworm-killed conifers, there doubtless would have been clearer selection for these stands in mid-March. Mean size of yards in March and the percentage of forest types they covered, were generally larger in L-blocks than in H-blocks (Table 4). This trend was not strong enough for the statistical analysis to indicate significant relationships (p > 0.1) between either variable on one hand, and Moose density on the other. Neither was the relationship between percentage of the area used by Moose in March or in January (Crête and St-Hilaire 1979) significantly (P > 0.1) related to mean group size in January nor to yard size in March. Other factors (e.g. climate and behaviour) could also influence yard size and percentage of forest types occupied by track networks.

Table 4. Mean size of Moose yards in mid-March and percentage of the area they covered according to the six blocks studied, southwestern Quebec, 1977-1979. H = high hunting pressure; L = low hunting pressure. The number following H or L indicates the year when the block was surveyed

<table>
<thead>
<tr>
<th>Area</th>
<th>Mean size (km²)</th>
<th>% area used¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>(standard error; n)</td>
<td></td>
</tr>
<tr>
<td>H-77</td>
<td>0.39 (0.12; 25)</td>
<td>3</td>
</tr>
<tr>
<td>L-77</td>
<td>0.56 (0.11; 43)</td>
<td>7</td>
</tr>
<tr>
<td>H-78</td>
<td>0.36 (0.04; 54)</td>
<td>4</td>
</tr>
<tr>
<td>L-78</td>
<td>0.65 (0.10; 96)</td>
<td>12</td>
</tr>
<tr>
<td>H-79</td>
<td>0.79 (0.08; 36)</td>
<td>6</td>
</tr>
<tr>
<td>L-79</td>
<td>0.67 (0.06; 81)</td>
<td>11</td>
</tr>
</tbody>
</table>

¹Including water bodies.

Balsam Fir, Mountain Maple and Beaked Hazelnut accounted for 74% (±0.6 = s) of the available twigs in the 18 yards studied. It was then reasonable to limit the regression computation of browsed and unbrowsed twigs to those three species. Potvin (1978) showed that it is preferable to compute regression curves for each locale, because regional variations produce non-representative general curves; the compromise we chose should have prevented biased estimates of browse consumption.

Mean dry-weights of browsed twigs (Table 5) were rather constant for a given species among years and between blocks, with the possible exception of Mountain Maple. The sign test revealed no difference (p > 0.5) between weight of browsed twigs in H- and L-block (all data combined). Also, there was no relationship between snow thickness and twig weight in contrast to the results of Crête and Audy (1974) for Moose in central and eastern Quebec and by Crête (1976) for White-tailed Deer. A snow accumulation index, computed in a manner similar to Coady (Bishop and Rausch 1974), reached 9245, 13 503 and 12 724, respectively, for winters of 1977, 1978, 1979, in a deer yard located 100 km south of the study area (Joly 1977, 1978, 1979). Weights of browsed twigs in this study had the same amplitude as Joyal's (1976) estimates from a study in La Vérendrye Reserve. Weights of unbrowsed twigs (Table 6) were similar (p > 0.2) in H- and L-blocks. Neither did the sign test indicate any difference among weights of unbrowsed twigs (p > 0.33) when the three species were pooled.

Percentage of browse removed by Moose rarely exceeded 10% in the 18 yards studies (Table 7); it

<table>
<thead>
<tr>
<th>Species</th>
<th>1977</th>
<th>1978</th>
<th>1979</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies balsamea</td>
<td>H-block</td>
<td>L-block</td>
<td>H-block</td>
</tr>
<tr>
<td>-</td>
<td>1.1</td>
<td>1.3</td>
<td>2.8⁴</td>
</tr>
<tr>
<td>Acer pensylvanicum</td>
<td>-</td>
<td>2.0²</td>
<td>-</td>
</tr>
<tr>
<td>Acer rubrum</td>
<td>0.9⁴</td>
<td>2.0⁴</td>
<td>-</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>-</td>
<td>-</td>
<td>3.3⁴</td>
</tr>
<tr>
<td>Acer spicatum</td>
<td>14.3</td>
<td>7.6</td>
<td>0.8</td>
</tr>
<tr>
<td>Cornus alternifolia</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Betula papyrifera</td>
<td>0.6</td>
<td>0.9</td>
<td>-</td>
</tr>
<tr>
<td>Corylus cornuta</td>
<td>0.3</td>
<td>0.4</td>
<td>0.4</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>5.4</td>
<td>1.9</td>
<td>3.9⁴</td>
</tr>
<tr>
<td>Prunus pensylvanica</td>
<td>0.9⁴</td>
<td>0.7</td>
<td>-</td>
</tr>
<tr>
<td>Nemopanthus mucronata</td>
<td>-</td>
<td>-</td>
<td>0.7</td>
</tr>
<tr>
<td>Salix spp.</td>
<td>-</td>
<td>1.2²</td>
<td>-</td>
</tr>
<tr>
<td>Thuja occidentalis</td>
<td>-</td>
<td>4.8</td>
<td>-</td>
</tr>
<tr>
<td>Viburnum alnifolium</td>
<td>-</td>
<td>1.4⁴</td>
<td>1.3</td>
</tr>
<tr>
<td>Viburnum cassinoides</td>
<td>1.2⁴</td>
<td>0.5</td>
<td>-</td>
</tr>
</tbody>
</table>

⁴Less than 10 DPB measured.
Table 6. Average dry-weight of unbrowsed twigs for the three common species in southwestern Québec, 1977-1979, according to the six blocks studied. Weights were estimated from In weight-ln distal diameter regression curves. H-block = area with high hunting pressure; L-block = area with low hunting pressure.

<table>
<thead>
<tr>
<th></th>
<th>1977</th>
<th>1978</th>
<th>1979</th>
</tr>
</thead>
<tbody>
<tr>
<td>H-block</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L-block</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Abies balsamea</td>
<td>0.5</td>
<td>0.9</td>
<td>1.4</td>
</tr>
<tr>
<td>Acer spicatum</td>
<td>1.2</td>
<td>1.3</td>
<td>1.0</td>
</tr>
<tr>
<td>Corylus cornuta</td>
<td>0.4</td>
<td>0.5</td>
<td>0.4</td>
</tr>
</tbody>
</table>

averaged 3.3 and 8.3% respectively in H- and L-blocks. The Mann-Whitney U test indicated that browsing pressure was higher in L-blocks (p < 0.02). However, even in L-blocks, browsing pressure was lower than that observed in Matane Reserve, Québec (Crète and Bédard 1975; Bédard et al. 1978). In our study area, Crète (1980) found that Moose generally did not use the same stands in consecutive winters. Available biomass ranged between 50-600 kg/ha (dry weight) and averaged 230 and 261 kg/ha respectively in H- and L-blocks; this difference was not significant (p > 0.05). Available biomass in late winter years was 3 or 4 times greater than annual twig production in the study area (Crète and Jordan 1982). Inclusion of more than twig current-year growth in the biomass estimate for the present study, and the fact that yards are probably not representative of the region sampled, can explain this discrepancy. Available biomass in the yards studied was slightly lower than estimates in Matane Reserve (Crète and Bédard 1975, Bédard et al. 1978), but the poor condition of Balsam Fir after the epidemic is probably responsible for the difference. Proportion of twigs browsed by hare was identical in H- and L-blocks (p > 0.10) and averaged 0.8% for the 18 yards: the competitive effects by hare on Moose appeared minimal.

Telfer and Cairns (1978) suggested that heavy browsing and stem breakage, which generally occur in late winter, had greatly slowed the vegetation succession in Elk Island Park, Alberta. Breakage there affected 5.4% (n = 7549) of stems greater than 0.61 m in 1971, and even summer breakage was observed. In our area, stem breakage was uncommon in both H- and L-blocks; it averaged 0.1 and 0.4% (n = 5251 and 6537) respectively; this difference was not significant (p > 0.10).

The difference in the number of pellet-groups ha⁻² (Table 8) was insignificant (p > 0.10) between yards of H- and L-blocks, even where the overall mean was more than twice as great in L-block. If differences were real, small sample size and large within-block

Table 7. Percentage of browse removed by Moose in 18 late winter yards according to the six blocks studied and to forest types in which they were located, southwestern Québec, 1977-79. H-block = area with high hunting pressure; L-block = area with low hunting pressure; H₁ = tolerant hardwoods; H₂ = intolerant hardwoods; C = close canopy i.e. ≥ 50% closure; O = open canopy.

<table>
<thead>
<tr>
<th></th>
<th>1977</th>
<th>1978</th>
<th>1979</th>
</tr>
</thead>
<tbody>
<tr>
<td>H-block</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L-block</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₁C</td>
<td>1 (610¹, 68²)</td>
<td>16 (327; 45)</td>
<td>1 (130; 82)</td>
</tr>
<tr>
<td>F₁C</td>
<td>0 (61; 63)</td>
<td>8 (221; 70)</td>
<td>1 (171; 91)</td>
</tr>
<tr>
<td>F₁O</td>
<td>16 (400; 67)</td>
<td>6 (424; 68)</td>
<td>3 (93; 101)</td>
</tr>
</tbody>
</table>

¹Browse available (kg/ha).
²Plots surveyed.

Table 8. Number of pellet-groups per ha in 18 late winter yards according to the six blocks studied and the forest type in which they were located, southwestern Québec, 1977-1979. H-block = area with high hunting pressure; L-block = area with low hunting pressure; H₁ = tolerant hardwoods; H₂ = intolerant hardwoods; C = close canopy i.e. ≥ 50% closure; O = open canopy.

<table>
<thead>
<tr>
<th></th>
<th>1977</th>
<th>1978</th>
<th>1979</th>
</tr>
</thead>
<tbody>
<tr>
<td>H-block</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>L-block</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F₁F</td>
<td>9 (34³)</td>
<td>109 (33)</td>
<td>20 (41)</td>
</tr>
<tr>
<td>F₁F</td>
<td>0 (31)</td>
<td>6 (35)</td>
<td>23 (43)</td>
</tr>
<tr>
<td>F₁O</td>
<td>41 (34)</td>
<td>21 (33)</td>
<td>23 (44)</td>
</tr>
</tbody>
</table>

³5-m² plots counted.
variation precluded this being shown. The highest values in the L-blocks were but one-third those found in Matane Reserve (Crête and Bédard 1975). A comparison of the ratio of kg browsed ha\(^{-1}\) to pellet-groups ha\(^{-1}\) for H- and L-block yielded insignificant differences (p > 0.10), suggesting comparable digestion rates. The overall ratio averaged 0.55 kg/group; since mean pellet-group dry weight was estimated at 0.23 kg on Isle Royale, Michigan (Jordan, unpublished data), digestion rate of woody browse would have been 58%. However this statistic exhibited large variation.

The chi-square test, applied to the pooled number of twigs counted in the 18 yards, indicated that Moose were selective when browsing (p < 0.001). The Spearman rank correlation coefficient, using only common species (available browse > 5 kg ha\(^{-1}\)), indicated that Moose preference varied symmetrically in H- and L-blocks (r\(_s\) = 0.61; n = 20; p < 0.02). Overall, the most preferred species were Shadbush, Mountain Maple, Mooseberry (Viburnum alnifolium), and uncommon species (Table 9). The most common species in Moose diets were Mountain Maple and Balsam Fir. Joyal (1976) in La Vérendrye, and Reserve and Brassard et al. (1974) over all of southern Québec, also found those two species the most commonly taken in winter. In addition, Crête and Jordan (1981) showed that Mountain Maple represented the most frequently-used species in the study area during the snow-free period.

Plant composition was highly variable among all blocks, and chi-square tests indicated significant difference (p < 0.001). Crête (1977) also found great variation in plant composition in the study area. However these differences were apparently not the result of replacement of preferred species in L-blocks due to selective browsing.

Conclusion
Notable differences in winter habitat use were not found between high and low Moose density areas. Habitat selection in January and March was difficult to illustrate in either H- and L-blocks. When group size was larger, in the L-blocks, yard size was also larger, so that each animal there occupied roughly the same area as did individual animals in the H-blocks. Even where densities were high, the mean weight of browse twigs was not large and the frequency of stem breakage was low; moreover, browsing pressure was low, and the preferred browse species were generally the same, in both H- and L-blocks. Only the proportion of browse removed reached higher values in L-blocks; the smaller yards in the H-blocks may have been sampled more heavily in their peripheral areas leading to an underestimation bias of browse impact. Because there appeared to be no extensive pressure on

<table>
<thead>
<tr>
<th>Species</th>
<th>H-block</th>
<th>L-block</th>
<th>Average</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acer saccharum</td>
<td>0.59</td>
<td>0.13</td>
<td>0.35</td>
</tr>
<tr>
<td>Amelanchier alnifolium</td>
<td>0.12</td>
<td>0.55</td>
<td>0.33</td>
</tr>
<tr>
<td>Balsam fir</td>
<td>0.15</td>
<td>0.17</td>
<td>0.16</td>
</tr>
<tr>
<td>Droecia glauca</td>
<td>0.06</td>
<td>0.07</td>
<td>0.06</td>
</tr>
<tr>
<td>Garrya camaldula</td>
<td>0.08</td>
<td>0.09</td>
<td>0.08</td>
</tr>
<tr>
<td>Ipomoneae rugosa</td>
<td>0.10</td>
<td>0.11</td>
<td>0.10</td>
</tr>
<tr>
<td>Viburnum alnifolium</td>
<td>0.12</td>
<td>0.13</td>
<td>0.12</td>
</tr>
<tr>
<td>Other species</td>
<td>0.15</td>
<td>0.16</td>
<td>0.15</td>
</tr>
</tbody>
</table>

Table 9. Average percentage of browse removed by Moose in three yards according to the six blocks studied and to plant species, southwestern Québec, 1977-1979. H-block = area with high browsing pressure; L-block = area with low browsing pressure.
preferred browse, and no density-related difference in the browsing pattern, we conclude that winter forage was not limiting to the animals studied here.

Acknowledgments
We express our gratitude particularly to D. St-Hilaire who was closely involved in the field work. We wish to thank M. Bourgon, J. Lambert, K. Levine and M. Monette who also worked in the field. R. Joly provided valuable advice in statistics and J. Bouchard drew the figure.

Literature Cited


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Cannibalism by a Free-Ranging Bobcat, *Felis rufus*

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Maine Cooperative Wildlife Research Unit, University of Maine, Orono, Maine 04469


An adult female Bobcat (*Felis rufus*) apparently killed and consumed a kitten. This cannibalism may have been partially influenced by territorial behavior since it occurred on the edge of the adult's home range.

Key Words: Bobcat, *Felis rufus*, cannibalism, territoriality

We observed an incidence of cannibalism by a Bobcat (*Felis rufus*) while conducting a study of their ecology in eastern Maine. On 31 January 1981, at ca 1230 h, one of us (MO'D) traversed a dense stand of hardwood shrubs and observed the remains of a Bobcat scattered in about a 20 m² area on the snow. The remains included a portion of the skull with canines, a foreleg, intestines and pieces of skin and hair. An open canine root canal indicated the Bobcat was a juvenile (Crowe 1975). It appeared from the tracks in the snow and the scattered remains that the victim was attacked and fed upon by another Bobcat. A 1.5 m long trail of blood and hair indicated a struggle had occurred. The carcass appeared to have been dragged 2 m. Numerous tufts of hair were found in the immediate area. Urine markings were observed at this site and the apparent kill site. The observer left the area at ca 1250 h.

At 1340 h the senior author arrived and observed a Bobcat leaving the carcass remains. A Bobcat (probably the same) was observed approaching the site at 1350 h. The Bobcat walked directly to the remains and fed. The senior author approached within 3 m of the feeding Bobcat several times, causing it to back away. However, the Bobcat returned each time. At ca 1435 h the senior author tossed a flesh-covered Beaver (*Castor canadensis*) skull toward the Bobcat. After consuming the fleshy remains of the victim Bobcat, the feeding Bobcat grasped the Beaver skull with its mouth and walked about 15 m north of the kill. The senior author then departed, and at 1530 h returned with several assistants. The Bobcat was observed within 10 m of the kill site. At 1600 h a portion of a Beaver carcass was placed at the kill site with four leg-hold traps around it. The observers left, returned at 1635 h, and found the Bobcat trapped. The animal was a 4.3 kg female, greater than one year old, based on dental characteristics. Although the Bobcat appeared underweight, it seemed in good health and no injuries were observed. We equipped the Bobcat with a radio collar and released it at the capture site at 1800 h. As of 1 January 1982, approximately 275 locations were recorded. Using these to estimate the minimum area home range (Mohr 1947), we found that the capture site was on the edge.

The results of Bobcat movement studies indicate that Bobcat home ranges are apparently exclusive territories with limited intrasexual range overlap, especially between adjacent adult females (Marshall and Jenkins 1966, Bailey 1974, Hall and Newsom 1976). Bailey (1972) indicated that Bobcats utilize visual contact and scent marking/avoidance behavior rather than overt aggression in territorial maintenance. This pattern has also been reported to exist in the territorial maintenance schemes of other solitary felids (Leyhausen 1965, Schaller 1967, Hornocker 1969).

Few Bobcat interactions have been reported. Provost et al. (1973) reported observing an adult male Bobcat chasing a juvenile male up a tree. Juvenile Bobcats often disperse during winter before the mating season (Erickson 1955) and may encounter resident individuals. The kill and capture site location suggest that the cannibalism we observed may have been influenced, in part, by territorial behavior as well as by hunger and opportunity.

Acknowledgments

This research was supported by Pittman-Robertson Project W-69-R; the Maine Cooperative Wildlife Research Unit, U.S. Fish and Wildlife Service, Maine Department of Inland Fisheries and Wildlife, Wildlife Management Institute and the University of Maine, cooperating.
Literature Cited


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Accepted 28 February 1982

Occurrence and Foraging Habits of Prairie Falcons, *Falco mexicanus*, at Beaverhill Lake, Alberta

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3819-112A Street, Edmonton, Alberta T6J 1K4


At Beaverhill Lake, Alberta, Prairie Falcons (*Falco mexicanus*) were recorded on 31 dates between 21 April and 21 October, 1967-1981. Hunting attempts, mostly on small passerines and shorebirds, were observed on 44 occasions, and all involved prey on the ground or in shallow water. In 26 cases, the prey appeared to have been spotted from afar while the falcon was soaring or in flapping flight. In 11 cases, the prey was detected just ahead while the falcon flew low over the ground. The last phase of these 37 hunts was a high-speed, low-level surprise attack, of which one was successful. The capture of a Baird's Sandpiper (*Calidris bairdii*) is described. In seven cases, falcons flying at 10-30 m stooped perpendicularly at small passerines that flushed below them.

Key Words: Prairie Falcon, *Falco mexicanus*, Alberta, Beaverhill Lake, foraging habits.

Prairie Falcons (*Falco mexicanus*) are usually associated with "arid plains and steppes of interior North America, wherever cliffs or bluffs are present for nesting sites" (Brown and Amadon 1968:834). The breeding range in Alberta is restricted to the southern portion of the province up to the latitude of Red Deer (Salt and Salt 1976), although there are a few recent nesting records from an area roughly 50 km WSW of Edmonton (G. Erickson, Alberta Fish and Wildlife Division, personal communication). Salt and Salt (1976:98) stated that "as a transient it has been seen as far north as Edmonton," and Lister (1979) cited an old record from Beaverhill Lake, 70 km east of Edmonton. Beaverhill Lake is roughly 15 X 20 km in size, situated in a shallow basin and surrounded by open or brushy pasture land. Its shoreline includes mudflat habitat, narrow sandy beaches and marshy bays with extensive reed beds.

From 1967 to 1981, I frequently visited Beaverhill Lake to survey migrations of raptorial birds. I saw Prairie Falcons on 31 dates: 3 in April, 5 in May, 7 in August, 12 in September and 4 in October. Earliest date was 21 April, last date 21 October. On several dates, two or three sightings were made, probably of the same bird. Some falcons, sitting on fence posts or shoreline rocks, were viewed through a 20x scope. Flying falcons were watched through 10x50 binoculars for as long as they remained in view. The black axillars, which are diagnostic for the species (Godfrey 1966), were noted in all 31 sightings.
Foraging activity on 24 dates included a total of 44 interactions with potential prey, which were all on the ground or in shallow water when attacked. In 37 cases, the hunting strategy used was a high-speed, low-level surprise attack. The initial phase of these hunts showed the following variations.

**Stoop from soaring flight**

During sunny and windy weather, falcons often soared and reached altitudes estimated to be in excess of 1000 m at times. Presumably after sighting prey, the falcons pulled in their wings partly or completely and stooped at angles varying from 30° to 60°. In the terminal portion of their attack, the falcons levelled off and travelled distances of 10 to 300 m low over ground or water without beating their wings. The prey was flushed at close range. Of 12 such stoops seen, 4 were aimed at flocks of shorebirds, 1 at flocks of unidentified blackbirds or Starlings (*Sturnus vulgaris*), and 6 at unidentified birds. One stoop appeared to be directed at Richardson's Ground Squirrels (*Spermophilus richardsonii*). The falcon involved in this last hunt attacked in curious, undulating flight; alternately dropping very low and rising 3-6 m.

**Oblique descent from flapping flight**

While travelling in flapping flight at altitudes varying from 10 to 150 m, and presumably sighting prey far ahead, some falcons suddenly descended obliquely, thereby increasing their speed, and flew low over ground or water. They attempted to seize a bird from flocks that flushed just ahead. During the very last stage of the attack, the falcon sometimes sailed with wings partly or completely flexed. Fourteen such hunts were seen; four aimed at shorebirds, two at blackbirds or starlings, and eight at unidentified birds along the lake's shore.

**Opportunistic low flight**

Travelling in flapping flight very low over ground or water, some falcons appeared to hunt prey at random, attempting to seize it as it flushed just ahead. Eleven attacks were observed; three on small shorebirds, one on blackbirds, and seven on unidentified species along the lake's edge.

On seven other occasions, I observed falcons, flying in flapping flight 10 to 30 m over open pasture land, suddenly stoop down perpendicularly with wings slightly flexed in an attempt to seize a small passerine that flushed from the ground. Mounting steeply after the unsuccessful stoop, the falcon continued on its course. The nearly vertical attacks set these attempts clearly apart from all the others.

The only successful hunt I observed took place on 10 September 1978 at 1400. I was sitting on the south shore of Beaverhill Lake and scanning the horizon through binoculars when I noticed a large falcon about 1500 m to the west flying at an estimated 70 m altitude. Twice it hovered briefly against the light wind, then suddenly beat its wings vigorously, pulled them in and headed east in a long curving stoop. The falcon covered the last 100 m just over mudflats until it flushed six Baird's Sandpipers (*Calidris bairdii*), which I had been observing prior to sighting the falcon. The sandpipers rose at the last instant, and one appeared to be hit by the falcon; I heard the sound of an impact. The sandpiper dropped back into the shallow (5 cm±) water, while some feathers drifted down. The falcon mounted steeply, turned and descended, seizing the splashing, wing-flapping prey without alighting, and carried the sandpiper to open ground some 60 m away. Upon noticing me, the falcon rose, flew towards me a little way, circled back and disappeared from view behind reed beds. While in flight, it brought its feet forward and bent its head down as if to bite and kill the prey.

On two occasions I encountered Prairie Falcons feeding on Starlings. One falcon was eating a Pectoral Sandpiper (*Calidris melanotos*) and another was flushed from the nearly consumed carcass of a Northern Pintail (*Anas acuta*). The observations reported here suggest that Prairie Falcons occur regularly north of the known breeding range to at least the latitude of Beaverhill Lake, where they hunt resting or feeding flocks of passerines and shorebirds in the same surprise technique used by Peregrine Falcons (*Falco peregrinus*), although they do not attack and pursue flying prey as the Peregrine often does (cf. Dekker 1980).

**Acknowledgments**

Most of these records were obtained while I was doing raptor surveys under contract to the Alberta Fish and Wildlife Division. I thank R. Fyfe and A. J. Erskine for critically reading the manuscript.

**Literature Cited**


Received 11 January 1982
Accepted 12 May 1982
News and Comment

Honorary Membership and Ottawa Field-Naturalists' Club Awards

Four new Ottawa Field-Naturalists’ Club awards were presented for the first time in 1982, along with one Honorary Membership. The four new awards are described in The Annual Report by Council to the Ottawa Field-Naturalists’ Club The Canadian Field-Naturalist 96(3): 367 and have previously been announced in Trail & Landscape 16(4): 185-189.

Honorary Member: Thomas H. Manning

Thomas H. Manning, O.C., has been a member of The Ottawa Field-Naturalists’ Club since 1941. In the 1930s and 1940s he surveyed large parts of Canada’s Arctic, including Southampton Island, Baffin Island and Repulse Bay, mapping areas by combining ground and air photographic surveys. His vast experience in arctic exploration has been recognized by many organizations. He has served as a consultant to the Defence Research Board, as executive director of the Arctic Institute of North America, and as leader of various expeditions.

Concurrent with his earlier geographical activities, and increasingly in later years, T. H. Manning has spent much of his life on biological work. He has made large collections of birds and mammals for the National Museum of Natural Sciences and the Royal Ontario Museum. More than fifty of his papers have been published by the National Museum and the Canadian Wildlife Service, a number of these in The Canadian Field-Naturalist. He continues his prolific biological work and arctic activities today.

He has been given many other distinguished awards recognizing his important contributions to the knowledge of the Canadian Arctic. In 1944 he was awarded the Bruce Medal of the Scottish Geographical Society and the Royal Philosophical Society of Edinburgh. In 1948 he was awarded the Patron’s Medal of the Royal Geographical Society. In 1974 he became an Officer in the Order of Canada, and in 1977 he was awarded the Massey Medal of the Royal Canadian Geographical Society.

Member of the Year: Joyce M. Reddoch

Joyce is the naturalists’ dedicated naturalist, and has done more to further Club goals than any other member in 1981. Her conservation activities in the Ottawa area are known and appreciated by most members of the Club, and her knowledge and expertise are also recognized by many people outside the Club. Since she started the Conservation Committee in 1972, Joyce has been working to protect important natural areas in the Ottawa area, and these efforts continued throughout 1981.

During the year, Joyce wrote several articles in Trail & Landscape, including two instalments in her series Conservation Activities. She also continued her work, with Allan Reddoch, on the Orchids in the Ottawa District, and she supplied much of the material for the Club’s display at the Wetlands Policy Workshop at Carleton University in early January 1982.

Joyce also served as Editor and Production Coordinator of Trail & Landscape, and continued to increase its reputation as an outstanding local natural history journal.

Service Award: Ellaine M. Dickson

Since joining the Club in 1968, Ellaine has been a very active participant in Club activities, taking as much interest in the Club and its members as in natural history. She maintains the accuracy of both the membership history cards and the mailing list. She has also been involved in the compilation of a list of volunteer work members. Since 1976 Ellaine has generously answered the Club phone and has taken most reservations for Club activities as well as general inquiries by members and non-members.

This year three of Ellaine’s beautiful bird carvings were presented to the three winners of the Anne Hanes Natural History Award. She is serving currently on the Council (since 1978) and on both the Membership and the Excursions and Lectures Committee. She has served on the Education and Publicity and the Nominations Committees in the past. Her knowledge of the membership has been invaluable for all the committees she has served with.

Many of Ellaine’s activities have been involved with maintaining good communications with the membership for important events. Without a doubt, Ellaine has played a key role in the smooth running of the Club in recent years.

The Anne Hanes Award for Natural History: Ross A. Layberry, J. Donald Lafontaine and Peter W. Hall.

This award is shared by three naturalists, in recognition of the outstanding calibre of their field studies on our local butterflies. These studies culminated in the publication of Butterflies in the Ottawa District in
**Trail & Landscape** 16(1): 3-59. This work represents years of keen field study, discriminating observations and meticulously collected data. While each of the authors has made significant individual contributions to our knowledge of local butterflies, together the three have produced a landmark publication which will undoubtedly be the standard reference for Ottawa Valley lepidopterists for many years to come. The May/June 1982 newsletter of the Lepidopterists’ Society included the following comments in its review of *Butterflies of the Ottawa District*: “This publication . . . is an outstanding example of how a local butterfly guide can be put together. . . . [It] should serve as a model for local guides being contemplated elsewhere.”

**Conservation Award: Albert W. Dugal**

Albert served on the Conservation Committee from 1975 to 1980. Because he has spent many hours in the field around eastern Ontario, he has been a very knowledgeable spokesman for the Club’s conservation interests. His main activities have centred on the South Gloucester area, where he has found over 500 plant species including 147 plants of regional significance and several of provincial significance.

Albert has made many presentations to planning groups and other groups of interested citizens. He has served on the Regional Municipality’s Citizen’s Advisory Committee on Conservation Lands in the southeastern area of Ottawa-Carleton.

As well as his dogged efforts for conservation of the South Gloucester area, Albert has been instrumental in the protection of the Shaw Woods, which the National Museum of Natural Sciences and the Nature Conservancy of Canada have purchased, and has led many groups through this area.

Albert has authored or co-authored 10 *Trail & Landscape* articles and Club reports (see *Trail and Landscape* 16(4): 189).

**Stephen J. Darbyshire**

and members of the

Ottawa Field-Naturalists’ Club Awards Committee.

**XIX Congressus Internationalis Ornithologicus: First Announcement**

At the XVIII International Ornithological Congress in Moscow the International Ornithological Committee accepted the invitation of the National Museum of Natural Sciences of Canada and of the Canadian ornithological community to hold the XIX Congress in Canada. The Congress will be held in Ottawa, Canada, from 22-29 June 1986. It elected Dr. Prof. Klaus Immelmann (West Germany) as President of the Congress. Dr. Henri Ouellet (Canada) was designated as Secretary-General.

Details about the general and scientific programs, field excursions, and other activities during the Congress will be available later.

Those interested in participating in the Congress are urged to inform the Secretariat in order to obtain announcements and application forms. Correspondence should be addressed to The Secretary-General, Dr. Henri Ouellet, XIX Congressus Internationalis Ornithologicus, National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario, Canada K1A 0M8.

**Fourth International Theriological Congress**

The IV International Theriological Congress (ITC) will take place 13-20 August 1985 on the campus of the University of Alberta in Edmonton. The purpose of this notice is to solicit names for a preliminary mailing list of potential participants, and to request comments and suggestions.

The names of all who attended any of the first three congresses will be placed on the provisional mailing list for IV ITC, but, if your address as listed in the Transactions of the Congress you attended is no longer correct, please send a current address.

If you have not attended any of the previous congresses but have any intention of coming to Edmonton in 1985 please send your name and address to the undersigned so that you will receive the first mailing, probably early in 1983.

It is expected that IV ITC will follow the general format adopted at Helsinki. If you have comments or suggestions for improvement please pass them along.

Finally, if you have suggestions for symposia or work-
shops or plenary speakers please pass them along too. We are particularly interested to hear from anyone with a burning desire to organize, or help to organize, a symposium or workshop.

W. A. FULLER

Common Tern Colour-marking by the Canadian Wildlife Service: Request for Information

The Canadian Wildlife Service, Ontario Region, is continuing its program of colour-marking Common Terns at two colonies in the lower Great Lakes to determine their post-breeding dispersal, migration routes and winter range.

In 1981 adults were marked with orange wing-tags and chicks with pink tags. Many of the adult tagged birds returned to their colonies in 1982 still carrying their tags. The tagged birds appeared fit and nested normally. Most tags were still clearly legible and showed little wear.

In 1982 bright blue wing tags (with black lettering) were put on all adults Common Terns and black tags (with yellow lettering) on chicks just prior to fledging. Tags were put on both wings of all birds. All tags have combinations of letters and numbers (the two tags on any bird have the same combination). When you observe a tagged tern would you please report the date, location, colour of the tag, and, if possible, the number/letter combination to:

Banding Office
Canadian Wildlife Service Headquarters
Ottawa, Ontario, Canada K1A 0E7
All reports will be acknowledged.

HANS BLOKPOEL
Wildlife Biologist, Ontario Region, Canadian Wildlife Service, 1725 Woodward Drive, Ottawa, Ontario K1A 0E7

International Society of Cryptozoology: Invitation For Charter Membership

The purpose of the International Society of Cryptozoology is to serve as a focal point for the investigation, analysis, publication, and discussion of all matters related to animals of unexpected form or size, or unexpected occurrence in time or space. The Society will promote the scientific examination of all evidence related to these matters.

The Society recognizes that much emotional debate has resulted over the possible existence of such animals, and that future work in this area will not be without controversy. However, the Society will attempt to address these issues in a strictly objective manner, following established scientific methods.

One of the principal aims of the Society is the dissemination of cryptozoological information among biological scientists, who might otherwise not be aware of its existence. This includes information on cryptozoological claims, and on the anayes of such cryptozoological evidence as photography, sonar tracks, footprint casts, tissue samples, and hair samples. The Society, which is governed by a Board of Directors composed of scientists with eminent credentials, will also serve as a forum for public discussion and education, and for providing reliable information to appropriate authorities and to the news media.

Although the Society is primarily intended for biological scientists, membership is open to all interested persons. The Society will publish both a quarterly newsletter and a scholarly, refereed journal, entitled Cryptozoology, which will appear once a year. While published articles will meet the highest standards of academic scholarship, they will be presented in a format appropriate for a non-specialized audience.

Many animals which today are well-known and accepted were once controversial — or at least “unexpected.” Some of the more interesting of these cryptozoological precedents are:

- The gorilla, described in 1847;
- The okapi, a Miocene giraffid, described in 1901;
- The pygmy hippopotamus, collected in 1913;
- The coelacanth fish, found in 1938, a true “living fossil;”
- The “Pleistocene peccary” described in 1975;
- “Megamouth,” a totally new species, genus, and family of shark, found in 1976.
Today we are confronted with a wide variety of reports of such "unexpected" animals — often appearing under the popular label of "monster." Some of those which the Society is concerned with are:

- Reports of very large octopuses (spanning 50 feet or more);
- Reports of "sea serpents" in many global marine environments, which may represent unknown species of large seals or supposedly extinct primitive whales known as archaeocetes;
- Reports of northern latitude "lake monsters" in Loch Ness, eight other Scottish lochs, and in Irish, Swedish, Soviet, Canadian, and U.S. lakes;
- Reports of large, long-necked animals in the swamps of Central Africa (Mokele-Mbembe), said to resemble Mesozoic sauropod dinosaurs;
- Reports of large hominoids in the Himalayan region (Yeti), Soviet Union and Mongolia (Almas), China (Wildman), and North America (Sasquatch).

Membership is $25 a year (Sustaining Members may contribute any amount above that), and includes the receipt of all Society publications. Couples may take out a joint membership for $30. Individuals wishing to subscribe to the Society's publications without membership, as well as libraries and institutions, may do so for $35 a year.

J. Richard Greenwell
Secretary and Treasurer
International Society of Cryptozoology
P.O. Box 43070
Tucson, Arizona 85733

National Museums of Canada Announces New Book Distributors

The National Museums of Canada has announced that, effective immediately, McClelland and Stewart Limited, Toronto, and Les Éditions France-Amérique, Montreal, are the exclusive distributors of National Museums of Canada (NMC) publications in Canada. These two firms were selected by competitive process earlier this year.

Over 300 NMC publications will be carried by the two publishers, who will be responsible for sales, promotion, warehousing and order fulfillment in Canada. Éditions France-Amérique will also be responsible for sales of French-language and bilingual titles outside Canada. The University of Chicago Press will continue to handle marketing and distribution of English-language and bilingual publications outside Canada.

The NMC publishes for both the scholarly and popular market in a wide variety of disciplines, including the natural sciences, anthropology, fine art and history. Natural sciences publications include Natural History Notebook No. 5 (paperback, $2.50), on Canadian prehistoric life, The Birds of Canada, and the Edible Wild Plants of Canada series.

Soon to be published is the first of a seven-volume series entitled Handbook of Canadian Mammals, and Moss Flora of the Maritime Provinces.

The Alfred B. Kelly Memorial Fund of the Province of Quebec Society for the Protection of Birds, Inc.

Annual Research Grants up to $1,000 will be available for studies pertaining directly to Quebec ornithology. Applications will be accepted from any interested person regardless of place of residence.

For application forms write to
Marianne G. Ainley
P.Q.S.P.B. Research Committee
4828 Wilson Avenue
Montreal, Quebec
Canada H3X 3P2

Applications must be postmarked by March 31, 1983. Applicants will be notified of the committee's decision by April 30, 1983.

Erratum
Please note on the inside front cover of the Canadian Field-Naturalist 96(1), (2), and (3) that "1981 Council" should read "1982 Council".
A long-time member and honorary member of the Ottawa Field-Naturalists' Club died in Ottawa on 8 September 1981, just 10 days short of his 96th birthday. For 38 years he served on the staff of the Geological Survey of Canada and the National Museum of Canada, and although his formal education stopped with high school, he retired with academic honours and memberships and an international reputation as a vertebrate palaeontologist. The two institutions for which he worked have had an admirable policy of giving their non-academically trained staff members the opportunity to make scholarly contributions to their branch of science. One thinks of T.C. Weston in geology, Clyde Patch in zoology, and W.J. Wintemberg in archaeology. Charlie Sternberg was an outstanding example of this progression from technician to scientist. He was born in Lawrence, Kansas, in 1885, the second son of Charles H. Sternberg, one of the most famous of professional fossil collectors. All three sons, George, Charles, and Levi, were trained in this work, and had collaborated with their father in making outstanding discoveries of fossil vertebrates in Kansas, New Mexico, and Wyoming. In 1912 the family moved to Ottawa and joined the staff of the Geological Survey of Canada.

The cause of this move was the arrival two years earlier of Barnum Brown, the highly successful dinosaur collector of the American Museum of Natural History, in the valley of the Red Deer River in Alberta. This rich fossil field had been known to Canadian geologists for 26 years, but had never been properly exploited. In fact, there was no Canadian with the skill and experience to direct the safe removal of these large but fragile skeletons. That was why Dr. Reginald Brock, Director of the Geological Survey of Canada, had to turn to an American to insure that Canada got some share of these palaeontological riches, and Charles Sternberg and his sons were the ideal choice.

The Sternbergs were in the Red Deer River Valley by 1912, and by 1916, in spite of war restrictions, had found, excavated, and shipped to Ottawa 16 skeletons or parts of skeletons. These were the subjects of papers and monographs by Lawrence Lambe, the Survey's vertebrate palaeontologist. But Sternberg senior did not agree with Lambe on plans for future work, so in 1916 he left the Survey, accompanied by his youngest son Levi. George, the eldest son, left in 1918, leaving Charlie as the only technical assistant to Lawrence Lambe. Then in 1919 Lambe died, and Charlie was left to maintain a programme in vertebrate palaeontology under Dr. E. M. Kindle, the Chief Palaeontologist.

Lambe had left an incomplete description of an armoured dinosaur, Panoplosaurus mirus, and Dr. Kindle encouraged Charlie to finish the description. This was published in 1921 and was his first written contribution to palaeontology. From now on his work had a dual purpose, to find and bring to Ottawa the skeletons of prehistoric animals, and to study the anatomy and systematic significance of these remains and publish his findings.

Most of Charlie's field work continued to be concerned with the still-rich dinosaur deposits of the Red Deer River Valley, but he had several interesting digressions. In 1921 he visited the Morgan Creek badlands southwest of Wood Mountain, Saskatchewan, where George Dawson had made the first find of Canadian dinosaurs in 1874. Charlie found several fine specimens, which enabled him to show that the Saskatchewan dinosaurs dated from the latest (Lancian) stage of the Cretaceous period. In 1922 he made a reconnaissance of fossil localities in Nova Scotia, the principal acquisitions being interesting fossil footprints. In 1928 and 1929 he collaborated with the invertebrate palaeontologist Dr. F. H. McLearn, who was making a geological map of southern Saskatchewan. Charlie found Lancian dinosaurs in the Eastend district and Miocene mammals near Wood Mountain. A trip to the Peace River Canyon of British Columbia in 1930 enabled him to make plaster moulds of remarkably extensive trackways of dinosaurs. The summer of 1937 was spent in the Manyberries district of southeastern Alberta, where he found dinosaurs that provided connecting links between those of the Red Deer River badlands and those of the Missouri River Valley of Montana.

But the Red Deer River badlands continued to be the main area of Charlie's field work. From 1923 to 1925 he explored the northern portion, north of Drumheller, finding and collecting 12 skeletons or skulls of dinosaurs. In 1928 he was in the Steeveville badlands, where he had first come with his father in 1913. Three important skulls and a partial skeleton were found, as well as parts of two interesting small dinosaurs. The Geological Survey sent a topographer to Alberta in 1935 to map the Steeveville-Dead Lodge Canyon badlands, and Charlie collaborated by locating the sites of the principal fossil discoveries. In the course of this work he discovered another new dinosaur. Charlie's last expedition to the Red Deer River badlands was in 1946, this time to explore the northern margin of the fossil field in the vicinity of Scollard and Big Valley. Here he found interesting dinosaurs that enabled him to date these upper beds of the Edmonton "Formation" as of Lancian age, like those.
Charles M. Sternberg photographed in the field, August 1928, near Steveville, Alberta by Delmer L. Bruers.
of the Saskatchewan badlands, and younger than those of the Drumheller and Steveville areas.

In 1948, the division of vertebrate palaeontology was transferred from the Geological Survey of Canada to the National Museum of Canada, and Charlie was promoted to the rank of Assistant Biologist. This was in recognition of his many scholarly contributions to palaeontology, which appeared in 47 published papers, and involved the description of 17 new genera or species of dinosaurs. In 1949 he was elected a Fellow of the Royal Society of Canada, the country's most prestigious learned society. The following year he retired from the National Museum staff, but continued, as a research associate, to publish descriptions of dinosaurs.

The Government of Alberta created Dinosaur Provincial Park in the Steveville-Dead Lodge Canyon area, and Charlie was engaged to plan the displays. In 1958 he found and set up two partial skeletons in the rock, protected by buildings with windows, and prepared another skeleton for outdoor display. This was his last field project. He spent his later years in semi-retirement, but retained an office in the vertebrate palaeontology (later paleobiology) laboratories of the National Museum(s) of Canada. The importance of his scientific contributions was recognized by the University of Calgary in 1960 by conferring on him the honorary degree of L.L.D. In 1974 Carleton University conferred on him the degree of D.Sc. He was an honorary member of the Society of Vertebrate

Paleontology, of which he had been a member for many years.

Charlie's partner of many years, his wife Myrtle, died in 1977. They are survived by three sons, all distinguished professionals, 11 grandchildren, 6 great-grandchildren, and a host of friends among the vertebrate palaeontologists of Canada and the United States.

LORIS S. RUSSELL
Royal Ontario Museum, 100 Queen's Park, Toronto, Ontario M5S 2C6
C. M. STERNBERG BIBLIOGRAPHY: 1917-1970

Compiled by: Richard Gordon Day

Paleobiology Division, National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario K1A 0M8


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Book Reviews

ZOOLOGY

The Doomsday Book of Animals: A Natural History of Vanished Species


The original Doomsday Book compiled in England around 1086 offers modern man a unique glimpse into the deep past of Great Britain: who owned what, where, how much was paid, etc. The book is a priceless treasure of British heritage.

Nearly 900 years later, a second Doomsday Book has been published which also offers us a look at the past. There is a crucial difference, however. While the original Doomsday Book marks the beginning of a continuing tradition of property ownership, the modern Doomsday Book shows us a heritage lost forever. The modern book chronicles the recent extinction of wildlife species (excluding invertebrates and plants) around the world.

The author, David Day, spent his early years in the woods of British Columbia. The book found its inspiration in that beautiful wilderness. The book depicts the extinctions of vertebrate species over the last 300 years — nearly one per year, a frantic pace of extinction. Even during the 'great dying' of dinosaurs, species went extinct at a rate of about 1 per 1,000 years. Divided into three main sections (Birds, Mammals, and Reptiles and Amphibians), the book is made up of a number of chapters. Chapters in the Birds section include: The Giants, The Fierce and The Wise, Talking Birds, The Singers, The Timid and The Brash. For each species discussed, the exact date of extinction is given where possible. Each species also gets an informative discussion and, often, a hair-raising description of its final demise.

Mr. Day writes with both clarity and emotion. These extinct creatures are carefully depicted. Although the focus is not "scientific", interesting information is sometimes passed along concerning the biology of the species. Unfortunately, for a good number of species, the end came before anything was known about them.

The book also contains some beautiful color and black and white illustrations. The color plates are especially intriguing. While many are beautiful, they are also disquieting. In many cases, the species depicted is extraordinarily interesting or elegant: the Passenger Pigeon, the Round Island Boa, or the Thylacine for example. Each full color portrait in this book is haunting — because all that is left of their existence is a picture.

While the Doomsday Book is packed full of martyred saints, it also depicts the devil. Throughout, man’s foolishness, greed, short-sightedness and ignorance abound. In some cases, the actions of our forefathers are truly unbelievable. The extinction of the Great Auk has to be read twice to be believed. The end comes with two gestures of thoughtless callousness which epitomize man’s role in these species’ demise.

"So it was that on June 3, 1844, on Eldey Island off the coast of Iceland, three Icelandic fishermen discovered the last two living Great Aucks. They were a breeding pair with a single egg. Jon Bradsson and Sigourer Isleffson killed the two adult birds with clubs. Ketil Ketilsson smashed the egg with his boot."

The book provides plenty of opportunities for the reader to shudder with disgust at our forefathers’ ignorance. But the book also asks a question: Are things any better now? In 1982 there are 400 critically endangered vertebrate species. More frightening perhaps, the book tells us in an appendix on plants that experts estimate there are over 20,000 species of vascular plants on the verge of extinction! Will these species find themselves in Volume Two of The Doomsday Book of Animals?

There is no doubt that endangered species are faring better now in a couple of ways. First, public awareness of and concern for endangered species is growing. The plight of the Giant Panda and the tiger are well-known. Perhaps the best examples of the general concern for endangered species are the world’s whales. These marine mammals have become symbols of the world’s vanishing natural heritage. It is interesting to note that, although some species of whales are critically endangered (the Bowhead), no whale species have entered the Doomsday Book.

Second, the unrestrained destruction of entire species which characterizes the Doomsday Book would not happen today — at least not in the same way. Species would no longer be simply blasted or bludgeoned to certain extinction.

Despite improvements, however, the list of endangered species continues to grow. The central reason is that the endangering of species is now happening at arm’s length. Although we may no longer actually pull the trigger, we remain responsible for diminishing
wildlife populations. Our tools of destruction are no longer the gun or club; they are, among others, the parking lot, the need for wood for fuel in developing countries, and the developed world’s insatiable appetite for energy. In many ways, and usually with harmful effect, we are destroying wildlife habitats around the world. Wildlife species are being eliminated now by misfortune rather than design. The distinction is of no solace to the species affected.

The Doomsday Book of Animals clearly describes and beautifully illustrates the extinctions of the last 300 years. In doing so, the book inspires us to look closely at the present situation and to change it to ensure there is no need for a second volume. A dramatic first step would be a major change in our basic perception of our world. Rather than as an afterthought, wildlife species should be seen as integral parts of our world. In protecting them, we protect our natural heritage — our most priceless and most important possession.

DAVID LOVE
World Wildlife Fund, 60 St. Clair Avenue East, Toronto, Ontario M4T 1N5

Fool Hen: The Spruce Grouse on the Yellow Dog Plains


Read this book if you want to be entertained while learning about a little-known bird. There are a lot of technical data but the text maintains a non-technical aspect. In other words, it is written for the layman and the scientist.

The book, which includes 15 figures, 25 tables, and 12 photographs (4 in full color), is the result of five years of study by the author and his Northern Michigan University students. The setting is the Yellow Dog Plains, approximately 30 miles northwest of Marquette, Michigan. It is a 25 square-mile island of Jack Pine (90% of the trees) surrounded by deciduous forest.

Of the 10 species of North American grouse, the Spruce Grouse has the second largest range but probably has the smallest body of literature. As the dust jacket states, this should remain the definitive treatment of the species for some time to come.

The longest of the book’s 15 chapters are on behavior of the female and broods and on population ecology. Also featured is a good index and approximately 175 references. Of major importance to the success of the study was color banding. Between 1965-69, over 700 observations of 315 color-banded individuals were made. Since 1969, another 30 have been banded and an additional 116 observations made.

From his first encounter with a Spruce Grouse in 1965, Robinson describes it as being a brown and patterned bird, a little bigger, a little plumper, and a lot prettier than a pigeon. His last chapter contains some sobering thoughts about Spruce Grouse, Man, and Nature. A two-page appendix is devoted to where and how to see a Spruce Grouse in Upper Michigan. He concludes that if you try 1-2 days without success to find the species as directed, call him in Marquette and he’ll try to help find a Spruce Grouse.

It is pleasing to read a book where it is evident that the author loves the species he is describing. The author has fulfilled his stated hope that the volume will further our understanding of the species and help us to appreciate more fully one of the other creatures that share the earth with us.

NOEL J. CUTRIGHT
Wisconsin Electric Power Company, 231 West Michigan, Milwaukee, Wisconsin 53201

The Birds of Manitoulin Island and Adjacent Islands within the Manitoulin District


This book is what is commonly known as a species account. At a minimum, such an endeavor is little more than a list of bird species with a brief comment regarding the status of each in the given area or locality. In its more grandiose form the list will include additional information, such as how to identify the bird, historical perspective on each species and even anecdotes. In the preface the author tells us that his offering “lies close to the centre, between the polarities”.

The book covers a total of 299 species in varying detail. It starts off with a chapter entitled “A Testament to Birdwatching”. This chapter rambles. Although there is the occasional interesting or
humorous anecdote, it serves no real purpose in a work of this type. Once past the testament one gets into the kind of information which is more appropriate. This reviewer found the "General Social History" chapter very interesting. It is followed by the species accounts.

Nicholson is consistent in the format of each species account. Each usually has five sections. The first is a single line providing a brief summary of the abundance and status of each species using a defined set of terms. These terms basically adhere to standard usage except that Nicholson adds a new twist to "transient", which he uses to describe a bird straying out of season.

The next section gives general information on the species. All sorts of information makes its way into this section. For many, historical details are included, along with comments on the species' status elsewhere. For casual and accidental birds the normal range is noted. Often, high counts are given, and, for quite a few, favoured localities are cited.

The third section covers spring arrival dates, the fourth deals with breeding information, and the last section covers fall departure dates. However, this format varies for species which don't fit into the "normal" pattern (e.g., vagrants from afar and birds which only come for winter).

Scattered throughout the book are line drawings. These are somewhat abstract but serve a useful purpose in breaking up the monotony of the printed word. On flipping through the book some of the illustrations (corn crake and seabirds) seem out of place in a book on Manitoulin Island. They depict species in the testament chapter.

The reviewer's opinion: a useful book for those going to, or interested in, Manitoulin Island but unfortunately the writer's prolixity makes the book much longer than it should have been. He also has an annoying, or amusing (depending on your point of view), habit of misusing words.

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Spider Communication Mechanisms and Ecological Significance


This excellent volume is broader than its title indicates. The nine chapters between the editors' introduction and epilogue provide thorough reviews of many aspects of the behavioural biology of spiders and, in many cases, syntheses of the authors' research. The first three of these nine chapters deal with core issues. Krafft gives an overview of the significance and complexity of spider communication, including social contexts and roles, mechanisms, ontogeny, and the central influence of silk. Barth discusses the sensory physiology and behaviour associated with vibration, and Uetz and Stratton consider acoustic communication and its functional role in reproductive isolation. The next three chapters focus on aspects of communication in specific groups of spiders. Forster presents behavioural sequences and the underlying visual mechanisms in interacting jumping spiders. For the same group, Jackson analyzes communication in the context of W. J. Smith's semiotic approach of messages and meanings. Tietjen and Rovner discuss chemical communication in wolf spiders. The last three chapters present other topics in spider behaviour. Riechert considers competitive interactions within the framework of optimization theory, providing another instance of the widespread applicability of this approach to biology. Burgess and Uetz deal with spacing patterns and Riechert and Luczak with foraging behaviour, including prey selection and predatory sequences.

The contents of the book thus carry the reader beyond communication but short of a comprehensive treatment of arachnoethology. Illustrations, tables, and indices are used effectively, and the overall composition is excellent. Earlier conclusions are re-evaluated in the light of more recent research, new methods of data collection and analysis are pertinently introduced, and useful suggestions for further work are made. Some of the authors provide comments comparing spiders with other animals. More such discussion would no doubt have been welcomed by readers whose chief interests are with other groups or topics. For instance, near-field and far-field effects are relevant in the sensation of fish as well as that of spiders. Additionally, if a glossary is not to be included, then specialty terms should be cross-referenced or defined when introduced: we stumble on "trichobothria" on p. 51 but they are not described until p. 85. A few sentences and paragraphs are unclear or apparently irrelevant. Notwithstanding these blemishes, this work is a valuable addition to the literature.

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The Freshwater Molluscs of Canada


This well-illustrated, readable book has the potential of stimulating much interest and research activity in freshwater studies. This is a teaching-reference tool, not a coffee table curio. Should it fall into the hands of an interested layman, naturalist, student or scientist, this book could be put to equally good use in ecological field studies or in identification and casual observation of snails or clams in the home aquarium.

A foremost malacologist and author of both scientific and popular articles, Clarke explains how to collect shells and provides an excellent index, reference section, and glossary to scientific terms. Each of the 1979 species is described in an organized but repetitive style. The scientific name is followed by a common name, important aspects of the ecology, representative black-and-white photos, and a distribution map. Noteworthy is that all freshwater mussels are depicted by beautiful colour paintings. This deserves special mention since accurate colour rendition is important when working with these clams. The maps indicate that most species are distributed in relation to ecological factors. There are, however, a number of species that apparently show strong political preference at the provincial level by their truncated distribution along certain boundaries. It is here that amateur and professional study is needed to clarify some of the distributional anomalies and to provide range extensions.

As I learned many years ago when working on Schistosomiasis—a snail-borne debilitating human disease in the tropics—"you cannot expect to understand the snail unless you stoop to its level." Through field work and/or home study, much can be learned. For the interested naturalist it is a wide-open field and much scientific research remains to be done here.

Clarke’s attention to detail is reflected by the remarkably few typographical errors. Although the cost is significant, this book, like Clarke’s monograph entitled The Freshwater Molluscs of the Canadian Interior Basin, will probably be out of print within a couple of years. A French version is also available.

I strongly recommend this book to the aquatic scientist or the naturalist who would like to get involved in something new.

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Caribou and the Barren-Lands

By George Calef. 1981. Canadian Arctic Resources Committee, Ottawa. Firefly Books, Toronto. 176 pp., illus., $34.95 plus $1.25 shipping.

Since the news spread that George Calef was working on a Caribou book for the Canadian Arctic Resources Committee, its publication has been awaited with considerable interest. Calef was already recognized as an excellent popular writer and an accomplished photographer. The question was: how would he deal with controversy over the threats to the survival of the Canadian herds?

George Calef commenced his northern caribou studies in 1971, as a field biologist for the Environmental Protection Board that was supported by the Canadian Arctic Gas consortium. The Board was given a large degree of freedom in developing its own environmental appraisal. At the Mackenzie Valley Pipeline Inquiry, 1975-77, it was Calef’s predictions of detrimental effects upon the Caribou that most influenced Judge Thomas Berger’s views. In his summary report, Judge Berger went beyond Calef’s testimony in predicting dire consequences to the Caribou if the gas pipeline was built. After his association with the pipeline project Calef remained in the North and eventually joined the Northwest Territories’ Fish and Game Branch as its Caribou biologist. In this position he participated in research and management of all the major herds in the Territories.

Calef has applied knowledge that he gained during a decade of involvement with Caribou (involvement that ranged from being an ardent conservationist to becoming a government researcher and manager) to the production of a popular, authoritative book on the Barren-ground Caribou of northern Canada and Alaska.

In Part 1, Calef describes the annual cycle of the Caribou in five chapters: Spring — the river of life; Calving — a birthright of snow; Summer — the great herds; Autumn — the hunter’s moon; and Winter — the time of testing. He initially uses a narrative style, following an individual, hypothetical animal, and traces its movements and subtle biological changes. In order to broaden the reader’s geographical appreciation of the distribution of the herds, he picks his animals from several different herds. So the spring migration and calving are those of the Bathurst herd,
while the summer and autumn travels described are those of the Porcupine herd. After the narrative part of each chapter, Calef describes the biological implications to the Caribou of each season. At this point he draws heavily upon the recent research findings and theoretical explanations of many authors without referencing them (as is acceptable in a popular scientific book). He acknowledges the contributions and assistance of his associates earlier, in the Preface.

Part 2 deals with the controversial subject of Man-Caribou relationships. Here Calef shows that, in perceiving the modern threats to the survival of the Caribou herds, he has been more influenced by his latter years as a Caribou biologist than the earlier ones as a traditional environmentalist. He commences by reviewing the prehistoric and historic relationships between the primitive hunter and his Caribou prey. He describes the important differences that formerly existed between human and Wolf predation. He senses that these ancient relationships have been broken by the modern use of firearms, aircraft and snowmobiles. He concludes that unless Caribou hunting is controlled, the Caribou will be destroyed. As an example, he cites the Western Arctic herd of Alaska and foresees the same tragic effect of overhunting on the Caribou.

Calef pays little attention to the threat of industrial development, except harassment by aircraft. He supports the planning process for the location of roads and transportation corridors. He states that the most destructive harassment is by hunters on snowmobiles.

The author concludes with a selected bibliography of the important Caribou literature and a brief review of the contributions of many naturalists and scientists to our knowledge of Caribou.

The Mismeasure of Man


Scientific hypotheses which originate in the prior beliefs of scientists are often treated as corroborated theory despite major contradictions with observed data. They can have profound social consequences when they form the basis of public policy. Gould treats a field prone to such bias, the study of intellectual differences among groups of people. He reviews the history of "biological determinism": the idea that much human variation is along a common scale ranging from more apelike, less intelligent individuals to those less apelike and more intelligent, and that position on this scale is heritable and varies with race, class, and sex.

Racially unified civilizations — Egyptians, Greeks, Chinese — have always considered themselves superior. European imperialism, colonial slavery, zoological classification, and quantitative science inevitably led to attempts to classify peoples on the "Great Chain of God > angels > man > animals. In immature evolutionary theory this ranking was perpetuated by projecting geographic variation onto an inferred temporal sequence of increasing humanness, assuming that this ranking measured individual or group worth. This is the kind of anti-Darwinian linear arrangement of lineages that Gould delights in exposing.

The story begins with Agassiz' attempts to fend off the theory of organic evolution with a creationist scenario indistinguishable from it. He supposed that even
interbreeding taxa were created in situ in their present numbers, geographically and taxonomically close to a pre-existing form. If the races of Painted Turtles are separately created species, then so are human races. Gould's discovery of Agassiz' violent reversion towards Negroes suggests that history ran the other way, and that Agassiz clung to creationism to avoid kinship with non-European people.

Starting here, the main body of the book documents inadvertent error (and some fraud) by white male scientists in defense of hypotheses of white and male superiority: biased measurement by Samuel George Morton and Robert Bennett Bean; persistent application of inappropriate measures of intellect by Cesare Lombroso, H.H. Goddard, and L.M. Terman; tortuous interpretations of adverse data by Paul Broca, R.M. Yerkes, and C.C. Brigham; and the over-interpretation of multivariate statistical analyses by Charles Spearman, Cyril Burt, and L.L. Thurstone.

The tale, in a word, of the perils which any scientist faces in forming and testing hypotheses, told to the beat of the usual fate of unitary explanations of complex phenomena: "Lombroso's retreat . . . Goddard recants . . . Terman recants . . . Spearman recants . . . Spearman finally recanted."

There is no longer any objective support for biological determinism among groups. Neither morphology nor behaviour can be linearly ranked. The electrophoretic study of isozymes has set the age of human divergence at a few tens of thousands of years, and shown that 85% of human allelic variation is within populations.

Gould argues that since among-group biological determinism is wrong, then so is both within-group determinism and the sociobiological hypothesis that much variation in human character traits may be heritable. But if a paucity of genetic variation between populations argues against determinism, then the great allelic variation within populations must in some sense argue for it. Heritable variation in human behaviour, like that in the stature of plants, is hard to measure and much affected by the environment. It may well exist, but we cannot study it directly, because we cannot put people in transplant gardens to see how they grow. The repressive use which has been made of past results argues against indirect studies. Gould also calls for the suppression of "human sociobiology" because some of its early hypotheses are ad hoc and adaptationalist. But sociobiology is a discipline, not a theory, and does not stand or fall with the genetics of, e.g., homosexuality.

Except for these lapses into his own biases, Gould is thorough, lucid, and amusing. He re-analyses old data to find biased errors in calculations, has given World War I U.S. Army intelligence tests to students at Harvard, and expounds factor analysis simply yet clearly.

This book is important to scientists and nonscientists both as history and as a catalogue of scientific pitfalls.

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Wild Mammals of Western Canada

By Arthur Savage and Candace Savage. 1981. Western Producer Prairie Books, Saskatoon, Saskatchewan. 209 pp., illus. $34.95.

This book should be used by amateur naturalists seeking a well-researched introduction to geographic ranges, behaviour, and other features of some of the mammals of Western Canada. Nine orders are introduced, each with representative species. Each species is discussed over 2-3 pages of mostly correct text accompanied by photographs and range maps. The 100 full-colour photographs are some of the most detailed natural depictions of species seen in any guide of this stature. Also appearing is a mostly correct binomial listing of most mammalian species of Western Canada, a well researched 23 page listing of publications dealing with specific species and/or groups of mammals, and a good index.

The manuscript had been read in part by seven scientific advisors. However, I found on average one misleading statement on every other page of text. Many of these are caused because the authors try to make generalizations from seldom observed behaviour of species. I found this to be the book's only real problem. Plenty of factual information exists, so I recommend the book for general readership by beginning naturalists interested in mammals.

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The Pronghorn Antelope in Alberta


This technical monograph contains much of the important early research and management data on pronghorns in Alberta. The author began his research in 1952 and combines many of his relevant findings in one well-documented, illustrated publication. Although based almost entirely on data from Alberta, in my view the basic findings should also be generally representative for pronghorns in Saskatchewan. Based on a search of relevant documents and government files, the author begins by presenting information on the distribution, numbers, legislation, and harvest of pronghorns in Alberta from early 1900's to the mid 1970's; the early historical information represents a particularly valuable contribution to the literature.

The author devotes a major portion of this publication to distinct aspects of the biology of the pronghorn. Range characteristics, including vegetative canopy coverage and forage yield, for two study areas are presented and compared with pronghorn food habits in the same areas. In one chapter the author details the morphological characteristics of neonatal, immature and adult animals; presentation of data on the cranial and mandibular characteristics is particularly well done.

Reproductive biology of the pronghorn is examined in two chapters. The size and cellular composition of testes and stages of the spermatogenic cycle are detailed. Information on the eight stages of the spermatogenic cycle suffers from lack of clarity and interpretation of photomicrographs and limited seasonal sample size. The chapter on female reproductive biology provides useful information on the morphology and composition of the ovary in relation to time of year and ages of the females, fetal development and growth, and in-utero fetal rates. Although it is no longer new information, this section provides a useful documentation and review of the remarkable reproductive characteristics of this species whereby there is a high ovulation and conception rate combined with extensive early intra-uterine mortality.

The size, composition and movement of pronghorn herds during the period 1952-65 are documented. Information on the movements of neonates and adults can only be viewed as preliminary data because of limited relocation information on marked animals; this research was conducted prior to the use of new routine telemetric procedures. A relatively brief, somewhat anecdotal, but useful discussion on mortality factors observed during the course of field research is also included.

This monograph is most significant when considered in proper context. The author pioneered much of the original research on pronghorns in Canada and portions of his work still stand as the best information available. This publication is based on field research conducted almost entirely before 1966 and, to some extent, the contents are dated. Similarly, more than 80% of the references deal with publications prior to 1970 and as a consequence, this monograph has limitations in providing a comprehensive review of recent research on pronghorns.

Individuals who not only enjoy natural history but have an interest in the basic biology and management of this uniquely North American animal will enjoy this publication. Serious scholars concerned with pronghorns should regard this work as an important prerequisite to further research.

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Wildlife Management Techniques Manual


This is still the most comprehensive guide in the world for studying wild birds and mammals. This fourth edition is an updated expansion of the decade-old 3rd edition. There are now 32 chapters, 8 appendices, and 85 pages of literature citations. New or expanded subjects appearing in this edition are: techniques for studying physiology of reproduction, body condition, nutrition, ecological diversity, remote sensing, sustained yield, models, and administrative policy. Subject headings are: Basic Research Techniques, Working with Wild Animals, Studying Wildlife Populations, Studying the Environment, Management, Administration and Policy, and Specialized Techniques.

The sections regarding wildlife literature searching and cataloguing are intensively complete. There is now much more on determining the reproductive condition and litter size of mammals, a subject noticeably missing from the third edition. The sections on estimating numbers, habitat improvement, and tele-
The Audubon Society Handbook for Birders


When I first learned in March 1979 that another book was being planned on the topic of bird watching, my initial reaction was, “Oh no, not another birding handbook.” It seems that as the numbers of Americans interested in birds increased during the 1970’s, authors and publishers seemed compelled to tell these “new birders” how to enjoy their new activity. The majority of these recent efforts have been of dubious value and do not compare with Hickey’s early classical work A Guide to Bird Watching published in 1943. I’m happy to report that I believe Kress’ product is the best birding handbook on the market today. Undoubtedly, having the book’s title associated with the Audubon Society also will aid sales.

The book is subtitled “A Guide to Locating, Observing, Identifying, Recording, Photographing and Studying Birds.” The first four chapters or approximately one-third of the book are devoted to field trip techniques; selecting binoculars, telescopes, cameras, and telephoto lenses; locating, identifying, and observing birds and noting their behavior; and photographing and tape-recording techniques. The chapter on binoculars and telescopes is especially well written and accurate. One problem with reviewing writings aimed at the beginner is that I suspect most reviewers, including myself, have passed through this stage years ago. One finds it difficult to assess what appeals to the beginning birder. What Kress has selected as topics in these opening chapters is presented in a clear and concise manner. I am glad he avoided the topic of “Attracting Birds” as there have been a number of books in recent years addressing this subject. The book contains 169 titled black-and-white photographs or line drawings. Many of the line drawings by Anne Senechal Faust should have been omitted.

Kress should be commended for his effort in assembling the information contained in the last four chapters and the three appendices (sources of birding supplies, books, and publications). Chapters 5 and 6 cover a comprehensive listing of educational programs (bird courses, museum programs, birding tours, research stations) and research programs welcoming amateurs. The “professional” ornithologist in North America is beginning to take a renewed interest in the amateur birder and to explore how the professional and amateur can join ranks to enhance ornithological research. The beginning birder should welcome this listing of professionally organized programs in which he may participate and broaden his knowledge. However, a caution to the user of this listing: information about these research programs (and on periodicals and organizations, the subject of Chapter 7) quickly becomes outdated. Unsuccessful attempts were made to contact a couple of unfamiliar research programs (Operation BIRD and New York Bight Pelagic Bird Study Project). I suspect they never actually were started or were ephemeral in nature. The list of periodicals in Chapter 7 does contain a few omissions (regional bird-banding journals) and incorrect categorizations (Western Birds with state journals). In the last chapter on bird books, checklists, and recordings, I quibble with his treatment of other recent bird books with Audubon Society included in their title. I could
never recommend the Audubon Society field guides to a beginning birder, and his relegation of Terres' fantastic The Audubon Society Encyclopedia of North America Birds to the "Other Choices" section is a shame.

I recommend the Handbook for those with a beginning interest in birds for it should help the novice bird watcher become involved with activities beyond simply identification and listing.

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Snakes — A Natural History


This book is a revision of The Natural History of Snakes (1965) by H. W. Parker, only slightly enlarged by A. G. C. Grandison (108 vs 95 pages). Both authors had long and distinguished careers in herpetology with the British Museum. An opening section deals with "The Origin and orders of living reptiles" (10 pp) followed by "Lizards and Snakes" (17pp), "The senses of snakes" (3pp), "Snakes and their environments" (6pp), "Nutrition" (7pp), and "Reproduction, growth and development" (7pp). Five sections deal with snakes group by group: "Primitive and burrowing snakes" — families Leptotyphlopidae, Typhlopidae, Anomalepididae, Aniliidae, Uropeltidae, Xenopeltidae (7pp), "Boas, pythons and wart snakes" — families Boidae and Acrorhoriidae (6pp) "Colubrid Snakes" — family Colubridae (10pp), "Cobras and sea snakes" — family Elapidae (7pp), "Vipers" — family Viperidae (5 pp.). A two-page glossary of technical terms and one page of selected reading conclude the text.

Simple and informative charts are strategically placed through the text; geological time-scale, comparison of selected characters of recent air-breathing vertebrates (classes) and of living reptiles (orders), differences between the suborders of the Squamata (amphibiaenians, lizards and snakes), classification of snakes, and comparison of some characteristics of the eleven families recognized. Similarly distributed are detailed figures of the skulls of representative reptiles and of the major families of snakes, and a ventral view of snake anatomy. There are eight black-and-white photographs and 32 in colour of selected snakes.

Perhaps the only aspect that the uninitiated should beware of in this treatment is that snake classification is still an evolving art. The division of the large family Colubridae (which contains 67 per cent of all recognized species of snakes) into sub-families, or the inclusion of the sea snakes with the Elapidae rather than as one or two additional distinct families, is not nearly as settled as this text might lead one to assume.

Overall, this is an authoritative and concise introduction to world snakes suitable for both those casually or seriously interested in an overview of these fascinating but often maligned animals.

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A Bibliography of Pacific Northwest Herpetology


Every naturalist and biologist, specialist to generalist, hobbist to professional, is aware that the amounts and sources of literature are proliferating at an incredible rate in every field. Those with access to large institutions can look to computer memory and retrieval to deal with the problem. Elsewhere, individuals may be forced to become more narrowly specialized or superficially generalized to have any hope of being both up-to-date and historically well-grounded. Whatever one's facilities or choice, the latest effort by the British Columbia Provincial Museum is a welcome aid.

The core of this publication is a numerical listing of 1156 entries. The case for its need is best illustrated by a count for the 1970-80 period alone: 508 — over 43 per cent of the total. Of the latter, 56 are from 1980, the last year included. It is perhaps a sign of our times that the authors excuse the haphazard sequence of this list with the remark that they did not have computer facilities available.

The book's comprehensiveness is impressive. I had to scrape my files for even 14 titles which could con-
conceivably have been added; the best of this obscure lot was J. F. Whiteaves (1887). On some Marine Invertebrates dredged or otherwise collected by G. M. Dawson, in 1885, in the northern part of the Strait of Georgia, in Discovery Passage, Johnstone Strait and Queen Charlotte and Quatsino Sounds, British Columbia; with a Supplementary List of a few land and fresh water shells, fishes, birds, etc., from the same region. Proceedings and Transactions of the Royal Society of Canada for the year 1866. Volume IV, Section IV, Article IX, pp. 111-137. The “etc.” in Whiteaves’ publication includes localities for both newts and garter snakes. Other examples are four articles by J. S. Bleakney on Canadian amphibians, lizards, snakes and turtles buried in the Encyclopedia of Canada (1957-58), and (with the exception of my 1980 Checklist) the Canadian Amphibian and Reptile Conservation Society “Bulletin”, which has had only a few items relevant to British Columbia in its 20 years of existence.

A grey area that is included is the extensive citation of the growing “shadow literature” of Canadian biology: the unpublished reports submitted to federal and provincial governments. This material is unreviewed and is not literature in the scientific sense. However, because its existence is often not generally known and it does contain useful (though unevaluated and sometimes unreliable) information, the inclusion is defensible; though it might better have been indexed separately. Its availability is assured, as copies of all references are on file with the Vertebrate Zoology Section of the British Columbia Provincial Museum. Some of the shadow entries are a surprise — among them, for example, is a draft manuscript, planned for eventual publication but still incomplete, by Fred Schueler, Don Rivard and myself. A preliminary copy had been sent by one of us to the British Columbia Museum for their information in connection with another project and was duly absorbed here as an “unpublished report” of our museum.

Preceding the numerical list is a section giving the majority of the 428 sources consulted, including 148 journals, and the extent to which they were searched (usually from inception to 1980).

A checklist gives the 51 species recorded from the coverage area: Alaska, Yukon, British Columbia and Washington. Thirty-six of these species occur in British Columbia.

Three indices, which allow access to the unstructured citation section, give species, geographical areas, and authors, all by number of entry.

One flaw in the species index is that only currently valid names are given. The reference itself may use an older and different name, so some knowledge of synonyms is useful and occasionally essential. Some older uses have completely escaped citation under species. The historically important remarks of John Keast Lord on turtle distribution in the Pacific Northwest in the mid-1800’s, which he gave under Clemmys marmorata but which are now recognized to apply to Chrysemys picta belli, appear under neither species.

The geographical index has a feature of enormous benefit to regional naturalists and consultants: British Columbia is indexed in five general regions and in 61 map grid squares (1° latitude by 2° longitude) of a possible 89; Washington is indexed in three general regions and its 38 counties. There are also indices to the “General Literature” (covering a large portion of a species range) and the “Additional Literature” (studies done elsewhere but important to understanding a species that occurs in the region).

The author index includes 805 individual authors, of which five are institutions or committees. The ubiquitous “anonymous” is credited with 17 entries. The book is dedicated to the late G. Clifford Carl (British Columbia) and to James R. Slater (Washington). Their contributions dominate all others with 29 and 27 entries respectively. Only two of the bibliography authors have citations: Campbell with 16 and Gregory with nine.

One very attractive feature of the book is the scattering of artwork throughout. Keith Taylor has produced 44 amphibian and reptile drawings and four scenes and Brigitta Van Der Raay 19 and three. Only a few of these appear too dark or unnatural. Most nonherpetologists, and some herpetologists, may be irritated by the complete omission of identifications. Elizabeth M. Taylor drafted the four maps. Renie Knowlton and Clover Tobin produced the cover.

This contribution is only part of the British Columbia Museum’s impressive and commendable vertebrate program. Yet to come in herpetology are two new guides — Reptiles (by Gregory and Campbell) and Amphibians (by David M. Green and Campbell) — listed in this bibliography as “unpublished manuscripts”. I am assured this does not rule out early future publication. Also in preparation is a comprehensive atlas of distribution. Similar projects are completed or underway for birds and for mammals.

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The stimulus for this publication was the retirement in 1981 of Professor Bengt Pettersson from the Chair of Ecological Botany at Umeå University. The volume is dedicated to Professor Pettersson and its main aim is to provide an overall view of the plant ecology research that is being carried out at Umeå University. The volume certainly achieves that objective. Fourteen of the papers have authors associated with the Department of Ecological Botany while there is one paper each from the Archaeology Department, Umeå University; the Department of Forest Site Research, Swedish University of Agricultural Sciences, Umeå; the Swedish Museum of Natural History, Stockholm; and the Department of Botany, University of Helsinki, Helsinki, Finland.

The studies reported are descriptive field studies rather than experimental studies. Many hypotheses have been raised but many remain to be tested. The 18 papers, which average less than 10 pages each, can be grouped into the fields of river communities (5 papers), paleoecology (4 papers) and terrestrial communities (9 papers).

Most of the river community studies are related to hydroelectric development on these North Sweden rivers. Sten Backlund has investigated the changes in diatom flora and water quality caused by the diversion of water from old river beds into a hydroelectric power station. Gunno Erixon reported on the relation of aquatic macrophytes to environmental factors in a North Swedish river. Gunnar Grellsson reported on the erosion and vegetation response along a river that was dammed for hydroelectric power production. Christer Nilsson has also studied the riparian vegetation on both unregulated and regulated rivers in North Sweden. Krister Jakobsson has studied the impact of the European beaver on the tree and shrub vegetation following colonization of the area.

The four paleoecological studies reported in this volume all support the hypothesis that the North Swedish landscapes are far from pristine. Widespread human activity has taken place since the Early Iron Age (0-200 A.D.). Roger Engelmark has interpreted Early Iron Age activity from carbonized fruits and seeds in soil samples collected from hearths and post-holes of house complexes in North Sweden. Philip A. Tallantire described sub-fossil fruits, seeds and leaves in a late glacial pool in northeast Scotland. The results suggest a similar present-day environment in the relatively oceanic or sub-oceanic parts of northern Fennoscandia. Ingemar Renberg and Ulf Segerström reviewed the usefulness to paleohistory of the varved lake sediments that are found in many areas of North Sweden. Kimmo Tolonen studied the sub-fossil leaf spines of *Stratiotes aloides* in an attempt to determine post-glacial spread of plants.

The studies of terrestrial ecosystems varied from vegetation descriptions through to the study of vegetation in relationship to environmental factors. Carl Gustav Thögersen described the establishment, the present characteristics, and the future plans of the northern-most arboretum (Arboretum Norr) in Sweden. Åke Strid recorded a polyposa as a new range extension into Fennoscandia. Per-Anders Esseen described the growth of epiphytic macrolichens by tree height on a range of tree hosts in spruce forests while Lars Soderström described the distribution of bryophytes in spruce forests on hill slopes. Leif Kullman reviewed the present state of knowledge on the adaptations to environmental factors (particularly snow) in the Scandinavian subalpine birch forest belt. Jan Elveland described a ten-year change in vegetation in seashore fens while Lars Ericson described how shore vegetation on the Gulf of Bothnia is affected by environmental factors, with particular reference to sea level. Finally, Ola Engemark described the influence of climate, fire and humans on forest vegetation in Muddus National Park while Lars Westman provided more detailed studies on soil activity on burned and unburned areas near Umeå.

There are a number of strong points about this volume. The papers are very readable and well illustrated. For those who read only English, a good deal of information is made available in this volume for the first time, but since the range of subjects is extremely wide, I would assume that few readers would read the volume cover-to-cover. The volume will be useful to anyone who wishes to work on, or learn more about, Fennoscandia boreal plant ecology. I think the volume is a useful addition to the recent volumes on the subject by Tamm (1975), Pruitt (1978) and Larsen (1980).

**Literature Cited**


ROSS W. WEIN

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Pocket Flora of the Redwood Forest


The Redwood forest once covered some two million acres of the west slope of the Coast Range of mountains from southern Oregon south to mid California. Now only about one eighth of the virgin trees remain, and these stately trees form cathedral-like forests.

The author presents keys, descriptions and illustrations for 212 of the most frequently seen plants in the Redwood forest, both native and exotic. A half page is devoted to most species, consisting of line drawings of habit, flowers and fruit, together with a quite detailed descriptive paragraph, with flowering and fruiting times, followed by an indication of habitat and general range.

The sequence followed is alphabetical by family, genus, and species. Thus it may be rather disconcerting to some to find the genus Trillium segregated in the family Trilliaciae rather than in the Liliaceae beside such familiar genera as Lilium and Smilacina. Perhaps even more puzzling is the separation of the various families of ferns and fern allies, and the similar separation of such related families as the Taxaceae, Cupressaceae, Pinaceae, and Taxodiaceae.

There is a useful short introduction which tells some of the Redwood story. It also provides instructions on how to use the keys, several pages of illustrations of flower parts, kinds of fruits, leaves and leaf arrangements, an illustrated glossary, a species list, and an index.

This book will certainly serve the purpose of introducing visitors to the Redwood forests to other plant species found growing there. It is important however, to remember that these are only the more commonly found species and not the more difficult to determine grasses (only one described) and sedges (some described), or other easily overlooked species.

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Genera of the Western Plants


Every naturalist working west of the Ontario-Manitoba border who is interested in the flora of the area will want to have a copy of this compact volume. It offers well-designed non-technical keys to the families and genera of the vascular plants known to occur naturally or to be commonly cultivated out-of-doors west of the 98th meridian and north of Mexico.

Professor Batson has followed the same format as in his most valued earlier work, The Genera of the Eastern Plant, the third edition of which is available through Wiley.

Vascular Plants of Glacier National Park, British Columbia, Canada


This pamphlet presents and discusses the authors' botanical observations and collections in Glacier National Park, British Columbia, together with the work of previous collectors. It commences with a brief history of the park and a review of past botanical activity. It discusses the climate, geology, and topography in relation to the flora and describes the major plant communities of the park, the Interior Subalpine Forest, the Northern Columbia Forest, and the Alpine Zone. The principal trees, shrubs, ferns and herbs associated with each area are discussed.

In addition to incorporating the work of previous collectors the authors discuss their own observations in several diverse but accessible regions of the park. They note and discuss particularly the association of
25 calciphilic species with localities where there are limestone outcrops or calcium rich springs (Fidelity Mountain, Cougar Valley, and the Beaver River Fen). The bedrock in most of the park gives rise to acidic subsoils which are said to prevent establishment of these species.

The last part of the work, and its kernel, is a checklist of vascular plants for the park, showing occurrence of each species for five generalized areas, each representing a different habitat type. Altogether, about 340 species are listed. The list is keyed to indicate which reports are based on sightings and which on collections. A list of dates and locations of collections is also included. I know of no other easily available checklist for the park. Park interpretive staff maintain an herbarium in Revelstoke and keep records of reported sightings.

The rather limited flora of the park presents an opportunity for botanists who are not familiar with the flora of the region. All common species which occur in the park are listed, so using the checklist serves to confirm identifications.

The checklist does not list every species occurring in each of the five representative areas. There are unusual species which occur in the park and are not listed. The authors remark upon how easily they added several new species to the list by visiting the alpine areas near the NRC station on Fidelity Mountain. In the course of a day's trip to the same area I observed two species (Pinus albicaulis and Phylodoce glanduliflora) which the authors do not list for that area. Both occur in greater abundance in, and were listed for, other areas of the park. I also observed Zygadenus elegans, one of the 25 calciphiles, at the site of Glacier House, an area where it should not occur according to the discussion of soil types. A visit to the Beaver River Fen yielded Spiranthus romanziiflorma, a species not included in the checklist.

These observations do not detract from the principal value of the publication: the ease with which it permits a newcomer to become acquainted with the flora of the park. Recommended references to accompany it would be Hitchcock's Flora and Hosie's Native Trees of Canada. There is also an attractive picture flora for Mount Revelstoke, written by Soper and Szczawinski.

The presentation and preparation of this publication are for the most part very good. The text is photo-offset from typewritten copy. It is free from unsightly failures of the production process, as well as from any obvious errors. The photographs are poorly reproduced, however. The nomenclature follows that of Taylor and McBride's Vascular Plants of British Columbia, A Descriptive Resource Inventory, an inconvenience since it differs from that of the regional floras as well as from that of Scogan's The Flora of Canada. Taylor's nomenclature is also used in the park records in Revelstoke.

I do not hesitate to recommend this publication as an essential inclusion in the library and among the field references of anyone interested in the flora of Glacier National Park.

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ENVIRONMENT

Threatened and Endangered Species and Habitats in British Columbia and the Yukon


Appeals for co-operation between naturalists/conservation groups and government agencies entrusted with preservation of the environment are common. Positive action does not often result. This volume exemplifies the usefulness of co-operation. The book contains papers presented at a symposium co-sponsored by the Federation of British Columbia Naturalists, the Institute of Environmental Studies at Douglas College, and the Fish and Wildlife Branch of the British Columbia Ministry of the Environment.

It begins with a brief introduction by Stace-Smith, followed by the texts of addresses by the Hon. Stephen Rogers, B.C. Minister of the Environment, and by Ian McTaggart Cowan. The bulk of the text consists of the papers presented, arranged in the six symposium sessions. While this organization will be meaningful to the participants, I would have preferred the published papers arranged by topic group. For example, Cowan's address fits well with the "other consideration" topics in session V; Wilma Robinson's account of the Greater Sandhill Crane fits more logically with other papers on particular species than with reviews of broad taxonomic groups, and the recommendations listed in session VI might better have been
placed at the end of each session. This minor fault is, however, readily offset by the inclusion of a complete table of contents.

In his opening address, Rogers points out that this was the first public forum in British Columbia on threatened species and habitats, and emphasizes concern over human-accelerated declines rather than natural extinctions. Cowan’s review on endangerment serves as an excellent précis on this topic at the World level. In addition to outlining some of the known causes of endangerment, Cowan discusses some of the problems in determining cause(s) in specific cases. Many readers will be shocked to learn that North America has the worst record of all continents in destruction of native animals, a record which Cowan attributes to the concept of local autonomy in resource management, making assertive action to save a species or habitat difficult at best.

Session I, entitled “Habitat Concerns,” contains three general reviews and three more specific accounts. Bristol Foster reviews the history and progress of the Ecological Reserves Program in British Columbia, and Jim Pojar presents reviews of both threatened forest systems and threatened habitats of rare vascular plants. These three general reviews are followed by a detailed pessimistic account of the Osoyoos-Arid Biotic Area by G. G. E. Scudder, and essays on winter habitat for ungulates by G. Gary Runka and on coastal habitats by R. Hunter.

Sessions II and III review the status of endangered species in British Columbia. An important paper by W. T. Munro and D. J. Low outlines plans by the British Columbia Government for the designation (and thereby protection) of threatened and endangered species in the province. An invitation by the government to respond to drafts of this plan was the original stimulus for the conference. In general, other speakers found the plan agreeable with minor faults. The intention of excluding peripheral species from possible designation as threatened or endangered, however, stimulated considerable controversy. Reviews of major taxonomic groups are presented for plants (R. L. Taylor), freshwater fish (J. D. McPhail), amphibia (D. H. MacIntyre and R. V. Palermo), reptiles (S. A. Orchard), and birds (W. C. Weber). All are excellent overviews of the groups concerned. Missing are reviews on any invertebrate groups, marine fish, and mammals. In addition to these overview papers, the species sessions for British Columbia contain specific status reviews on White Pelican (D. Dunbar et al.), Peregrine Falcon (K. Hodson), Greater Sandhill Crane (W. Robinson), Burrowing Owl (R. Howie), Spotted Owl (R. Howie), Vancouver Island Marmot (M. D. Miller), and Sea Otter (A. C. M. Farr and F. L. Bunnell).

In Session IV, attention is shifted to the Yukon, where the state of knowledge is less advanced, but rapidly advancing. The preliminary assessment of the current status of all birds and mammals in the territory by G. F. Hartman and R. Hayes should stimulate further work. D. Mossop presents a brief overview of vulnerable bird species, followed by a more detailed account of a Peregrine Falcon recovery project. Additional papers concern Gyrfalcons (N. L. Barichello and F. L. Bunnell), Grizzly Bears (Barney Smith), and the much-discussed Porcupine Caribou herd (N. R. LaBlond and W. E. Rees).

The papers in session V, “other considerations,” are more general. In addition to Joslin’s discussion on peripheral species, two papers by F. L. Bunnell and R. G. Williams are well worth reading. These concern the importance of subspecies to ecosystem diversity and “threatened species and habitats — why bother?” Both provide useful background material for use in any public forum. The fifth session ends with a brief look by V. C. Brink at the role of non-government organizations, and a summary by R. D. Muir of the work and progress of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). The sixth and concluding session “Where to next?” is a three-page list of recommendations arising from issues raised in the previous sessions.

The cover on my review copy had begun to disintegrate in the mail. There are far too many typographical errors scattered through the book. The table on Yukon birds is especially littered with minor errors. A new species, the Double-breasted Cormorant, is invented on p. 191, and “extinction” is used where extirpation is intended on p. 68. These minor faults should not deter any serious naturalist in British Columbia or the Yukon from purchasing this valuable document. Although the papers range from essays to progress reports to thorough reviews, all provide important material on threatened habitats and species in British Columbia and the Yukon.

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Watershed Red: The Life of the Dunk River, Prince Edward Island


Good natural history writing embodies the fruits of patient observation, the insights of science, and the skill of the word craftsman. These elements, brought together by Kathy Martin in Watershed Red, have been packaged with pleasing illustrations and attractive layout to form a fine example of the natural history genre.

This book deals with the natural life of a small Prince Edward Island watershed, whose transition from green to red each autumn is due not so much to the changing colours of the maples as to the overturning of the red soil by fall ploughing. After a geographical and historical introduction, the book becomes a series of essays on the major kinds of wild plants and animals of the area. The watershed is really a peg to hang these accounts on, rather than a theme. Most of the book's contents easily apply across Prince Edward Island, and indeed to much of eastern Canada.

The author of Watershed Red is a biologist by training, and her professional instincts are reflected in the preponderance of fact over feeling in the book. Nevertheless, the style is light and clean, and only occasionally encumbered by formal phrasing and unnecessary qualifiers. An example of the latter fault is the declaration that the oyster is "largely" unaware of its key position in the estuarine community, from which follows the unlikely inference that oysters have sufficient grasp of the principles of community ecology to be at least dimly aware of their importance.

The text is amply accompanied by clean and attractive black-and-white sketches by Connie Pound-Gaudet. The artist's renditions are slightly stylized, so she may be forgiven for the occasional lapse from accuracy, such as furnishing her Osprey's wings with an excessive, and unequal, number of primaries.

Watershed Red was written for the general public, and will serve a useful end if it helps awaken interest in natural history among lay Prince Edward Islanders. But because of the widespread applicability of its contents and the breadth of its scope, the book will provide profitable reading for other eastern Canadian naturalists, professional as well as amateur.

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Advances in Environmental Science and Engineering


This book is a collection of 10 papers, on a variety of subjects, that attempt to present recent research in the general field of environmental science (environmental management, planning, or engineering if you prefer). The subjects of the 10 papers are, in order: the 1977 amendments to the United States’ Clean Water Act; integration of biological and chemical processes in wastewater treatment; modeling of warm water effluent from large industrial plants to natural bodies of water; the acid production of vegetation communities compared to atmospheric fallout; the modelling of atmospheric activity in regards to SO2 (sulphur dioxide), NO2 (nitrogen dioxide), CH4 (methane), CO (carbon monoxide), and O3 (ozone) from anthropogenic sources (four papers); the influence of pollution on urban climates; and the design of electrostatic precipitators for particulate control.

The prediction and mitigation of future environmental impact as well as the amelioration of ongoing impact is dependent upon valid scientific models of environmental activity. This understanding of processes is developed by a long process of experimentation, field testing, and knowledge sharing. This book is one of a series that gives state-of-the-art reports on various aspects of environmental management. The editors state in the preface that:

"Progress in environmental science may be regarded as occurring on two fronts. The first is increasing depth of knowledge within a specific field. The second is concerned with a greater understanding of interactions among a number of related disciplines.".

The authors appear to have been consciously aware of the need for making their papers understandable to workers in other specialities. The majority of the papers succeed at this effort, but the readers nevertheless must have a good background in advanced chemistry and mathematics to be able to comprehend the papers.

Before any issue can be defined as an environmental problem, there is a period of time where limits on thresholds are defined and generally accepted. Such a process is now underway in atmospheric science in regards to the issue of acid rain specifically, and pollution generally. Seven of the papers discuss in detail the
existing knowledge in various aspects of atmospheric pollution. It is obvious that modelling of the world’s atmospheric machine is an immense job, but I was impressed with the level of understanding now extant in various fields, such as SO₂ and NO₃ atmospheric activity. Nevertheless, trying to trace atmospheric elements around the world is much like attempting to push a chain down the street. The numerous links in the complex, atmospheric machine make prediction difficult, but within the realm of possibility.

One of the most interesting papers discusses the influence of vegetation on the acidity of fresh water. I. T. Rosengvist of the University of Oslo points out that vegetation is a major acid generator and probably contributes more than does acid precipitation. Over geological time the steady exposure of new unweathered rock material to the soil-forming processes neutralizes the acid generated by biological excreta. I have often wondered about the impact of forest tree removal on the fertility of forest soils. This author adds an interesting component to this issue when he states that:

"Modern logging methods will, on average, more than double the extraction of K⁺, Na⁺, Ca²⁺ and Mg²⁺, thus adding considerably to natural acidification".

J. K. Bewtra of the University of Windsor gives a good treatise on the design and operation of wastewater treatment. He emphasizes that both biological and physical-chemical processes should be considered in facility design. His paper would be a useful introduction to the subject for process engineers or applied chemists.

K. Muraoka from the National Institute for Environmental Studies for Japan and K. Nakatsuji from Osaka University discuss the modeling of the mixing of warm water effluent from industrial plants with natural waters. They point out that a 1000-MW output of a power plant requires 35 to 40 m³/s of cooling water for a fossil fuel power plant and 60 to 65 m³/s for an atomic energy plant. This huge volume of water has relevance to me personally because of a tour I once took of the construction site at the Bruce Nuclear Development on Lake Huron. I was shown the construction site of the intake pipe that was to bring cooling water in from the lake. This pipe was a huge hole heading into bedrock that appeared to be well over 100 mm diameter. I stood on its edge looking down into this round cavern heading down into the dark and attempted to grasp the volumes of water that would ultimately come through it. The authors end their paper with the statement that further research "will soon yield valuable insights into the solution of real problems". In other words the existing state of knowledge in this field does not allow accurate prediction of the mixing of warm water effluents with the receiving body. This is not an optimistic sign when one realizes the potential impact on cold water fisheries that could result from the input of warm water effluents. For example, many biologists are still concerned about the long-term impact of the Nanticoke Power Plant on Long Point Bay and its biota.

The papers have a strange mixture of metric and imperial (American version) measurement units. In one case both types were found in the same sentence. I find this to be inappropriate, but even a journal such as Scientific American allows it to take place.

The papers are written for a general scientific audience, but are still full of detail. While working my way through them I was reminded of the comments of a senior Bay Street lawyer who works in the general field of environmental management. As the scientific discussions become technical he likes to interject. "What is the bottom line, gentlemen?"

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Structure and Function of Northern Coniferous Forests: An Ecosystem Study

Edited by T. Persson. 1980. Ecological Bulletins No. 32. Swedish Natural Science Research Council (NFR), Stockholm. 609 pp., illus. 290SK.

The 1960's found increased public awareness in ecological matters, which paralleled an increased scientific capability in systems analysis research and quantitative ecology. At the same time, the exploitation of Sweden's conifer forests was having untold ecological consequences. In response to this, and to increased public pressure, the Swedish National Science Research Council commenced the Swedish Coniferous Forest Project (SWECON), a longterm "systems" study on the effects of logging conifer forests. The program would fulfill the two functions of developing the methodology to enable the studies to progress while providing basic forest ecology information. Mathematical modeling was used to aid understanding of experiments and simulated processes.

The study was broken down into six components:
1. Energy exchange and microclimate;
2. Water turnover;
3. Dynamics of above-ground plant biomass;
4. Dynamics of assimilated and NPK in plant biomass;
5. Dynamics of below-ground plant biomass;

This book presents a glimpse of the ongoing study, beginning with the site descriptions of the two research areas and data gathering and simulation techniques. The main portion of the book, 37 papers, presents detailed information in a discussion type of approach, where problems are presented along with results. The text provides details and glimpses of the "system", but does not try to synthesize the results. The book ends with an honest discussion of the project's progress, the different phases of development of research, and the researchers' paradigm as they gained experience and insight into the study problem and methodology.

Naturalists will rarely need such a text. Both scientific and management findings will be of interest to scientists in forest (especially of northern conifer forest) ecology and systems analysis.

The book is in four parts: Part 1 describes the All figures and tables are clear and easily read. The editors must receive praise for their blend of information and data with discussion.

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Ecological Land Survey Guidelines for Environmental Impact Analysis


The federal government established an environmental assessment policy in 1973. It is meant "to ensure that the environmental effects of federal projects, programs and activities are assessed early in their planning, before any commitments or irrevocable decisions are made". Since 1973, the responsible agencies have been slowly building up a body of experience and knowledge on carrying out such assessments. This publication is essentially a guideline that describes an outline for undertaking an ecological land survey, i.e. an inventory of the terrain, soils, wildlife, vegetation, climate and water of an area. Such data can then be used to assess the potential impact of a proposed development.

The book comes in four parts: Part 1 describes the federal assessment process; Part 2 outlines the planning; Part 3 the undertaking of a survey; and Part 4 discusses the use of the data.

The process is obviously meant for large projects with major impacts, such as new roads, oil-and-gas developments or nuclear installations. The smallest scale discussed is 1:3 000 000 (ecoregion) while allowance is made for work to the larger scale 1:2 500 (ecoregion). Important elements such as the selection of the field survey team, the development of a work schedule, background research and pretrip remote sensing are presented. Unfortunately, the guidelines for actual field data collection are quite sparse. For example, the terrain mapping section refers the reader to six other publications and never gives directions on how-to-do-it. The authors assume, somewhat naively in my experience, that the specialists in the various fields will know how to undertake the surveys at the appropriate level. I am constantly dismayed to find zoology graduates who can not identify wildlife and botany graduates who can not do field surveys. If you are looking for detailed field survey methodology suggestions you must look elsewhere.

The selected references appendix concentrates on federal government publications in the field and ignores much of the excellent environmental assessment literature now available. For example, Jain, Urban and Stacey's, Environmental Impact Analysis and Myers and Shetton's, Survey Methods for Ecosystem Management fill in many of the gaps found in this publication and should have been mentioned.

The most valuable part of the book, for me, is Appendix B — Sources of Information. It lists federal sources of maps, reports and data sources such as topographic maps, hydrographic charts, ecological land surveys, geological maps, air photos, satellite imagery, forest inventory maps, and so on. Finally, I now know where to obtain satellite photographs.

Environmental impact assessment is a vitally important component of land-use planning that now is under development in Canada. But, it is not easy. Let me outline a few of the major problems that the environmental planner must solve before he starts any field work. There is an infinite amount of data in any landscape. What kinds of data need to be collected and at what scale? What geographical area is to be investigated and how does one choose the boundaries?
What level of accuracy is acceptable? Acting as an umbrella covering these issues are the overall constraints of time and money.

EIA is also a classic case of comparing apples and oranges. Once the data are collected the planner must attempt to assess the level of importance given to each landscape feature. How does one compare wildlife habitat to aesthetic views or soil type to climatic zone? The development has to go somewhere and how much disturbance is acceptable?

This book provides a general level treatment of the planning and implementation of an ecological survey. It does not answer the questions raised above but it does make the planner aware that such issues must be faced and solutions arrived at.

Polynyas in the Canadian Arctic


In 1980, Stirling published a paper (Arctic 33: 303-315) in which he concluded that polynyas are "of critical importance to arctic marine birds and mammals for feeding, reproduction and migration". The work reviewed here is essentially an expanded version of that earlier paper, and attempts to describe in detail how and why polynyas are so 'critical'. The results of this attempt are uneven. Although much useful information is presented, there is also a disappointingly large number of inaccurate statements and misused data. The net result is to leave a reader no closer to understanding the biological phenomena of polynyas, and indeed, wondering if polynyas are in fact as important as claimed.

A major problem is the confusing and inconsistent use of the word 'polynya'. Although properly defined as 'any non-linear opening enclosed in ice', the authors found this definition (from the Pilot of Arctic Canada) too "technical" or too "restrictive" and so arbitrarily included shoreleads, ice edges and several other areas of open water in or near ice. From a biological point of view these areas are very different. They have very different origins and causative forces, different characteristics of productivity, and greatly differing importance to marine birds and mammals. This lack of rigor of definition is compounded by the inclusion of such bizarre terms as "former polynya areas" and the "west Greenland polynya", which even the authors admit is not a polynya! The latter is in fact contiguous with the North Atlantic Ocean. The net result is the attribution to polynyas of biological phenomena that were documented in non-polynya areas. Indeed, references to biological information on polynyas, per se, are few.

But the tough questions remain. How important are each of the elements of this landscape? Under the federal assessment procedure an appointed panel has been given the responsibility of hearing all the evidence and making the overall judgment. No amount of objective field measurement changes the fact that the final decisions are essentially subjective. The underlying current is not scientific objectivity but one's philosophy and approach to the environment.

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covered with fast ice in winter. White Whales, Narwhals, Harp Seals and, particularly, Bowhead Whales, rarely, if ever, migrate to Queens Channel and Penny Strait.

The seabird chapter suffers from similar problems. Many of the arguments about the importance of polynyas to birds in winter are based on the 'west Greenland polynya'. Other 'evidence' concerns guillemots in the Foxe Basin polynya; however, the sources cited all refer to sightings in pack ice 400 km south of that polynya. Similarly, the contention that polynyas are important in winter is supported by references to work done in summer. The authors' correlation between seabird colonies and polynyas is not supported by the data. This chapter also has many inaccuracies. Photosynthesis can and does occur before the surface of the water is free of ice. The eastern end was the only part of Lancaster Sound where open water was present in summer 1978. Seabirds at colonies near this open water nested as late and with as poor success as those at ice-bound colonies further west. Dovkies do not visit the ice edge and loose ice at the entrance of Lancaster Sound in spring. In fact, they avoid such areas and occur almost exclusively offshore in heavy pack ice. The assertion that alcids cannot fly 50 km over ice is incorrect. Also incorrect is the statement that cliffs at Bellot Strait are too low-lying for cliff-nesting birds. The cliffs along the north side of the strait are higher than those near Cape Hay. Bylot Island, the site of a large seabird colony. What is the source for the ice conditions shown in Figure 1?

The brevity of the chapter concerning the relationship of polynyas and seaducks is an indication of the amount of evidence supporting such a relationship. The authors, in fact, suggest that polynyas are probably not important to high arctic duck populations. There are inaccuracies in this chapter too.

The attractive packaging and well-known authors involved in this work will undoubtedly lead those unfamiliar with the Arctic to believe that this is an important contribution to arctic biology. In fact, great caution should be exercised when quoting from the papers on birds and mammals. Judging from remarks in the Introduction, this publication is intended as a background document to a proposal to secure funding for arctic research. It seems to me, however, that the focus for future arctic research (and much does need to be done) could have been more properly determined with a publication that did not try to address a variety of issues under a single catchy title.

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Soil Conservation


The 16 chapters of this book fall into one of two categories; either a description of the processes of soil erosion in all of its intricate detail in various parts of the world or a "how to" manual in terms of combating erosion.

I reviewed this book as an ecologist interested in the soil fauna, which is poorly described and understood. The causes of soil erosion, its extent and geographical distribution, depending on landscape and soil type, are fairly well understood and are described clearly in this book. There are many excellent black-and-white photographs to illustrate the text. If there is a one-line message to this book I suppose that (although wind erosion is discussed) "soil erosion is proportional to rainfall" would be that phrase.

For the biologically oriented reader, only the first six chapters plus chapters 11 and 16 are essential to the understanding of the biological implications of this book. The intervening chapters would be of most interest to engineers and researchers concerned with the techniques of controlling erosion. They may still be read with profit by others, if for no other reason than to marvel at man's ingenuity in tackling these problems over time and a wide variety of terrain.

The prose is terse but readable. The detail available in some chapters can be overwhelming at times to the non-expert, but chapter sub-titles, plus a text unmudied by jargon, allow absorption of the general argument without having to grasp the underlying intricacies.

Chapters 3 and 4, "The Physics of Rainfall" and "The Erosivity of Rainfall" discuss the relationships among rain drop diameter, drop size distribution, terminal velocity of raindrops, kinetic energy of rainfall, (and related matters) and the soil, in brief but clear style. The author also points out how sparsely rain gauges are scattered around the world (a sample of 1 in 20 million in densely sampled experiments in developed countries to 1 in 200 billion in undeveloped countries. Both are sampling rates which, as Hudson points out, would be considered grossly inadequate for most experiments).

Hudson says: "Soil erosion is a work process in the
physical sense that work is the expenditure of energy, and energy is used in all phases of erosion — in breaking down soil aggregates, in splashing them in the air, in causing turbulence in surface run-off, in scouring and carrying away soil particles. If the available sources of energy are considered this explains why splash erosion is so vital in the erosion process" (p.64). A comparison of rain (splash) and run-off reveals that rain has 256 times more kinetic energy than surface run-off under fairly common circumstances (p.65). These statements illustrate Hudson's terse prose style and summarize the core of the book.

Chapter II (Control of erosion by crop management) will also be of interest to ecologists. There are a number of interesting statements here, generally well supported by data. For example, Hudson says: "Clearly improved conservation practices like terracing are important, but good crop management can be up to ten times more effective in reducing the amount of erosion" and "It is remarkable how often the management required for good erosion control coincides with intensive, efficient, profitable farming. There is no substance at all in the fear sometimes felt by farmers that conservation farming means restricted production or uneconomic practices" (p.209). Well said.

The soil provides us with our agriculture which was both the source of human civilization and its core to this day; this book provides a comprehensive review of a subject for which most of the "civilized" world remains unaware. Admittedly soil conservation as a research discipline does not have the glamour of biotechnology or the presence of ecology or the precision of physics. However, its importance to the continuance of human life and culture is essential. Loss of soil quality (primarily through erosion) is mankind's most serious environmental problem. Several chapters of this book should be required reading for field biologists, and the policy makers of agriculture, forestry, and land use.

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MISCELLANEOUS

Evolution in Age-structured Populations


This book should be used by those wanting all of the mathematical tools known to science for correctly analyzing age-specific natural selection in populations. The text is highly theoretical since few data sets exist concerning age-specific evolution in real populations under natural conditions. Those not able to grasp advanced, rigorous, mathematical treatment will find most of this book impossible to read. However, many of the mathematical discourses of models are terminated by impeccable summaries in clear English so that a few hours spent leafing through the text, looking for these summaries, will be well worth the effort. The good subject and author indices will aid a perusal of this type.

Generally, three chapters deal with the effects of age-structure on population genetics, one other on life-table analysis, and another on the evolution of life histories. Models for plants and animals are provided in many cases with respect to sex, age, discretely breeding, continuously breeding, density-dependent, and density-independent cases. Theories concerning density dependence and carrying capacity are discussed under new lights shed by differences in age-specific mortality and fecundity. Theoretical changes in gene frequencies with respect to age-structure are explored.

This book is an effort to introduce age-structure to conventional theories of ecology and population genetics. Unfortunately, evolution in populations has been studied as though it were not affected by the ages of the organisms concerned. Charlesworth makes it clear that evolution of most organisms can no longer be studied without knowing the ages of these organisms.

Novel interpretations introduced throughout the text are: 1) survival functions and fecundities should be defined for males as well as females; 2) perturbations away from the carrying capacity are usually followed by a return to an equilibrium population size unless other factors are promoted; 3) the rate of convergence to Hardy-Weinberg equilibrium of allelic frequencies is the same as the rate of convergence to a stable age-distribution of a survival series; 4) usually a population cannot simultaneously be in genetic equilibrium and have an unstable age-structure; 5) genotypic frequencies can change as a result of changes in age-specific demography without changes in the selective regime; 6) oscillations in population size caused by gene-frequency changes (Chitty's hypothesis,
Canadian Journal of Zoology 38:99-113 (1960) appear to be mathematically impossible; 7) the accepted idea that natural selection increases population density only if genotypes differ in their ability to survive density-dependent mortality does not appear to be valid; and 8) density-independent cases can be treated the same as density-dependent cases for determining the Evolutionarily Stable Strategy of a life history.

Any person working with life-table analysis, life history, or age-specific genetic problems should spend some time with this book.

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Weather for Outdoorsmen: A Complete Guide to Understanding and Predicting Weather in Mountains and Valleys, on the Water, and in the Woods


This book should be read by naturalists who want a practical understanding of the causes of present weather patterns and who want to know how to predict future patterns. The book is written by a professional meteorologist in an easy-to-understand popular style with a glossary. Its primary purpose is to allow the reader to know how to anticipate bad weather so he can take effective actions in the field and to know how to plan activities requiring good weather. How weather patterns on water differ from those on land and how they differ in mountains, valleys and forests is amply discussed.

The text discusses how to utilize weather recording instruments and the clouds in different types of environments appropriate to a field naturalist. It describes cloud formations, what causes different types of cloud formations, and what type of upcoming weather can be predicted from each type of formation. It describes how to predict upcoming weather with ±80% accuracy using barometric pressure, the most important variable. Using barometric pressure, wind direction and cloud type, one can accurately forecast upcoming weather ±90% of the time. How to interpret relative humidity and temperature readings to determine if dew or frost will form is explained.

The book explains how to ascertain the best location to pitch a tent depending on the cloud cover and temperature since many times only a few meters' difference in location will make a huge difference in how well you sleep. How to keep from getting caught in fog while boating and how to avoid electrocution from lightning storms when in the field are described.

In short, what causes wind, fog, rain, clouds, different temperatures, and sunny weather is discussed in this book. Changes in many of these parameters affect our nervous system, causing changes in behavior and emotion which lead to sociological and psychological implications. Persons reading this book will not have as many trips to the field prematurely ended because of rain since most of these days can be avoided simply by looking at the color of the sky and the cloud-type in the morning. I recommend this book for all field naturalists.

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The Weather Almanac


This volume contains a wealth of information about the weather. There are eleven principal sections. The first, titled "U.S. weather in atlas format", uses maps with charts at various localities to give monthly-by-month changes in temperatures, precipitation, snowfall and amount of sunshine. Prevailing wind directions are shown as arrows on a map and the growing season data are presented in tabular form.

The section on "Storms, severe weather and geo-

physical phenomena" discusses thunderstorms, winter storms, floods, volcanoes, etc., how to prepare for each, as well as how to react when caught in a severe situation.

Subsequent sections deal with atmospheric factors that influence health, air pollution, weather fundamentals, forecasting, energy (solar and wind), and record setting weather. The chapter on Round-the-world weather includes 33 Canadian sites from Aklavik, N. W. T. to St. John's, Newfoundland.

"Weather of 180 selected U.S. cities" occupies
nearly half the book. Each city has a four page entry. The first page describes the environment of the city and how it is influenced by the major weather systems, discusses growing seasons, temperatures and precipitation. The remainder of the entry is composed of tables on normals, means and extremes, heating and cooling degree days, snowfall, temperature and precipitation. Most of the tables have years and months on the two axes.

The last section is a "Special report: climatic changes", which discusses the process of change, the carbon dioxide problem and the effect of energy technologies on climate.

There are scattered photographs of such events as tornadoes, thunderstorms and volcanic eruptions but they are quite grainy and dark. In a few places, e.g., pages 33 and 179, the lettering on tables and graphs is so small that it is illegible. Throughout the book, temperatures are given in fahrenheit degrees and precipitation is in inches. There is a glossary and an index.

Overall this is an informative volume which provides an interesting introduction to weather and geophysical phenomena and a mass of detailed statistics for selected cities.

J. Ginns
RR 1, Cantley. Quebec J0X 1L0

The Guinness Book of Mountains and Mountaineering


Mountains affect people in different ways. Beautiful, exhilarating and foreboding are a few adjectives applied to mountains and they don't adequately explain the spiritual influence of mountains upon man. Edward Pyatt's book touches on these and many other aspects of mountains and their interaction with man.

The introductory 62 pages consider the definitions of a mountain, then give a synopses of plate tectonics, volcanoes, glaciers, weather, medicine, mapping, flora and fauna, recreation, living in the mountains, etc. The main part of the book treats the mountains of the world in geographic areas, e.g., The Alps, North America. Each page has (in the left column, occupying one third of the page width) an annotated listing of the principal mountains in the ranges found in that geographic area. For example, under Canadian mountains, we see that Mt. Waddington is also known as mystery mountain, is 3994 meters high, and was first ascended in 1936 by Weissner and House. In all, over seven pages are devoted to mountains in Canada. Mount Edith Cavell is shown in color and several other peaks are pictured in black and white.

The text emphasizes man's expeditions to conquer summits. It is nicely presented and written in a readable style. The photographs, maps and illustrations effectively complement the text. Overall it is an excellent introduction to mountains and mountaineering.

J. Ginns
R.R. 1, Cantley. Quebec J0X 1L0
NEW TITLES

Zoology


Botany


Environment


†The natural environment of Newfoundland past and present. 1981. Edited by Alan G. Macpherson and Joyce Brown Macpherson. Memorial University of Newfoundland, St. John’s. xviii + 265 pp., illus. $17.50.


Miscellaneous


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*Assigned for review
†Available for review
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