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Cover: Cascade Mantled Ground Squirrel, *Spermophilus saturatus*, at Cascade Lookout, Manning Provincial Park, British Columbia, 31 May 1990. Photograph courtesy of Maria Leung. See report of the status and distribution of this species in British Columbia by Maria C. Leung and Kimberly M. Cheng, pages 365-375.

Fisher, *Martes pennanti*, Home Range Characteristics in a High Density Untrapped Population in Southern Québec

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Garant, Yves, and Michel Crête. 1997. Fisher, *Martes pennanti*, home range characteristics in a high density untrapped population in southern Québec. *Canadian Field-Naturalist* 111(3): 359–364.

Most Fisher (*Martes pennanti*) populations in North America are moderately to heavily trapped. Trapping may reduce density and can indirectly affect spacing patterns of solitary terrestrial carnivores by creating vacant territories. From 1991 to 1993, we studied home ranges of radio-collared Fishers in Gatineau Park (Québec) where trapping had been prohibited for ≥ 20 years. We estimated density using median home range size and a track-count survey technique. Mean home range size determined by minimum convex polygon was 5.4 km² (n = 7) for adult females and 9.2 km² (n = 3) for adult males in the park. The observed home ranges in Gatineau Park were comparable to sizes predicted from body mass/home range size curves among carnivores, but smaller than those measured for trapped populations in northeastern North America. Density was estimated at 2.7 Fishers/10 km² using median home range sizes, when assuming saturation of the area by Fishers. An independent density estimate of 3.0 Fishers/10 km² was obtained using a probability sampling survey based on track counts in the snow. This was one of the highest densities reported in northeastern North America and was mainly attributed to the absence of trapping, a major mortality factor in Fishers.

La plupart des populations de pékans (*Martes pennanti*) de l'Amérique du Nord sont modérément ou fortement exploitées par le piégeage. Chez les carnivores solitaires, le piégeage peut réduire directement la densité des populations ou affecter indirectement l'espacement des individus en créant des territoires vacants. Entre 1991 et 1993, nous avons étudié, par la télémétrie, les domaines vitaux de pékans du Parc de la Gatineau, un site où le piégeage est interdit depuis plus de 20 ans. Nous avons estimé la densité des pékans à partir de la taille médiane des domaines vitaux et d'un inventaire des pistes en hiver. La taille moyenne du domaine vital, déterminée par le calcul du polygone convexe minimal, était de 5.4 km² (n = 7) pour les femelles adultes et de 9.2 km² (n = 3) pour les mâles adultes. Les tailles des domaines vitaux mesurées dans le parc étaient comparables à celles pouvant être prédites à partir de la relation générale reliant la masse corporelle et la taille du domaine vital chez les carnivores. Les aires vitales mesurées dans le parc étaient cependant plus petites que celles mesurées chez des populations piégées du nord-est américain. La densité a été estimée à 2.7 pékans/10 km² en utilisant la taille médiane des domaines vitaux et en assumant que les pékans occupaient la totalité de l'habitat disponible. Une estimation indépendante de la densité, par l'échantillonnage des pistes, a indiqué une densité de 3.0 pékans/10 km². Cette densité correspond à une des valeurs les plus élevées pour le nord-est américain; la forte densité résulterait vraisemblablement de l'absence de piégeage, le principal facteur de mortalité chez le pékan.

Key Words: Fisher, *Martes pennanti*, mustelids, density, home range, intrasexual territoriality, spacing, Québec.

Spacing and home range size of terrestrial carnivores may be affected by factors such as body size, age structure, mortality rates, sex ratio, and by the abundance and productivity of food (Powell 1994). Fishers (*Martes pennanti*), like many *Martes* species, generally exhibit intrasexual territoriality (Powell 1979) and show little or no overlap of home ranges between individuals of the same sex. Intrasexual intolerance probably begins when animals reach sexual maturity as observed in Pine Marten (*Martes martes*) (Selås 1990). Fishers attain sexual maturity

at one year of age (Wright and Coulter 1967; Leonard 1986; Cherepak and Connor 1992). Home range size was reported in many Fisher studies (Kelly 1977; Raine 1982; Buck et al 1983; Johnson 1984; Arthur et al. 1989; Jones 1991; Kohn et al. 1991), but all northeastern studies concerned harvested populations.

Harvesting affects population size by removing resident animals, which can indirectly influence social structure and spacing patterns of one or both sexes (Litvaitis et al. 1987; Strickland and Douglas

1987; Arthur et al. 1989; Powell 1994). Spatial organization of carnivores may remain stable if transient individuals from untrapped areas settle into ranges formerly occupied by residents (Litvaitis et al. 1987), or if territory size is determined primarily by energy requirements (Katnik et al. 1994). However, spatial organization can vary in highly exploited populations or in the absence of refugia (Bailey 1972; Litvaitis et al. 1987; Arthur et al. 1989); harvested populations do not generally exhibit natural population attributes (Powell 1994).

Most Fisher populations outside parks and reserves in the Northeast are moderately to heavily trapped (Douglas and Strickland 1987; Paragi 1990; Krohn et al. 1994). Annual trapping mortality in Maine ranged from 21 to 62%, depending on age and sex classes (Krohn et al. 1994), whereas it averaged 40% in Québec (Garant 1995). Such high trapping rates can maintain Fisher density below carrying capacity and provide vacant territories to transient individuals. Data from lightly harvested and unharvested areas are needed for a better understanding of Fisher population dynamics (Krohn et al. 1994). Knowledge of how territoriality affects spacing patterns and density in untrapped areas could provide useful information for the management of Fisher populations.

Our objectives were to determine Fisher population characteristics and to estimate home range sizes and density in an untrapped park of southern Québec. Because there was no trapping and there were limited human activities, we postulated that Fisher density would be high and predicted home range size smaller than those in trapped areas.

Study Area

We conducted the study in Gatineau Park, Québec (45°36'N, 76°05'E), a 350-km² mostly forested area located 30 km northwest of the Ottawa-Hull region (Figure 1). Our main study block was the western half of the park, in the La Pêche lake area. The landscape consisted of rolling hills typical of the Laurentian shield. Vegetation was representative of the Great Lakes — St.-Lawrence forest region (Rowe 1972); about 45% of the park was composed of hardwoods, and 35% of mixed woods with limited areas of pure conifers. The most common species was Sugar Maple (*Acer saccharum*), often associated with Yellow Birch (*Betula alleghaniensis*) and Beech (*Fagus grandifolia*) (Lopoukhine 1974). Balsam Fir (*Abies balsamea*), Eastern Hemlock (*Tsuga canadensis*), White and Red pine (*Pinus strobus*, *P. resinosa*), and spruces (*Picea* spp.) were the most common coniferous species. At the outset of the study, furbearer trapping had been prohibited for ≥ 20 years in the western part of the park, and for ≥ 40 years elsewhere, except for the trapping of nuisance Beavers (*Castor canadensis*).

Methods

Fishers were captured in Tomahawk live-traps (Model 107 and 207, Tomahawk Live Trap Co., Tomahawk, Wisconsin) in autumn and winter 1990 to 1992, mostly in the western half of Gatineau Park. Captured Fishers were anesthetized with intramuscular injection of ketamine hydrochloride (Ketaset™, Bristol Lab, Syracuse, New York) at an average dose of 15 mg/kg body mass or gassed with isoflurane (Aeranne™, Anasquest, Mississauga, Ontario) in a Plexiglas box. For most Fishers captured in the park, an upper premolar (PM1) was removed for age estimation by cementum annuli (Strickland et al. 1982). Fishers were fitted with ear tags and with radio-collars (Model SMRC-3, Lotek Engineering Inc, Newmarket, Ontario, or model 225, Telonics, Mesa, Arizona).

Radio-collared Fishers were monitored 2-5 times/month, between December 1990 and December 1993, from a Cessna 172 equipped with 2 Adcock (type H) antennas attached to the aircraft struts. Each location was plotted on a 1:50 000-scale topographic map. To respect independence of observations, only those locations that were separated by > 16 h were used for home range size calculation (Arthur et al. 1989). Telemetry accuracy was assessed by comparing known transmitter locations with those determined from the air. In these blind tests (n = 10), aerial locations were ≤ 150 m from the actual locations. Home range size was determined by the minimum convex polygon (MCP) encompassing 100% of locations, using MCPAAL software (M. Stüwe and C. E. Blohowiak, Smithsonian Institute, Front Royal, Virginia), for ease of comparison with published studies. The harmonic mean method was not used because it was found inappropriate for estimating total area used by Fishers (Arthur et al. 1989).

We estimated age structure of live-trapped Fishers by calculating frequency distribution of juveniles (< 1 year), yearlings (1.5 year), and adults (≥ 2.5 years) and compared it with the age structure of Fishers harvested by trappers in the surroundings of the park (Figure 1) using a chi-square test of homogeneity (Daniel 1978). We used G-statistic analysis, adjusted for our small sample size using Williams' correction (Sokal and Rohlf 1981), to test if Fisher sex ratio in the park departed from parity.

Density was estimated using median range size, assuming saturation of the area by Fishers, and intrasexual territoriality (Arthur et al. 1989; Thompson and Colgan 1987). We also derived a winter density estimate in late February 1993 using a probability sampling technique (Becker 1991). This sampling design assumes that the number of different Fishers encountered along a set of transects can be determined, and that movement data from a random sample of radio-collared animals can be measured. Three

sets of four transects were randomly distributed in February 1993 in a 58-km² block of Gatineau Park to tally Fisher tracks, 24 hours after a snowfall of 32 cm. Each east-west oriented transect was 4 km long and was walked by an observer on snowshoes. At the same time, nine radio-collared Fishers were monitored from a Hughes-500 helicopter, and their locations were recorded on a 1:20 000-scale topographic map three times/day. These radio telemetry data were used to determine the average distance travelled by Fishers along a north-south axis, referred to as the X axis. The use of a helicopter helped to accurately determine locations and distances travelled by Fishers. We then calculated the probability of encountering a Fisher track in the snow using mean distance travelled by radio-collared animals. Using the equations provided in Becker (1991), we estimated the number of animals within our inventory block and calculated confidence intervals on this estimate.

Results and Discussion

Home range

Twenty-two Fishers were caught and radio-tagged in Gatineau Park, and home range size was calculated for 10 resident adults, 3 males and 7 females. Data from other Fishers were excluded because they either dispersed from the park, were juveniles, or because of inadequate sample size (radio failure or loss of contact). From 17 to 35 independent locations were necessary before area-observation curves reached an asymptote.

Mean home range size (MCP) of females and males in Gatineau Park were 5.4 (range: 2.2-9.6) and 9.2 km² (range: 6.0-12.3) respectively (Table 1), a difference not statistically significant ($U = 4.00$, $P = 0.13$). Fisher home ranges in Gatineau Park were substantially smaller than those previously reported for harvested Fisher populations of Maine and New Hampshire (Table 1). Mean home ranges of 17 females and 9 males were 8 km² and 23 km², respectively, in a recent study in Massachusetts (E. York, University of Massachusetts, personal com-

munication), and 29.4 km² for 6 males in a trapped area in southeastern Québec (Garant 1995).

The ratio of male home range size/female home range size was 1.8 in Gatineau Park, a value of similar magnitude to their body mass ratio of 1.7 (Y. Garant, unpublished data). This home range size ratio was comparable to the value of 1.9 measured in Maine (Arthur et al. 1989) but greater than the ratio of 1.5 estimated in New Hampshire (Kelly 1977).

Adult Fishers exhibited a spacing pattern similar to animals from harvested populations and maintained a comparable ratio between male and female home range sizes. No intrasexual territory overlap was observed. However, although we trapped intensively in the western half of the park, some unmarked Fishers may have been present in our main study block.

Reduced home range size in mustelids can result from two confounding factors: abundant foods and high density. Thompson and Colgan (1987) found that in American Marten (*M. americana*), home ranges were the smallest and density the highest when prey was abundant; home ranges grew in size and Marten density decreased when prey was scarce. In a similar way, distribution and abundance of the Least Weasel (*Mustela nivalis*) in Sweden depended on the abundance of small rodents (Erlinge 1974).

Powell (1994) proposed a model for *Martes* species in which spacing behavior and home range vary with prey abundance. According to this model, spacing should evolve from completely exclusive territories when food resources are very low to ultimately extensive home range overlap, with members of both sexes, at high levels of prey. However, this model has not yet been experimentally tested in Fisher.

Powell's model predicts that intrasexual territoriality would prevail in situations with intermediate levels of prey abundance. Since little or no territorial overlap was observed for adults in most, if not all, studies across Fisher range (Kelly 1977; Buck et al. 1983; Johnson 1984; Arthur et al. 1989), this implies that food base was intermediate everywhere. Food was probably not a limiting factor for Fishers in

TABLE 1. Home range areas of adult Fishers in untrapped Gatineau Park and trapped areas of New England.

Location	Sex	N	Home range (km ²)		Reference
			\bar{X}	SE	
Untrapped area					
Gatineau Park	F	7	5.4	0.9	Present study
	M	3	9.2	1.8	Present study
Trapped areas					
Maine	F	6	16.3	4.7	Arthur et al. 1989
	M	7	30.9	9.3	Arthur et al. 1989
New Hampshire	F	5	15.1	2.1	Kelly 1977
	M	6	22.8	6.4	Kelly 1977

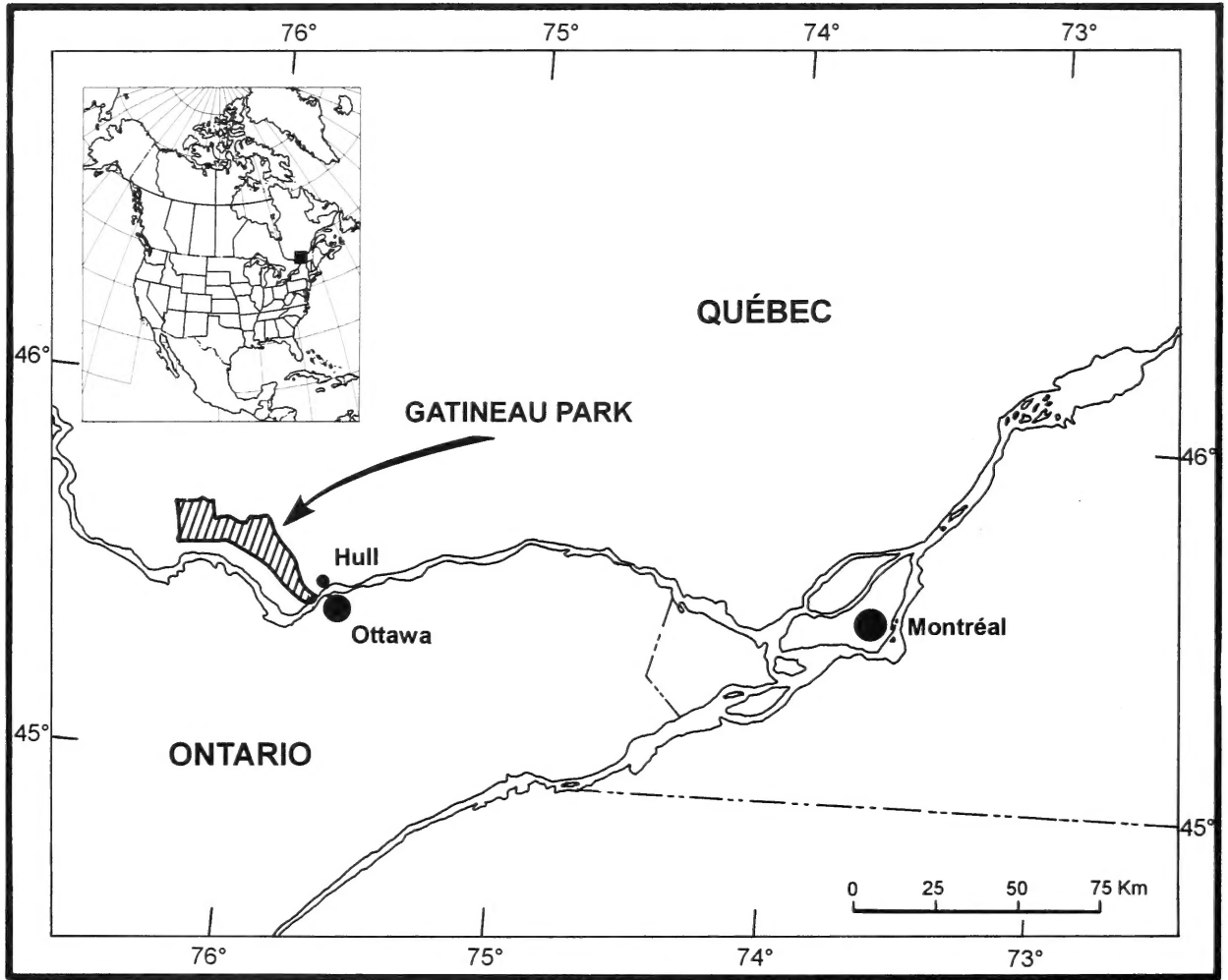


FIGURE 1. Location of Gatineau Park in southern Québec.

Gatineau Park since no sign of poor body condition or starvation was observed. Body mass in late autumn-early winter averaged 4.6 kg for males ($n = 13$) and 2.4 kg ($n = 15$) for females, which were among the highest values reported for this species (Powell 1993). Observed home range sizes in Gatineau Park were close to values predicted by the general equation $A = 170M^{1.03}$ linking body mass (M) and home ranges (A) in carnivores (Lindstedt et al. 1986). Home ranges of Fishers in other studies were consistently larger than those predicted on the basis of body size (Buskirk 1992).

In addition to food availability, we believe that spacing behavior and home range size may be influenced concomitantly by Fisher density. Fishers are known to defend their territory against intruders (Powell 1993), and instances of fighting have been documented (Arthur et al. 1989). When Fisher density increases after interruption of trapping, one way to minimize social interactions with members of the same sex and avoid overt aggression might be to contract home range size, as long as food resources remain sufficient to meet metabolic needs. Even if

males may adjust their home ranges according to female spacing (Sandell 1989; Powell 1994), home range contraction may not restrict exclusive access to mates in a densely populated area. These three factors (mate access, density, and energy requirements) that appear to influence home range size in Fisher are not necessarily exclusive. Conversely, when density decreases (e.g., because of exploitation) surviving Fishers could extend their territory into vacant ones without any social conflict. Recent studies on Fisher populations at relatively low densities (Jones 1991; Heinemeyer 1993) tend to support this hypothesis.

Density

Thirteen Fisher tracks were tallied along the transects during the February survey. According to telemetry locations of nine radio-collared animals, the average distance travelled by Fishers along the X axis was 0.90 ± 0.09 km during the day of the winter survey. These figures yielded a population estimate of 17.4 ± 2.0 Fishers for the 58-km² study block, i.e. 3.0 Fishers/10 km² ($\pm 11.1\%$, $\alpha =$

0.05). Assuming saturation, median home range sizes of female (5.6 km²) and male (9.3 km²) produced a density estimate of 2.7 Fishers/10 km². Both methods provided comparable density estimates, which were among the highest reported in the Northeast. In the White Mountains of New Hampshire, Fisher abundance varied from 1.3 to 2.6 Fishers/10 km² of suitable habitat (Kelly 1977). Arthur et al. (1989) estimated a winter density of 0.5 to 1.2 Fisher/10 km² in Maine. Coulter (1966) and Hamilton and Cook (1955) reported a density of 3.9 Fishers/10 km² based on snow tracking; however, their estimates are at best indices of actual densities (Powell 1994) and are less accurate than density estimates based on telemetry or probability sampling. In the highly trapped Algonquin Park in Ontario, density estimates varied between 1.5 and 1.9 Fisher/10 km² (Douglas and Strickland 1987), whereas a maximum density of 2.6 Fisher/10 km² was used in Maine for management purposes (Clark 1986).

Age structure and sex ratio

Juveniles accounted for 21% of the live-trapped Fishers in the park, whereas yearlings and adults comprised 42% and 37% respectively ($n = 24$). Age structure of Fisher in Gatineau Park differed significantly ($\chi^2 = 40.79$, $df = 2$, $P < 0.05$) from the age structure of Fishers trapped in the region surrounding the park, where juveniles comprised 75% of harvest ($n = 92$). This contrasted also with other harvested populations where juveniles usually represent > 60% of the harvest (Douglas and Strickland 1987; Powell 1994). In the lightly trapped Fisher population of Wisconsin, juveniles comprised 48% of the harvest (Kohn et al. 1993). The Fisher age structure in Gatineau Park was consistent with the survivorship of 80% that we estimated during the study (Garant 1995).

In Gatineau Park, we captured more females than males but our 0.6 M:F ratio did not statistically depart from parity ($G_{adj} = 1.60$, $df = 1$, $P > 0.05$) This high proportion of females is nevertheless surprising because live-trapping and kill-trapping tend to be skewed toward males, mainly because adult females are less susceptible to trapping than are adult males (Krohn et al. 1994). Males' greater vulnerability to trapping was attributed to their presumably greater food requirements (larger size) than females. Krohn et al. (1994) suggested that adult males may be less wary of traps because they are less familiar with their environment as they do not spend their entire adult life in the same home range, as do adult females.

Trap spacing can influence rates of capture between sexes since rate of encounter with traps is higher for males if traps are arranged in grids, but higher for females if traps are arranged in a line (Buskirk and Lindstedt 1989). Therefore, because many of our traps

were parallel to access roads, this may have increased females' rate of encountering traps as a result of the higher density of traps in their smaller home ranges.

Powell (1993) suspected that true M:F sex ratios for natural *Martes* populations were close to equality, but that harvested populations might be skewed toward females. Because of Gatineau Park's relatively small size, this Fisher population could be partially affected by kill-trapping on its periphery. By having larger home range sizes and greater mobility than females, males on the outskirts of the park may suffer a greater risk of being trapped. If this were the case, this higher exposure of males to trapping than females could explain to some extent why female Fishers outnumbered males in our study. However, we believe that unharvested populations could be skewed toward females if intrasexual territoriality is to be maintained and if male home range sizes exceed those of females. Such a social structure inevitably leads to a sex ratio skewed toward females because young males are forced to emigrate. This phenomenon was also observed in a well-established but harvested population in Maine: Arthur et al. (1989) estimated that three resident adult Fishers, one male and two females, could be present per 25 km² block of habitat, for a M:F ratio of 0.5.

Our data suggest that smaller home ranges in Fisher could result from increased social pressure resulting from high density. The untrapped population of Gatineau Park comprised more adults than in the adjacent harvested area and was skewed toward females. The characteristics of this untrapped Fisher population support Powell's (1994) assumption that trapping affects more than population size; it has repercussions on other population attributes (e.g., age structure, sex ratio) that we should consider for sound management of this furbearer.

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The Distribution of the Cascade Mantled Ground Squirrel, *Spermophilus saturatus*, in British Columbia

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The Cascade Mantled Ground Squirrel, *Spermophilus saturatus*, only occurs in southwestern British Columbia (Canada) and Washington State (United States). Little was known about the squirrel in British Columbia prior to this survey. Range and distribution were determined from museum records, survey forms, opportunistic observations, visual counts, and live-trapping. Visual counts were used most often and were more effective at locations where the relative abundance of *S. saturatus* was high. *S. saturatus* was found further north and west than previously reported, but not as far east as indicated by museum records. *S. saturatus* was uncommon and had a discontinuous distribution in British Columbia, which could be a result of frequent extinctions and slow recolonizations at the northern portion of their range. Marginal climatic conditions, drainage systems that delineate the range of *S. saturatus*, and displacement by the Columbian Ground Squirrel (*S. columbianus*) at the eastern extent of *S. saturatus* range in British Columbia, are all probable factors limiting the distribution of *S. saturatus*. Although the squirrel's distribution is limited, the population is not likely in danger of extinction at present. Trapping at four locations indicated good overwintering success of the most vulnerable age group, young born the previous year.

Key Words: Cascade Mantled Ground Squirrel, *Spermophilus saturatus*, range, distribution, British Columbia.

The Cascade Mantled Ground Squirrel, *S. saturatus*, is endemic to the Cascade Mountains of southwestern British Columbia and Washington State. Little was known about the squirrel's northern range and distribution in British Columbia (Trombulak 1988) except for data presented in Howell (1938), and Cowan and Guiguet (1965). The survey was conducted in 1989 to gather data on the squirrel's range and distribution, and to determine if there were any recent changes in the distribution which may have resulted from habitat alteration. Supplementary data were also gathered to outline recruitment success. The species was on the British Columbia provincial red list for "threatened or endangered" vertebrate species (Munro 1990) until the report resulting from the survey (Leung and Cheng 1991) was reviewed by the Committee on Status of Endangered Wildlife in Canada (COSEWIC). COSEWIC (1992) decided to let the species remain unlisted. It was also down-listed to the provincial blue list for vulnerable species which are species not considered threatened by imminent extinction or extirpation, but at risk of further disturbance (Harcombe et al. 1994).

Methods

Before beginning the field survey for *S. saturatus*, a preliminary range and distribution map was constructed from data presented in Howell (1938) and museum lists of locations where *S. saturatus* specimens were collected in British Columbia. The museums which contributed included the Royal British

Columbia Museum (BCPM; 6 specimens), the Canadian Museum of Nature (NMC; 19 specimens), the Cowan Vertebrate Museum (CVM, University of British Columbia; 15 specimens), the Royal Ontario Museum (ROM; 1 specimen), and the [United States] National Museum of Natural History (USNM, Smithsonian Institute; 1 specimen). Locations of other sightings were sought by distributing survey forms to interested individuals, regional naturalist clubs and other outdoors-oriented organizations. The survey form had a picture of *S. saturatus* and a description on how to distinguish it from chipmunks (*Eutamias* spp.) and Golden Mantled Ground Squirrels (*Spermophilus lateralis*).

In 1989 and 1990, locations where *S. saturatus* had previously been recorded from museum collections, were resurveyed. Locations inside and outside the previously delineated range were also checked, particularly in subalpine to alpine habitats. Survey locations were limited by road, trail and terrain access. Field surveys for the ground squirrels were conducted during the active portion of the squirrel's circannual cycle (Kenagy and Barnes 1988) between May and September in 1989 and 1990. Live-trapping, visual counts, and opportunistic observations (e.g., walking transects and road sightings) were used to detect the presence of *S. saturatus* and to identify the current range and distribution of the squirrel.

When trapping, Tomahawk #201 live traps were baited with peanut butter and oats. Traps were opened at 0800 hours, checked every two hours, and

closed at 1800 hours. In remote locations, each individual caught was marked with a metal ear-tag carrying a unique three digit number for future identification. In provincial parks and locations frequented by hikers, black hair dye applied to the pelage was used for marking and identification. For detecting the presence of *S. saturatus*, a minimum of 25 traps were set for one day.

To make relative abundance comparisons, trapping was conducted for four consecutive days at four known locations of *S. saturatus* between 29 May and 8 July 1990. Young of the year were not yet dispersing nor trapped during trapping sessions and therefore did not bias the density estimate upwards at locations checked later. Trapping effort totalled 160 trap-nights at the study areas on Iron Mountain (1650 m; 50°03'N 120°46'W) and Thynne Mountain (1950 m; 49°42'N 120°55'W), and 80 trap-nights at the Cascade Lookout in Manning Park (1750 m; 49°04'N 120°48'W and Brookmere Dump (1000 m; 49°40'N 120°52'W), — study areas which were approximately half the size. Iron Mountain is located in very dry cool montane spruce forest, Thynne Mountain and the Cascade Lookout are located in dry cold Engelmann Spruce-Subalpine Fir forest and the Brookmere Dump lies in dry cool Douglas Fir forest. Although the tree species differed between some sites, all sites were structurally similar in that they were all located in open forest with a developed understorey (Leung 1991). A population index was used to compare the population size of each of the four locations by dividing the total number of individual squirrels trapped by the trapping effort.

Aside from *S. lateralis*, *S. saturatus* is easily distinguished from other small mammals in the region by its pelage colouration and size (Hall 1981) which, together with its diurnal behaviour and high tolerance to human presence (Banfield 1974), facilitated the use of visual counts surveys to detect its presence. Prior to field surveys, study skins of *S. saturatus* and *S. lateralis* (subspecies *tescorum*) and associated skulls obtained from the CVM, the Conner Museum (University of Washington), the Burke Museum (Washington State University), and the Slater Museum (University of Puget Sound) were compared so that either species would not be mistaken for the other when observed in the field. The dark stripes bordering the longitudinal white stripe on each side of the back is well defined in *S. lateralis*, whereas, on *S. saturatus*, the median dark stripes are reduced or obsolete and the outer dark stripes are reduced or obscure (Howell 1938).

While we did not make an exhaustive examination of all the study skins available at other museums to confirm identification, we are confident that *S. saturatus* specimens have been correctly identified at museums for two reasons: 1) no collection localities for *S. saturatus* were unusually far from other collec-

tion localities; and 2) skulls (which often had corresponding study skins) identified as *S. saturatus* or *S. lateralis* measured at the four museums mentioned were found to be significantly different in size and shape (Leung and Cheng 1994). While misidentification was unlikely, we were not able to eliminate totally that possibility in the field observations.

Field observations were aided by 8 × 21 mm binoculars, a 20 × 60 mm spotting scope, and by intermittently sounding a high pitched whistle to attract the ground squirrels. The minimum observation time, including changing viewpoints at each place, was one hour.

The probability of sighting a *S. saturatus* within a certain time interval was calculated by correlating the cumulative percent sightings at locations of known inhabitation to cumulative time spent observing at these sites. This allowed us to predict the amount of time needed at each location in order to detect *S. saturatus* if it was there.

Results

Distribution of S. saturatus

Coordinates, elevations, and general habitats for locations where *S. saturatus* was sighted in 1989 and 1990 are listed in Table 1. Locations where specimens of *S. saturatus* were collected for museums and where *S. saturatus* were sighted during 1989 and 1990, including reports from survey forms, appear on Figure 1. Most locations associated with the specimens are approximate, but all known museum records are listed in Table 2. Locations where we searched for *S. saturatus* and did not detect any also appear on Figure 1. Coordinates and elevations for these locations are given in Appendix 1. UTM coordinates for locations where *S. saturatus* have been recorded are available from The British Columbia Conservation Data Centre (780 Blanshard St., Victoria, British Columbia, Canada V8V 1X4). Sightings of *S. saturatus* made in 1989 and 1990 indicate that their range is further north and west than documented by museum specimens.

In 1989 and 1990, *S. saturatus* was recorded at 36 locations. Of these, 16 locations were detected from visual counts, 13 from opportunistic observations, seven from survey forms and none from trap surveys. Nine of 35 survey forms distributed were returned, of which seven reported sightings.

S. saturatus was trapped where it had already been sighted, and were not trapped in all the attempts at locations where it had not been sighted. Therefore, trap surveys did not detect any new locations of *S. saturatus*. The results of trapping at the four locations where presence of the ground squirrel was known are shown in Figure 2. Seven squirrels were trapped at Iron Mountain, 11 at Thynne Mountain, 14 at Cascade Lookout and 23 at the Brookmere Dump for a total of 55 squirrels. The mean age and

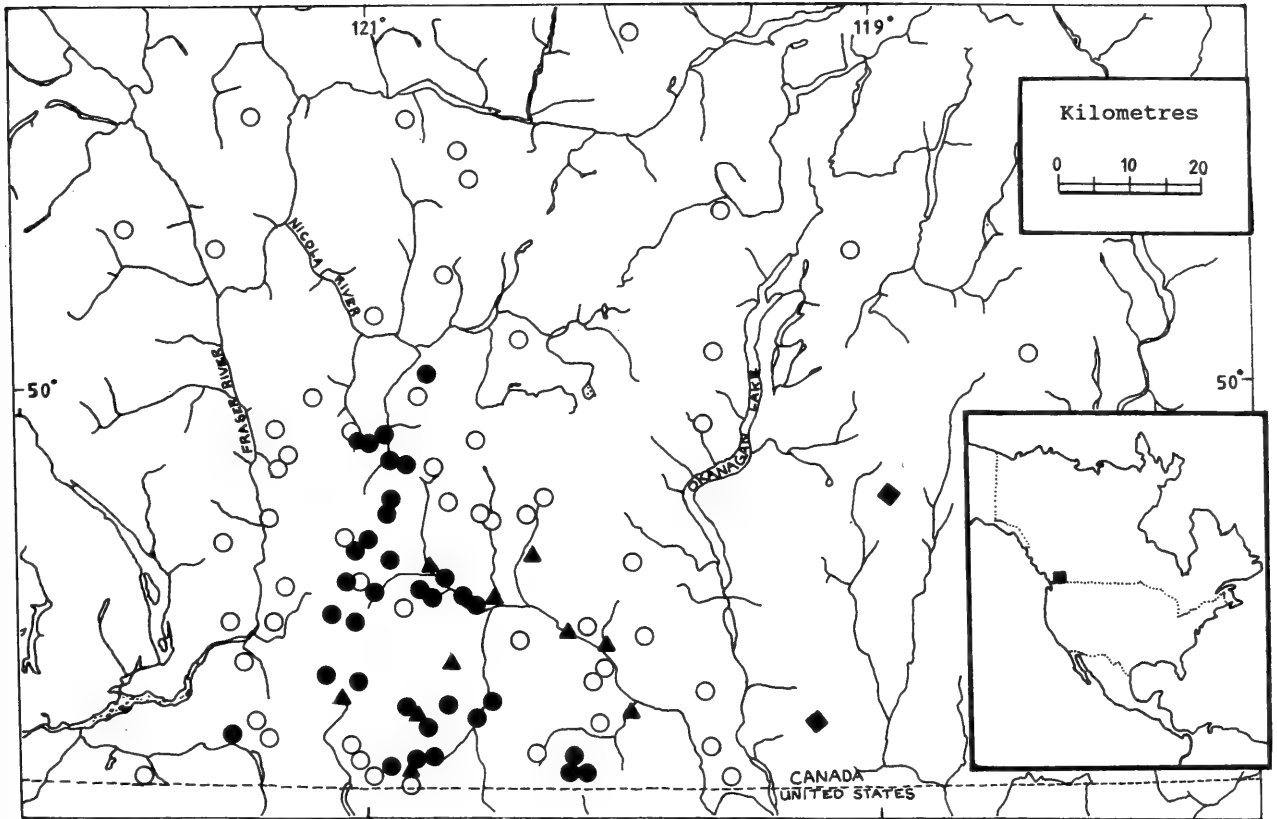


FIGURE 1. Map of survey area. ● = locations where *Spermophilus saturatus* was sighted during the survey; ○ = locations surveyed without any detection of *S. saturatus*; ▲ = locations where *S. saturatus* has been collected for museum specimens prior to 1989; ◆ = locations where *S. lateralis* was sighted during the survey.

sex composition of the 55 squirrels (Figure 2) was: adult female (31%), adult male (25%), yearling female (24%), yearling male (21%). Trapping in two consecutive years at Thynne Mountain showed that, of three adult females, four adult males, two young-of-the-year females and two young-of-the-year males (total of 11) marked in 1989, two adult females, two adult males, two yearling females, and one yearling male were recaptured in 1990. In addition, five new individuals (one adult female, one adult male, and three yearling females) were captured for the first time in 1990 at Thynne Mountain (Figure 2).

Sightings of *S. lateralis*

During the survey, *S. lateralis* was sighted at Big White Mountain (2300 m; 49°44'N 118°45'W) and Mount Baldy (2300 m; 49°08'N 119°16'W). Nagorsen (1995) also reported sighting of *S. lateralis* in Okanagan Mountain Provincial Park (520 m; 49°47'N 119°37'W) (Figure 1).

Visual counts survey method

For each of the four trapping locations, the proportion of total sightings for each time category was calculated (Table 3). The time to first sighting was less for larger populations (Table 3), and the likelihood of seeing a squirrel within the first hour

increased with the density of squirrels (Table 3; Figure 3).

Although observation periods did not always last until *S. saturatus* was sighted, the "60 +" time category in Table 3 assumes that *S. saturatus* would have been sighted given enough time. To support this assumption, four artificial points (one for each location) were created for a cumulative percent sighting value of 100 % at 10 000 cumulative minutes. These points were included in the data for finding the best fit curve, but are not depicted in Figure 3. The average cumulative percent sightings (y) for the four locations were plotted against cumulative time (t). The best fit curve, $y = 78(1 - e^{-0.14t})$ with $R^2 = 0.99$, reaches an asymptote at 78% (Figure 3). Although R^2 is high, the data points are widely scattered. If the four artificial points are excluded from the data set, the best fit curve is $y = 70(1 - e^{-0.21t})$ with $R^2 = 0.99$.

Discussion

The shorter time to first sighting and higher likelihood of seeing a squirrel within an hour of observation at the Cascade Lookout and Brookmere Dump sites as compared to the Iron Mountain and Thynne Mountain sites (Figure 3) suggests that *S. saturatus* is more easily detected where it occurs at higher relative abundance. The squirrels at the Cascade

TABLE 1. Location, coordinates, elevations and general habitats for locations where *Spermophilus saturatus* was sighted in 1989 and 1990. Survey methods include: survey form (F), road/opportunistic sighting (R) and observation by binoculars or spotting scope (O). Biogeoclimatic zones are based on Krajina (1959).

Elevation Survey Location	Coordinates	(m)	Method	Biogeoclimatic zone
1. Iron Mountain	50°03'N 120°46'W	1650	O	very dry cool montane spruce interior Douglas Fir
2. Gillis Lake	49°54'N 120°55'W	950	R	Montane Spruce
3. W of Gillis Lake	49°54'N 121°02'W	800	R	dry cold Englemann Spruce-Subalpine Fir
4. Gillis Mountain	49°54'N 120°59'W	1550	O	dry cool interior Douglas Fir
5. W of Brookmere	49°50'N 120°54'W	1000	R	dry cool interior Douglas Fir
6. Brookmere garbage dump	49°49'N 120°52'W	1000	O	dry cold Englemann Spruce-Subalpine Fir
7. N of Thynne Mountain	49°46'N 120°55'W	1450	R	dry cold Englemann Spruce-Subalpine Fir
8. Thynne Mountain	49°42'N 120°55'W	1950	O	wet mild Englemann Spruce-Subalpine Fir
9. S of Coquihala Lakes	49°38'N 121°00'W	1100	R	Montane Spruce
10. 4 km SW of Coquihala Lakes	49°36'N 121°04'W	1000	R	Montane Spruce
11. 8 km SW of Coquihala Lakes	49°35'N 121°06'W	1000	R	wet mild Englemann Spruce-Subalpine Fir
12. N of Grasshopper Mountain	49°35'N 120°54'W	1250	R	Englemann Spruce-Subalpine Fir
13. W of Needle Peak	49°34'N 121°07'W	1500	F	very dry hot interior Douglas Fir
14. NW of Coalmont road to Lodestone Lake	49°32'N 120°43'W	800	R	dry mild Montane Spruce
15. N of Tulameen River	49°30'N 120°46'W	1350	F	Montane Spruce
16. Blackburn Road	49°29'N 120°59'W	1000	R	dry cool interior Douglas Fir
17. between Coalmont and Princeton	49°29'N 120°44'W	1250	O	interior Douglas Fir
18. NW of Princeton	49°30'N 120°39'W	800	F	dry cool interior Douglas Fir
19. NE of Mount Snider	49°28'N 120°37'W	700	R	dry cool interior Douglas Fir
20. Treasure Mountain	49°26'N 121°07'W	1200	O	alpine tundra and Englemann Spruce-Subalpine Fir parkland
21. Mount Outram	49°25'N 121°03'W	1700	O	Englemann Spruce-Subalpine Fir
22. 3 km N of Dry Lake	49°17'N 121°10'W	1800-2100	O	alpine tundra and Englemann Spruce-Subalpine Fir parkland
23. W end of Manning Park	49°17'N 121°02'W	1200	F	Englemann Spruce-Subalpine Fir
24. Kicking Horse Campground, Manning Park	49°13'N 121°59'W	1000	F	Englemann Spruce-Subalpine Fir
25. Garrison Lake	49°11'N 121°49'W	1900	F	alpine tundra and Englemann Spruce-Subalpine Fir parkland
26. E of Copper Creek	49°13'N 120°41'W	1300	F	dry mild Montane Spruce
27. 8 km E of Manning Park	49°15'N 120°33'W	1000	R	dry cool interior Douglas Fir
28. First Brother Mountain, Manning Park	49°11'N 120°33'W	1050	R	dry cool interior Douglas Fir
29. William's Peak	49°10'N 120°46'W	2250	O	alpine tundra and Englemann Spruce-Subalpine Fir parkland
30. Strawberry Flats, Manning Park	49°07'N 121°30'W	1900	O	Mountain Hemlock
31. Coldspring Campground, Manning Park	49°04'N 120°53'W	1400	O	Englemann Spruce-Subalpine Fir
32. Cascade Lookout, Manning Park	49°05'N 120°48'W	1250	O	interior Douglas Fir
33. Resort Lodge, Cathedral Park	49°04'N 120°46'W	1750	O,F	dry Englemann Spruce Subalpine Fir
34. N of Ladyslipper Lake, Cathedral Park	49°04'N 120°12'W	2100	O	very dry cold Englemann Spruce Subalpine Fir
35. Lakeview Mountain	49°03'N 120°11'W	2250	O	very dry cold alpine tundra Englemann Spruce-Subalpine Fir parkland
36. Lakeview Mountain	49°02'N 120°09'W	2500	O	very dry cold alpine tundra Englemann Spruce-Subalpine Fir parkland

TABLE 2. Locations where *S. saturatus* specimens were collected in British Columbia

Location	Museum	ID#	Date
Princeton	BCPM	4956	1939
Princeton	BCPM	4955	1939
Manning Park, Easy Going Ridge	BCPM	5174	1945
Tulameen	BCPM	225	1917
Manning Park, Timberline Valley 6500 feet (2000 m)	BCPM	5175	1945
Manning Park, Mount Gordon 5500 feet (1700 m)	BCPM	5485	1949
Ashnola Forks	CVM	3554	1951
Ashnola Forks	CVM	3555	1951
Ashnola River	CVM	3556	1951
Princeton	CVM	3683	1943
Princeton	CVM	3684	1943
Princeton	CVM	3685	1943
Gibson Pass, Manning Park	CVM	4298	1952
17 miles (27 km) up Ashnola River	CVM	5629	1950
Blue River (NNE of Princeton)	CVM	5630	1947
12 miles (19 km) East of Princeton	CVM	5631	1952
Princeton	CVM	9305	1967
Manning Park	CVM	2966	1949
Manning Park	CVM	2968	1949
Manning Park	CVM	2969	1949
Ashnola Creek	NMC	28847	1950
Hope-Princeton Summit Pass	NMC	7856	1927
Hope-Princeton Summit Pass	NMC	7857	1927
Hope-Princeton Summit Pass	NMC	7858	1927
Near Princeton	NMC	28848	1950
Second Summit, Skagit River	NMC	1198	1905
Second Summit, Skagit River	NMC	1199	1905
Second Summit, Skagit River	NMC	1202	1905
Second Summit, Skagit River	NMC	1205	1905
Second Summit, Skagit River	NMC	1207	1905
Similkameen River, 2 miles (3 km) below mouth of Ashnola River	NMC	8966	1928
Similkameen River, 2 miles (3 km) below mouth of Ashnola River	NMC	8967	1928
Skagit	NMC	1165	1905
Stirling Creek mouth	NMC	8857	1928
Stirling Creek mouth	NMC	8883	1928
Stirling Creek mouth	NMC	8884	1928
Stirling Creek mouth	NMC	8889	1928
Stirling Creek mouth	NMC	8908	1928
Whipsaw Creek	NMC	1163	1905
Juniper Mountain, Similkameen, 1737 m	ROM	28577	1930
Lighting Lakes, Manning Park	USNM	235331	1920

Lookout and Brookmere Dump were also accustomed to human activity (i.e., sightseeing and feeding at Cascade Lookout and discarding garbage at the Brookmere Dump) and were likely not disturbed into hiding as much by our visual count surveys as the squirrels at the more remote sites, Iron Mountain and Thynne Mountain. Where species occur at low densities, caution should be taken when concluding that the species is absent at a site (Haila and Jarvinen 1983; McArdle 1990). A probability of the species absence at a site is a more realistic representation of data in which species could go undetected despite their presence. The average 78% probability of sighting *S. saturatus* within 60 minutes (Figure 3) gives

some credence to the conclusion of *S. saturatus*' absence on visits of an hour's duration. Herein, we assume that the survey for *S. saturatus*, including all methods of detection, give an approximate range and distribution of *S. saturatus*.

Our survey indicated that within the northern part of its range, *S. saturatus* is uncommon and its distribution fragmented. Three drainage systems surround the range of *S. saturatus* in British Columbia. To the west is the Fraser River; to the north is the Nicola River system; and to the east is the Okanagan system. Cowan and Guiguet (1965) state that *S. lateralis* extends westward only to the east side of the Okanagan Valley, rendering the ranges of the two

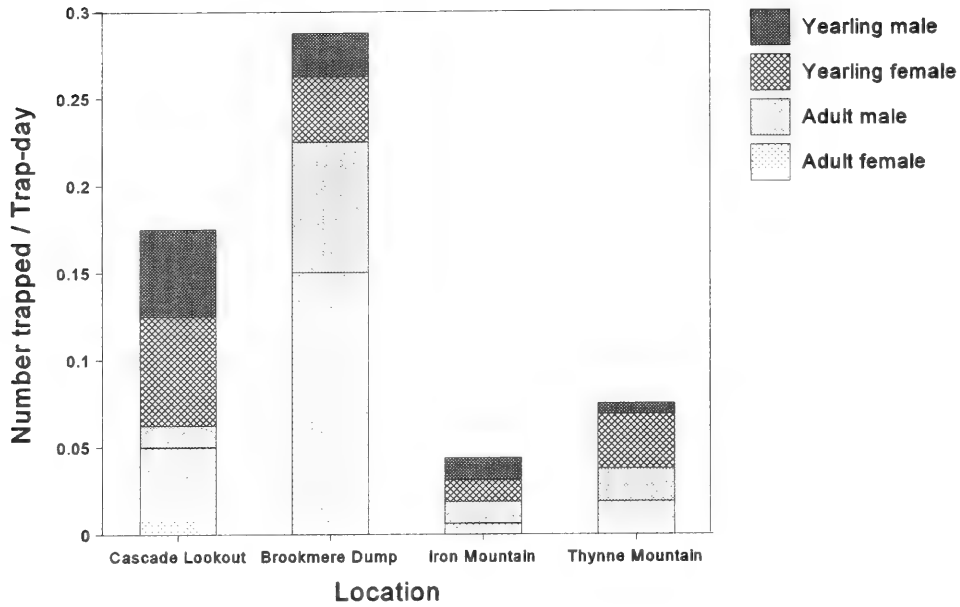


FIGURE 2. Age and sex composition and relative density of *Spermophilus saturatus* at four locations in British Columbia.

sibling species allopatric in Canada. The two species are not known to overlap elsewhere (Hall 1981), but there has not been any recent published survey of *S. lateralis*. A museum survey of locations of *S. lateralis* specimens collected from British Columbia (USNM, 36 specimens; CVM, 11 specimens; NMC, 21 specimens; ROM, 0 specimen; MMMN [Manitoba Museum of Man and Nature] 1 specimen; BCPM 0 specimens: see Appendix 2) did not reveal any location west of the Okanagan drainage and provided some substantiation that the two species do not overlap in the Okanagan Valley.

The increased range extending northward and westward as found during this survey probably reflects enhanced human access to these areas in recent years, and not a range expansion by the ground squirrel. Cowan and Guiguet (1965)

remarked that the squirrel's "northern limits are not known". The apparent shift of the eastern boundary westward in British Columbia (Figure 1) could be due to the competitive exclusion of *S. saturatus* by *S. columbianus*. While this hypothesis needs to be tested experimentally, circumstantial evidence for competitive exclusion includes observations of *S. columbianus* where *S. saturatus* used to be, such as the alpine meadows at Blackwall Peak (49°06'N 121°45'W) in Manning Park. *S. saturatus* has been residing in Manning Provincial Park prior to its designation in 1941 (USNM specimen # 235331 collected in 1920; Carl et al. 1952), but *S. columbianus* was first observed only after the construction of the highway traversing the park (Ted Underhill: personal communication) and was not included in the comprehensive natural history survey of Manning

TABLE 3. Percent of total first sightings occurring within consecutive ten minute intervals at four trapping locations

Time interval (minutes)	Iron Mountain	Thynne Mountain	Cascade Lookout	Brookmere Dump
0-10	20	23	73	50
11-20	0	31	0	33
21-30	0	15	9	17
31-40	13	0	0	0
41-50	0	8	0	0
51-60	13	0	0	0
60+	54	23	18	0
Number of sightings	15	13	11	6
Minimum number of <i>Spermophilus saturatus</i>	7	11	14	23

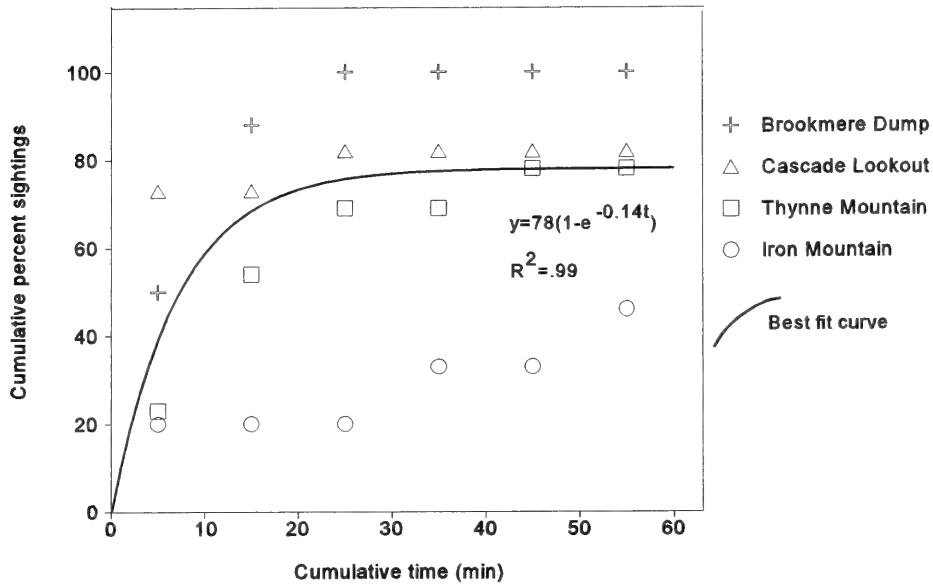


FIGURE 3. Probability of sighting *Spermophilus saturatus* within different time limits.

Park by Carl et al. (1952). Until 1959, the westernmost record of *S. columbianus* was still east of Manning Park (Sheppe 1959).

It is possible for *S. saturatus* to be outcompeted by *S. columbianus* because their ecological niches overlap and in some habitats *S. columbianus* would be dominant. Not only are both squirrels diurnal and semifossorial, but they also have some overlapping forage species, including Lupines (*Lupinus* spp.) and Sunflowers (*Taraxacum* spp.) (Elliot and Flinders 1985; Andrusiak and Harestad 1987; Trombulak 1988). Since *S. columbianus* occurs mainly in meadows, it could only exclude *S. saturatus* from meadow habitats, but not talus slopes or alpine forest where *S. saturatus* also resides (Reichel 1986). The larger size of *S. columbianus* (340-812 g) (Burt and Grossenheider 1976) and its cooperative social system (Michener 1983), would probably put *S. saturatus* (170-276 g) at a major disadvantage because resources would be used faster by *S. columbianus* and aggressive encounters are usually won by the larger animal. Evidence of competitive exclusion has already been observed between *S. lateralis* and *S. columbianus* in Rosland (49°05'N 117°49'W), British Columbia. At one site where all *S. columbianus* were removed, *S. lateralis* subsequently reclaimed the area (Leung 1991).

The discontinuous distribution of *S. saturatus* may be due to its poor colonizing ability and to the patchiness of its habitats. Brown (1971) presents data from the Great Basin suggesting that mammals on mountaintops are poor colonizers. Also, because *S. saturatus* is at the northern limit of its range in British Columbia, it likely experiences local extinctions in individual habitat patches and slow recolo-

nization (McCauley 1991), which may explain its sparse and unpredictable occurrence in British Columbia. Isozyme analysis of *S. saturatus* in British Columbia revealed very little genetic variation in the population (Leung and Cheng 1994). This indicates, at least theoretically, that the population may not adapt to rapid changes in environmental conditions.

For rodents, mortality is usually highest in the first year of life (Caughley 1977). However, overwinter survival of young born in 1989 at Thynne Mountain was not lower than that of adults. The presence of yearlings at all four trapping sites indicate that some individuals born the year before overwintered successfully and were recruited into the local population. The mean age and sex composition of the squirrels trapped at the four sites (Figure 2) was similar to that reported by Trombulak (1987) for *S. saturatus* populations in forest and meadow habitats in Washington State between 1980 and 1982. Decreased reproduction has been associated with *Spermophilus* species living in portions of their range where the growing season for plants is relatively short (Bronson 1979; Philips 1984). The recruitment and survivorship in the locations trapped seem to verify that *S. saturatus* does not have a high risk of imminent extinction in British Columbia. Since *S. saturatus* in British Columbia likely mature slower than their southern counterparts and hence begin breeding after the second winter of hibernation, a longer study is needed to follow individual reproductive success. We recommend long-term monitoring, at least every five years, of *S. saturatus* to assess changes in population structure and to address any threats to the ground squirrel.

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Appendix 1.

Coordinates and elevations for localities surveyed in British Columbia where no *Spermophilus saturatus* was sighted.

	Locality	Coordinates	Elevation (m)
1.	Mount Todd	50°55'N 119°56'W	2100
2.	Cornwall Hills	50°42'N 121°28'W	2000
3.	Mount Savona	51°42'N 120°49'W	1500
4.	Greenstone Mountain	50°37'N 120°38'W	1800
5.	Chuwahls Mountain	50°32'N 120°40'W	1900
6.	Tuktakamin Mountain	50°28'N 119°34'W	1800
7.	N of Devil's Lake	50°25'N 121°53'W	1700-2100
8.	Botanie Mountain	50°20'N 121°36'W	1400-1900
9.	Silverstar Mountain	50°22'N 119°03'W	1600-1850
10.	Swakum Mountain	50°18'N 120°42'W	1700
11.	Promontory Hills	50°12'N 120°58'W	1000,1700
12.	Mount Hamilton	50°08'N 120°21'W	1500
13.	Terrace Mountain	50°06'N 119°37'W	1600-1900
14.	Eureka Mountain	50°05'N 118°23'W	1900
15.	Stoyoma Mountain	49°59'N 121°13'W	2200
16.	Kane Valley Trail	49°49'N 120°44'W	1350
17.	Carrot Mountain	49°45'N 119°39'W	1500
18.	E of Boston Bar	49°54'N 121°23'W	1100
19.	W of Gillis Lake	49°55'N 121°05'W	1300
20.	Blue Lake	49°52'N 120°35'W	1100
21.	SE of Boston Bar	49°39'N 121°22'W	800
22.	Uztimus Road	49°47'N 121°20'W	500
23.	8 km E of Brookmere	49°49'N 120°40'W	1100
24.	Siwash Lake Road	49°43'N 120°21'W	1250
25.	Mount Pike	49°43'N 120°40'W	1400
26.	SE of Boston Bar	49°40'N 121°24'W	500
27.	Missezula Mountain	49°40'N 120°32'W	1500
28.	Chain Lake	49°44'N 120°19'W	1350
29.	Rampart Lake	49°39'N 120°30'W	1400
30.	N of Spuzzum Creek	49°38'N 121°34'W	1000
31.	Douglas Lake Trail	49°38'N 121°08'W	1300
32.	Isintok Mountain	49°34'N 119°58'W	1800
33.	E of Needle Peak	49°34'N 121°06'W	1500
34.	Emancipation Mountain	49°30'N 121°16'W	1100
35.	Lodestone Mountain	49°28'N 121°50'W	1850
36.	Dog Mountain	49°24'N 121°32'W	1000
37.	Oglivie Moutain	49°25'N 121°23'W	750-1000
38.	Stemwinder Road	49°25'N 120°09'W	1400
39.	Apex Mountain	49°28'N 119°55'W	2200
40.	Agate Mountain	49°23'N 120°24'W	1600
41.	S of Eureka Creek	49°20'N 121°28'W	500-900
42.	Whistle Creek Road	49°18'N 120°06'W	1600
43.	NW of IR10	49°16'N 120°09'W	2000
44.	Orofino Peak	49°15'N 119°41'W	1500
45.	Yola Creek	49°11'N 121°26'W	1000
46.	Crater Mountain	49°11'N 120°05'W	2000-2300
47.	Silverhope Creek	49°07'N 121°22'W	1000
48.	Shwatum Mountain	49°07'N 121°05'W	650
49.	Mount Kobau	49°07'N 119°40'W	1800
50.	W of Duruisseau Creek	49°06'N 120°23'W	1300-1700
51.	S of Nepopekum Mountain	49°03'N 121°00'W	600-1500
52.	Church Mountain	49°02'N 121°51'W	1000-1250
53.	Skyline Trail, Manning Park	49°02'N 120°55'W	1300-1700
54.	W of Mount Kruger	49°02'N 119°32'W	1000
55.	Frosty Mountain	49°01'N 120°50'W	1300-2400

Appendix 2.Locations of *Spermophilus lateralis* collected in British Columbia

Museum	Catalog#	Subspecies	Location	Collector	Date
CVM	1566**	<i>cinerascens</i>	Akamina River	J. Hatter	1945
CVM	3552*	<i>cinerascens</i>	Mount Rowe, Akamina Pass	I. McT. Cowan	1951
CVM	3553**	<i>cinerascens</i>	Mount Rowe, Akamina Pass	I. McT. Cowan	1951
CVM	447*	<i>tescorum</i>	Creston	Hatter and Cowan	1941
CVM	1568**	<i>tescorum</i>	Toby Creek	Cowan	1945
CVM	3207**	<i>tescorum</i>	Goat Peaks	P. W. Martin	1950
CVM	3208**	<i>tescorum</i>	Goat Peaks	P. W. Martin	1950
CVM	3686**	<i>tescorum</i>	Monashee Pass	A. C. Brooks	1937
CVM	5625**	<i>tescorum</i>	Pine River Pass	J. B. Boroch	1929
CVM	5626**	<i>tescorum</i>	Midge Creek	A. Racey	1935
CVM	5627**	<i>tescorum</i>	Monashee Pass	K. Racey	1937
USNM	106206	<i>tescorum</i>	Barkerville	A. C. Brooks	1900
USNM	106207	<i>tescorum</i>	Barkerville	A. C. Brooks	1900
USNM	106208	<i>tescorum</i>	Barkerville	A. C. Brooks	1900
USNM	106209	<i>tescorum</i>	Barkerville	A. C. Brooks	1900
USNM	106210	<i>tescorum</i>	Barkerville	A. C. Brooks	1900
USNM	106211	<i>tescorum</i>	Barkerville	A. C. Brooks	1900
USNM	106212	<i>tescorum</i>	Barkerville	A. C. Brooks	1900
USNM	106213	<i>tescorum</i>	Barkerville	A. C. Brooks	1900
USNM	106214	<i>tescorum</i>	Barkerville	A. C. Brooks	1900
USNM	106215	<i>tescorum</i>	Barkerville	A. C. Brooks	1900
USNM	106216	<i>tescorum</i>	Barkerville	A. C. Brooks	1900
USNM	174129	<i>tescorum</i>	Yellowhead Pass	J. H. Riley	1911
USNM	174149	<i>tescorum</i>	Moose River, South fork	N. Hollister	1911
USNM	174150	<i>tescorum</i>	Moose River, North fork	N. Hollister	1911
USNM	174151	<i>tescorum</i>	Moose River, North fork	N. Hollister	1911
USNM	174153	<i>tescorum</i>	Moose River, North fork	N. Hollister	1911
USNM	174154	<i>tescorum</i>	Moose Pass	N. Hollister	1911
USNM	174155	<i>tescorum</i>	Moose Pass	N. Hollister	1911
USNM	174156	<i>tescorum</i>	Moose Pass	N. Hollister	1911
USNM	174157	<i>tescorum</i>	Moose Pass	N. Hollister	1911
USNM	174159	<i>tescorum</i>	Moose Pass	N. Hollister	1911
USNM	174172	<i>tescorum</i>	Yellowhead Lake	N. Hollister	1911
USNM	180930	<i>tescorum</i>	Mount Selwyn	F. K. Vreeland	1915
USNM	209374	<i>tescorum</i>	Parsnip River, head	F. K. Vreeland	1915
USNM	209400	<i>tescorum</i>	Parsnip River, upper	F. K. Vreeland	1915
USNM	209405	<i>tescorum</i>	Parsnip River, middle	F. K. Vreeland	1915
USNM	210222	<i>tescorum</i>	Head Wapiti River	S. P. Fay	1914
USNM	222781	<i>tescorum</i>	Jarvis Pass	F. K. Vreeland	1916
USNM	257460	<i>tescorum</i>	Mount Selwyn, Peace River	W. G. Sheldon	1932
USNM	257461	<i>tescorum</i>	Mount Selwyn, Peace River	W. G. Sheldon	1932
USNM	257469	<i>tescorum</i>	Sukunka River, head	R. Borden	1932
USNM	257470	<i>tescorum</i>	Sukunka River, head	R. Borden	1932
USNM	257471	<i>tescorum</i>	Sukunka River, head	R. Borden	1932
USNM	257472	<i>tescorum</i>	Sukunka River, head	W. G. Sheldon	1932
USNM	257473	<i>tescorum</i>	Sukunka River, head	W. G. Sheldon	1932
USNM	551546	<i>tescorum</i>	Cranebrook	C. B. Garrett	1933
NMC	22833***	<i>tescorum</i>	Flathead	C. Wise	1952
NMC	22845**	<i>tescorum</i>	Flathead	C. L. Thatcher	1952
NMC	22846**	<i>tescorum</i>	Flathead	C. L. Thatcher	1952
NMC	9923***	<i>tescorum</i>	Goatfell	H. M. Laing	1929
NMC	9924***	<i>tescorum</i>	Goatfell	H. M. Laing	1929
NMC	9925***	<i>tescorum</i>	Goatfell	H. M. Laing	1929
NMC	10174***	<i>tescorum</i>	Goatfell, near Yahk	E.R. S. Hall 1	1929
NMC	47*	<i>tescorum</i>	Golden City	John Macoun	1885
NMC	10014***	<i>tescorum</i>	Green Mountain, Rossland	R. M. Anderson	1929
NMC	28840***	<i>tescorum</i>	Grouse Creek, Barkerville	L. Jobin	1946
NMC	28841***	<i>tescorum</i>	Grouse Creek, Barkerville	L. Jobin	1947
NMC	28843***	<i>tescorum</i>	Invermere	L. Jobin	1949

(Continued)

APPENDIX 2. *Concluded.*

Museum	Catalog#	Subspecies	Location	Collector	Date
NMC	28844**	<i>tescorum</i>	Invermere	L. Jobin	1949
NMC	9813***	<i>tescorum</i>	Old Glory Mountain, Rossland	H. M. Laing	1929
NMC	9814***	<i>tescorum</i>	Old Glory Mountain, Rossland	H. M. Laing	1929
NMC	9816***	<i>tescorum</i>	Old Glory Mountain, Rossland	H. M. Laing	1929
NMC	9824***	<i>tescorum</i>	Old Glory Mountain, Rossland	H. M. Laing	1929
NMC	9833***	<i>tescorum</i>	Old Glory Mountain, Rossland	H. M. Laing	1929
NMC	9761***	<i>tescorum</i>	Rossland	H. M. Laing	1929
NMC	892***	<i>tescorum</i>	Trail	W. Spreadborough	1902
NMC	893***	<i>tescorum</i>	Trail	W. Spreadborough	1902
MMMN	5496***	<i>tescorum</i>	British Columbia	Unknown	1973
BCPM	1156*	<i>tescorum</i>	Indian Point Mountain	T. McCabe	1927
BCPM	1191**	<i>tescorum</i>	Indian Point Mountain	T. McCabe	1928
BCPM	2117**	<i>tescorum</i>	Eva Lake	I. McT. Cowan	1937
BCPM	2118**	<i>tescorum</i>	Eva Lake	I. McT. Cowan	1937
BCPM	2119**	<i>tescorum</i>	Eva Lake	I. McT. Cowan	1937
BCPM	2120**	<i>tescorum</i>	Eva Lake	I. McT. Cowan	1937
BCPM	2121**	<i>tescorum</i>	Mount Revelstoke	K. Racey	1937
BCPM	2122**	<i>tescorum</i>	Monashee Pass	K. Racey	1937
BCPM	2123**	<i>tescorum</i>	Monashee Pass	I. McT. Cowan	1937
BCPM	2124**	<i>tescorum</i>	Monashee Pass	K. Racey	1937
BCPM	4957*	<i>tescorum</i>	Slocan Lake, Sandon	F. L. Beebe	1939
BCPM	4958*	<i>tescorum</i>	Ymir	F. L. Beebe	1940
BCPM	5034†	<i>tescorum</i>	Paradise Mine	C. G. Clifford	1944
BCPM	7519*	<i>tescorum</i>	Mount Mobley	F. H. H.	1959
BCPM	9641*	<i>tescorum</i>	Barkerville	J. Jobin	1946
BCPM	9662*	<i>tescorum</i>	Eigh Mile Lake near Wells	J. Jobin	1946
BCPM	9663*	<i>tescorum</i>	Invermere	J. Jobin	1949
BCPM	9664*	<i>tescorum</i>	Invermere	J. Jobin	1949
BCPM	9665*	<i>tescorum</i>	Invermere	J. Jobin	1949
BCPM	18500***	<i>tescorum</i>	Okanagan Mountain Provincial Park	D. Nagorsen	1992

*skin only; †skull only; **skin and skull; ***skin, skull, and skeleton.

The Recent Spread of Autumn-olive, *Elaeagnus umbellata*, into Southern Ontario and its Current Status

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Autumn-olive (*Elaeagnus umbellata* Thunb.) was extensively planted during the 1960s and 1970s to provide food and cover for wildlife, and has several other uses including reclamation, erosion control and interplanting in agroforestry. It has been discovered growing outside of cultivation throughout much of southern Ontario over the past 10 years. It has increased rapidly in parts of southern Ontario and the United States and is currently a competitive pest in some areas, hindering colonization of native species and competing with native vegetation. Autumn-olive is primarily a problem in open habitats on dry sandy soils. It has the potential to degrade native plant communities of natural sandy openings which contain significant native biodiversity.

Key Words: Autumn-olive, *Elaeagnus umbellata*, Elaeagnaceae, alien, weed, distribution, identification, invasion, Ontario.

Several alien woody plants have become serious competitive invaders of Canadian ecosystems and they pose major threats to the long term protection of native Canadian biodiversity. Information on the naturalization and spread of alien plants in Canada is relevant to the legislation restricting entry and to predictions which may enhance control. Here we report on naturalized occurrences of Autumn-olive (*Elaeagnus umbellata* Thunb.), also known as Umbellate Oleaster, Japanese Silverberry, or Asiatic Oleaster, a native of eastern Asia.

Economic Value

Autumn-olive has been available from plant nurseries and landscaping companies in Ontario for at least 30 years, and the cultivar “Cardinal” has been recommended for its attractive scarlet fruit and leaves silvery beneath (Sherk and Buckley 1968). It has also been planted to provide food and cover for wildlife and for erosion control (Henry 1980; Zarger 1980), and has been recommended as a nectar source for honey production (Sternberg 1982*). Autumn-olive is actinorhizal resulting in the improvement of soil quality through nitrogen fixation. Soil improvement capabilities make the plant valuable for reclamation of mine spoil (Brown et al. 1983; Hensley and Carpenter 1986) and in agroforestry. Interplanting with walnut

(*Juglans nigra*) for example, has improved the production of walnut in North America, resulting in the the highest yields and the highest return on investment (Schlesinger and Williams 1984; Campbell and Dawson 1989). It has been used extensively in European agroforestry. In Japan Autumn-olive is used for both pickles and the production of alcoholic beverages (Sakamura and Suga 1987). It is an easy shrub to propagate in nurseries and grows quickly producing visible results in a short time frame (Sternberg 1982). As a result of these qualities, it may have been more eagerly advertised than it should have, especially as a “wildlife enhancement shrub”. In fact, it ranks relatively low on the list of species used by birds as discussed in some depth by Sternberg (1982*).

History and Impact

A survey of all major Ontario herbaria (CAN, DAO, HAM, OAC, QK, TRT, TRTE, UWO, WAT) suggested that Autumn-olive has only recently escaped from cultivation in Ontario. The first Ontario collection of a possibly naturalized plant (*sub E. commutata*) was made by Aiken and Darbyshire at Bruce’s Pit near Bells Corners in Ottawa-Carleton in 1983. Very little spreading had occurred from equally spaced original plantings at this site by 1995. The earliest Ontario collection of a definitely naturalized plant was made in Haldimand-Norfolk by Sutherland and Gartshore in 1985, at which time it was reported by Sutherland (1987) as being uncommon in that region. This was the first

*Unpublished, see Documents Cited section, following Acknowledgments.

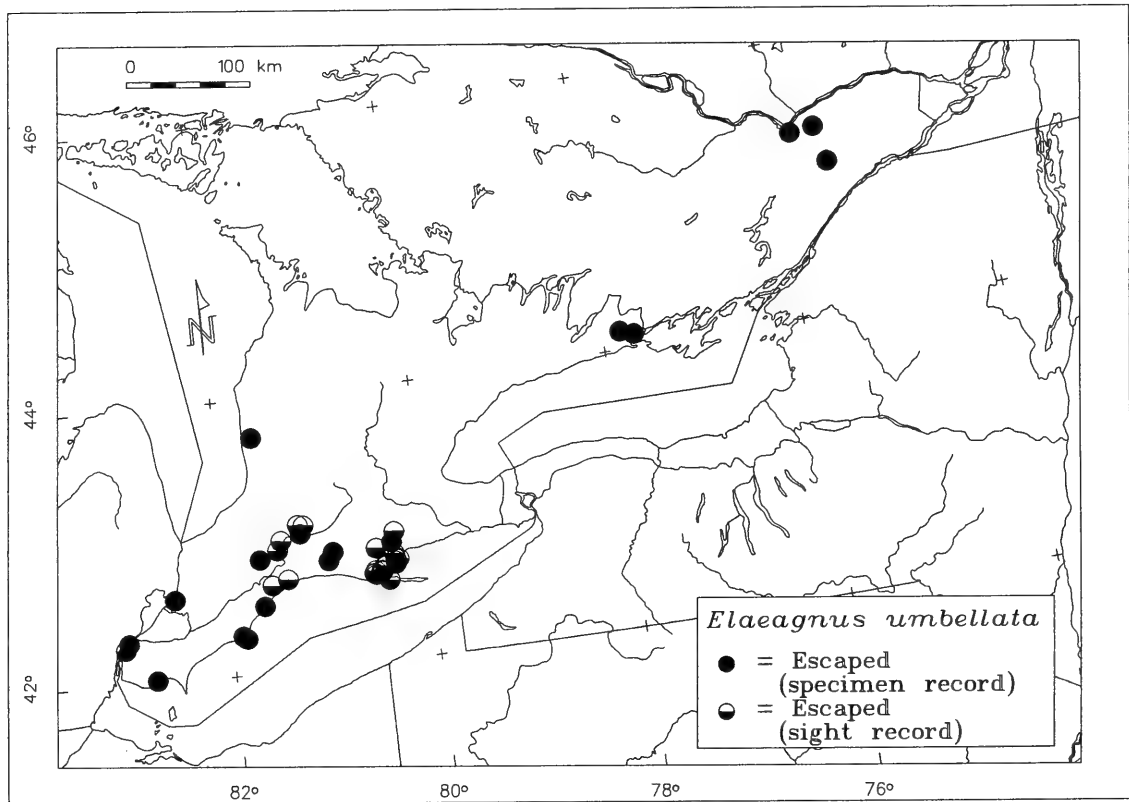


FIGURE 1. Distribution of Autumn-olive in Ontario based on specimens at CAN, DAO, MICH, TRT, TRTE and UWO, as well as sight records of M. J. Oldham and D. A. Sutherland.

published report for both Ontario and Canada. In the second published report for Ontario and Canada, Oldham et al. (1992), noted an adventive plant along a railway in Elgin County, but they noted also that it does not often escape cultivation (supporting this view by the observation that it was not listed by Morton and Venn (1990)). Over the past 10 years Autumn-olive has been discovered growing outside of cultivation throughout the southern part of the province (Figure 1). It has increased in both distribution and abundance on the Norfolk Sand Plain (Regional Municipality of Haldimand-Norfolk) to the point where it is now a very serious weed, largely as a result of being a significant competitor with native vegetation. Its soil improvement capabilities may lead to a reduction in significant native vegetation which is often associated with nutrient deficiency (Eckardt 1987*). The shrub has the potential to degrade natural sandy openings including prairie, savanna, barren, dune and shore communities that have been highly profiled for protection in Canada.

Naturalization and impact in other parts of North America appears to be similarly recent. For example, Autumn-olive was not recognized as adventive in Illinois in 1963, and was first planted in the state during the 1970s. It became a major problem about 10 years later (Ebinger and Lehnen 1981; Sternberg 1982*), as a result of becoming "highly

invasive" and forming dense stands at the expense of native vegetation. Ebinger and Lehnen (1981) reported up to 33975 stems/hectare with up to 30% being more than 5 dm high and frequencies of up to 97%. Zimmerman et al. (1993) recently reported it as a problematic invader of reestablished tallgrass prairie in Illinois.

Autumn-olive is a detriment to agriculture in some parts of Illinois and in West Virginia (Ebinger 1983). It is difficult to control since burned, mowed, or cut plants will resprout vigorously (e.g. Kuhns 1986*; Szafoni 1991), making the use of herbicides or hand pulling necessary. Eckardt (1987*) noted that Autumn-olive was only just beginning to be recognized as a potentially serious alien problem in the United States during the late 1980s, at which time it was still being distributed for use in wildlife plantings. Some university and museum-based botanists in the US have concluded that further planting of Autumn-olive would be "biologically unsound" or "biologically immoral". The shrub has also been described as having "the potential of becoming one of the most troublesome adventive shrubs in the central and eastern United States" (Ebinger and Lehnen 1981; Eckardt 1987*; Sternberg 1982*), based on prolific fruiting, rapid growth, site adaptability and avian dispersal. Few other introduced plants have so quickly become a subject of serious concern.

Regional variation in impact in Ontario

The escaped occurrences in the Ottawa district (Mountain Provincial Wildlife Area, Leitrim green-belt, Bruce's Pit) can all be traced to plantings 15 to 25 years old. Spread from these plantings has been minimal (5-8 plants from 10-25 planted shrubs), and the majority of the plants at each site are the original equally spaced plantings. At each of these sites other woody species are aggressively colonizing the open ground including *Rhamnus* spp., *Rhus* spp., *Populus* spp., and *Betula* spp. The sites included both sandy and clay-loam soils.

The situation further south in Ontario is very different. In the eastern Lake Ontario region and on the Norfolk sand plain the shrubs were aggressively invading sandy open habitat, and sometimes forming dense stands and evidently competing with native species in adjacent prairie and savanna relicts.

Dispersal

In many cases escaped plants appear to be a result of spread from nearby cultivated plants. At most of the Ottawa sites the shrubs produced fruit abundantly, at least on the lower branches. Younger shrubs appear to produce more fruit than older ones. The seeds, within juicy berries, are probably eaten and dispersed by many different mammals and birds. In the Ottawa area American Robin (*Turdus migratorius*), and Cedar Waxwing (*Bombycilla cedrorum*) have been observed eating the fruits (P. M. Catling, personal observation). These two birds as well as Eastern Bluebird (*Sialia sialis*), Swainson's Thrush (*Catharus ustulatus*), Hermit Thrush (*Catharus guttatus*), Gray Catbird (*Dumetella caroliniensis*), Northern Mockingbird (*Mimus polyglottos*), Bohemian Waxwing (*Bombycilla garrulus*) and European Starling (*Sturnus vulgaris*) have been observed eating fruits in other parts of southern Ontario (D. A. Sutherland, personal observation). Seeds regurgitated by, or passing through the digestive system of Robins remained viable (Sternberg 1982*). Raccoons (*Procyon lotor*), Skunks (*Mephitis mephitis*) and Opossums (*Didelphis marsupialis*) are also known to feed on the fruit (Szafoni 1991).

Habitat

Major infestations of Autumn-olive in Ontario are in areas of dry sandy soils. Although plantings exist on fine-textured, periodically wet soils over limestone, spreading has generally been very limited on such sites. In the eastern Lake Ontario area Autumn-olive was associated with Black Oak (*Quercus velutina*) and/or Trembling Aspen (*Populus tremuloides*) in semi-open areas with Canada Bluegrass (*Poa compressa*). On the Norfolk sand plain, Autumn-olive has been found most frequently in a variety of dry to mesic sandy, forested and open to

semi-open habitats including: deciduous and mixed forests dominated by Black Oak, White Oak (*Quercus alba*), White Pine (*Pinus strobus*) and Red Maple (*Acer rubrum*); Red Cedar (*Juniperus virginiana*) glades; prairie/savannah relicts dominated by Indian Grass (*Sorghastrum nutans*); and coniferous plantations. It has also been found in seasonally wet, open floodplain thickets; on open clay hillsides and roadside banks; on gravelly till in openings in White Cedar (*Thuja occidentalis*) floodplain slope woodland; on raised sandy knolls in an open to semi-open graminoid fen; and on low sand dunes in Eastern Cottonwood (*Populus deltoides*) savannah. Soil pH at these sites ranges from 5-7 and a similar pH range is reported from U.S. sites (Eckhardt 1987*).

Prospects

Although some of the places in the U.S. where it has been reported as a serious pest are distant and have a warmer climate than Ontario, it is a competitive invader in the adjacent states of Michigan (Voss 1985), New York (personal observation) and Ohio (Cooperrider 1995). In Michigan, Voss (1985) reported that it is "too freely escaping" and "thoroughly naturalized as a weed". Some of the shrubs at eastern Lake Ontario sites had dead upper branches suggesting winter kill, but the plants were still aggressively spreading. Sherk and Buckley (1968) indicate that it can survive up to the limit of hardiness zone 5, which includes the region south of a line from the the lower Ottawa Valley to Georgian Bay. Cultivated plants are known to vary in their hardiness (Sternberg 1982*), but at the very least a large portion of southern Ontario appears to be within the range hardiness.

Monitoring and research on reproduction and dispersal rates are necessary to further document the degree of threat (Eckardt 1987*). Research on the effects on the nitrogen cycle in infertility-dependent natural communities is also desirable. The decline of Autumn-olive in plantations in Illinois due to disease (Sternberg 1982*) suggests that natural controls may reduce the competitiveness of dense stands. Depending on the effectiveness of natural controls, biological control methods may have to be considered.

For a shrub that was not known as a wild plant in Ontario 10 years ago, Autumn-olive has spread very rapidly, but the main problems of competition with native flora may be limited to areas with sandy soils. In particular the sandy shores of the Great Lakes and the sandy areas of southern and eastern Ontario are the most susceptible. These areas are particularly important in terms of native biodiversity and are already seriously impacted.

Identification

Although this shrub is becoming common over

much of the northeastern United States (eg., Gleason and Cronquist 1991), it has not previously been reported as escaped from cultivation in Ontario in the standard reference texts (eg., Soper and Heimburger 1982; Morton and Venn 1990) or from Canada (eg., Boivin 1966-1967; Scoggan 1979). Consequently it is not expected and is not included in some of the keys frequently utilized to identify southern Ontario plants.

Autumn-olive is one of six species in the Elaeagnaceae occurring in Ontario. Soapberry (*Shepherdia canadensis* (L.) Nutt.) is a widespread

native species. Silverberry (*Elaeagnus commutata* Bernh.) is native only in northern Ontario. Russian Olive (also called Narrow-leaved Oleaster, *E. angustifolia* L.) is a cultivated and occasionally escaped in Ontario (but becoming more common). The other three including Sea-buckthorn (*Hippophae rhamnoides* L.), Thorny Buffalo-berry (*Shepherdia argentea* Nutt.) and Multi-flowered Oleaster (*Elaeagnus multiflora* Thunb.), are all cultivated, mostly in southern Ontario. These species can be separated using the following characteristics:

- 1a. Leaves opposite..... 2
- 2a. Leaves green and nearly glabrous above; plants not thorny
..... *Shepherdia canadensis* (L.) Nutt. (Soapberry, Canadian Buffalo-berry)
- 2b. Leaves silvery on both sides; plants thorny *Shepherdia argentea* Nutt. (Thorny Buffalo-berry)
- 1b. Leaves alternate 3
- 3a. Leaves linear *Hippophae rhamnoides* L. (Sea-buckthorn)
- 3b. Leaves lanceolate, ovate or elliptic 4
- 4a. Branchlets and leaves with only silvery scales; perianth tube as long as the calyx lobe;
fruit yellow with silvery scales *Elaeagnus angustifolia* L. (Russian Olive)
- 4b. Branchlets and leaves with both brown and silvery scales; perianth tube as long as or much longer
than the calyx lobe; fruit silvery or red 5
- 5a. Leaves silvery on both sides; fruit silvery *Elaeagnus commutata* Bernh. (Silverberry)
- 5b. Leaves silvery beneath, green above; fruit becoming red 6
- 6a. Perianth tube as long as calyx lobes; stalk of fruit 1.5-2.5 cm long
..... *E. multiflora* Thunb. (Multi-flowered Oleaster)
- 6b. Perianth tube longer than the calyx lobes; stalk of fruit approx. 1 cm long
..... *E. umbellata* Thunb. (Autumn-olive)

Specimens Examined: ONTARIO: DUNDAS, GLEN-GARRY & STORMONT: 10 km W of Winchester, 45°05'N, 75°29'W, 29 June 1990, *Shchepanek & Dugal 8628* (CAN), October 1995, *Catling s.n.* (DAO). ELGIN: Aylmer, Carnation Milk property, 13 Aug. 1991, *W. G. Stewart* (UWO). Springfield, UTM 054415, 31 July 1992, *Oldham 14042* (UWO). 1.5 km NE of Elgin-Kent border, UTM 461035, 9 Aug. 1993, *Oldham & Vanderjeugd 15374* (MICH). ESSEX: Cedar Creek, UTM 537529, *Allen & Sutherland 1340* (TRTE). Windsor, UTM 368836, 27 Oct. 1993, *Oldham 15956* (DAO). HALDIMAND-NORFOLK: 1.5 km NE of Jacksonburg, UTM 317159, 13 Sept. 1985, *Sutherland & Gartshore 6679* (TRTE). HURON: 1 km S Benmiller, UTM 495405, 11 June 1993, *Reznicek et al. 9483* (MICH). KENT: Rondeau Prov. Park, South Point trail, 42°15'25"N, 81°51'15"W, 11 Oct. 1994, *Larson 3664* (DAO), 30 July 1995, *Larson 3908* (TRT). LAMBTON: Walpole Island Indian Reserve, UTM 747167, 8 August 1986, *Allen et al. 2744* (TRTE). NORTHUMBERLAND: Brighton Twp., Goodrich-Loomis Conservation Area, 44°07'38"N, 77°49'17"W, June 1994, *Brownell s.n.* (DAO), 21 May 1995, *Catling 20722* (DAO). 4 km N of Smithfield, 44°05'40"N, 77°41'20"W, 18 Aug. 1995, *Catling s.n.* (DAO).

Murray Twp., Mayhew Cr. area, 4 km NW of Smithfield, 44°05'58"N, 77°40'11"W, 25 June 1995, *Blaney s.n.* (DAO). OTTAWA-CARLETON: Bells Corners, Bruce's Pit, 45°19'45"N, 75°48'20"W, 2 June 1983, *Aiken & Darbyshire s.n.* (DAO), October 1995, *Catling s.n.* (DAO). Leitrim, 45°20'50"N, 75°33'50"W, 15 Sept. 1995, *Catling s.n.* (DAO).

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The Distribution and Numbers of Bowhead Whales, *Balaena mysticetus*, in Northern Foxe Basin in 1994

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Aerial reconnaissance surveys were conducted in June, 1994, to document the distribution of Bowhead Whales in the coastal waters of Foxe Basin and Roes Welcome Sound during the spring migration. The summer distribution of Bowheads in northern Foxe Basin was examined using both aerial surveys and boat-based observers. Results indicated that there are potentially three migration routes used by Bowheads to enter Foxe Basin and that once in northern Foxe Basin, Bowheads aggregate in a well-defined area north of Igloolik Island. Three systematic aerial strip surveys were done in August to estimate the number of surface whales present in northern Foxe Basin. Estimates of 256 ± 31.3 and 284 ± 48.6 Bowheads were derived from two useable surveys.

Key Words: Bowhead Whale, *Balaena mysticetus*, eastern Canadian Arctic, Foxe Basin, distribution, numbers.

By the early 20th century, Bowhead Whale, *Balaena mysticetus* Linnaeus 1758, numbers in the eastern Canadian Arctic were depleted by commercial whaling (de Jong 1983; Reeves et al. 1983). Other than reports by local residents that stocks are recovering (Anonymous 1995*), little is known about the current status of these whales. The most recent published estimate of Bowhead numbers in northern Hudson Bay and Foxe Basin, is “at least a few tens” of animals (Reeves and Mitchell 1990) based on examination of opportunistic sightings. There has been no systematic attempt to document Bowhead numbers in this area. Spring and fall migration routes are not well documented (Moore and Reeves 1993) and there has been only one survey (McLaren and Davis 1982*) to locate the wintering area used by these Bowheads. In addition, the summer distribution of animals in this area, although generally known from whaling records and recent sightings (Reeves et al. 1983), has not been systematically studied.

In 1994, we began a study of Bowhead whales in Foxe Basin to gather information on spring and summer distribution and on the numbers of whales using Foxe Basin during the summer open water period. Aerial reconnaissance surveys were conducted in late June to gather information on spring distribution. Additional aerial reconnaissance surveys were flown in August to document summer distribution. Sightings from boats also provided information on both spring and summer distribution. Systematic aerial strip surveys were flown on three days in mid-

August to estimate how many Bowheads were present in northern Foxe Basin.

Methods

June reconnaissance surveys focussed on the coastal waters of Melville Peninsula, Roes Welcome Sound and the east and south east portions of Southampton Island (Figure 1). Fury and Hecla Strait was surveyed on 24 June. A flight on 28 June along the Igloolik ice edge was conducted in response to a hunter report of Bowheads having been seen along the ice. On this day, the survey aircraft departed from Hall Beach. On all other days, the aircraft left from Igloolik. Wind and ice conditions were noted during each survey.

In August, reconnaissance surveys were flown only in northern Foxe Basin, including Fury and Hecla Strait, Gifford Fiord and Steensby Inlet (Figure 2). Transects were also flown between Hall Beach and Rowley Island. Wind and ice conditions were recorded during each survey.

All reconnaissance surveys were flown with a deHavilland Twin Otter equipped with a Global Positioning System (GPS), at an altitude of 338 m at 204 to 222 km/h (110 to 120 knots). All windows were flat. In June, one observer sat in the co-pilot's seat and three observers (two on the pilot's side and one on the co-pilot's side) sat in the passenger section of the plane. For the surveys in August, one observer sat in the co-pilot's seat and two observers sat, one on either side, in the passenger section. Although the surveys were primarily for Bowhead Whales, incidental sightings of other species were also recorded. Belugas (*Delphinapterus leucas*) and Walrus (*Odobenus rosmarus*) made up the majority of sightings of other marine mammals.

*See Documents Cited section between Acknowledgments and Literature Cited.

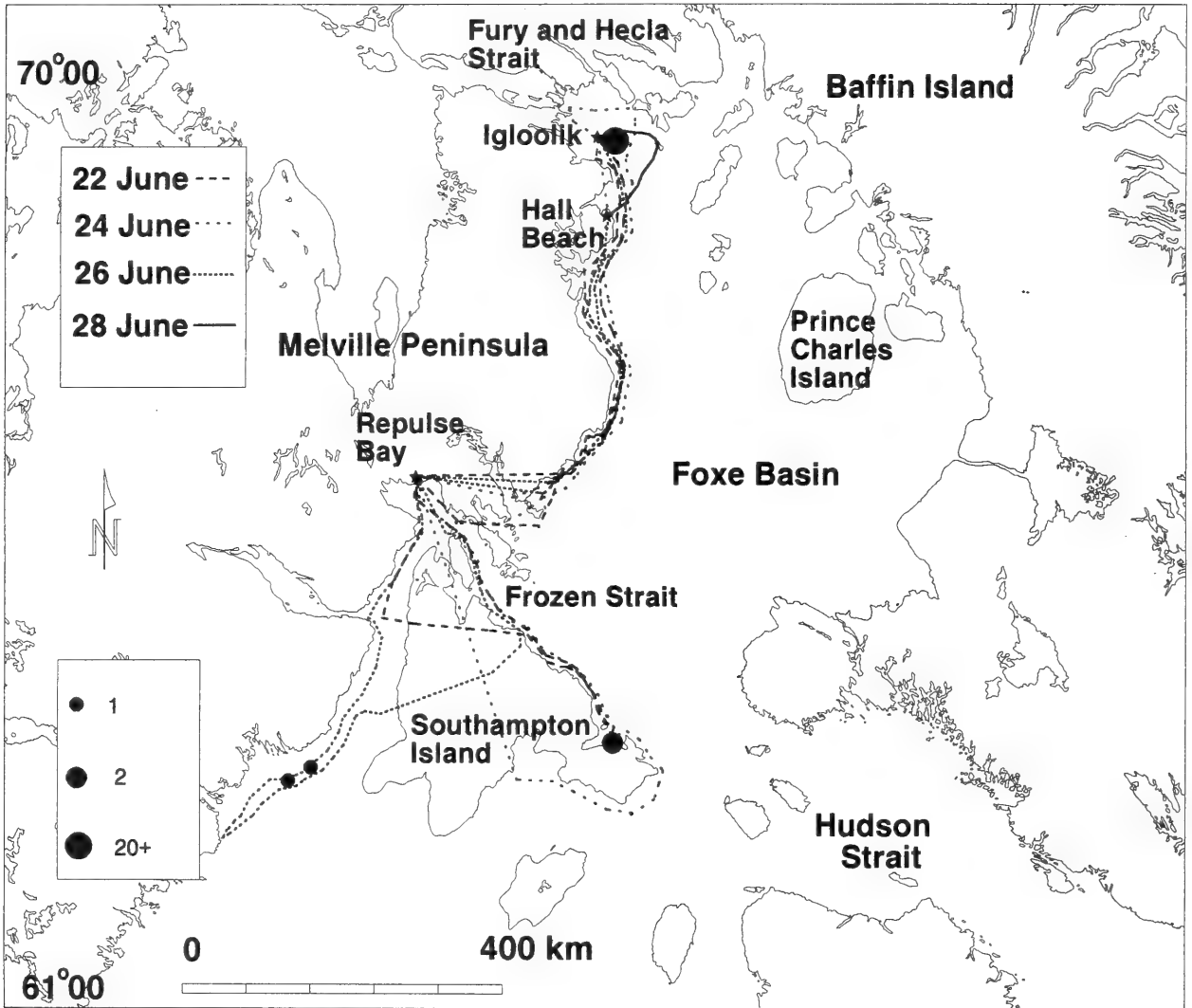


FIGURE 1. Aerial reconnaissance survey routes flown and Bowheads seen in June, 1994. Repulse Bay was used as a refuelling location.

Survey routes were documented by the observer in the co-pilot seat by recording the time of day and GPS location every 3 to 10 min or when the plane changed bearing. The GPS locations of marine mammal sightings were also recorded. Observers in the passenger section of the plane recorded the time of day of each sighting. The latitude and longitude of these sightings were later determined by matching time of day with the GPS data used to plot the survey routes.

Local hunters reported the date, location and number of Bowheads they sighted opportunistically, during their travels by boat in northern Foxe Basin. The authors (BP and TQ) recorded the date, location and number of whales seen during boat-based surveys to photograph naturally marked Bowheads.

Both boat-based sightings and aerial reconnaissance data indicated that, in August, Bowheads were aggregated in a relatively well-defined area north of Igloolik Island. Strip surveys were therefore flown to

estimate the numbers of Bowheads using the area. The survey block was located between $82^{\circ}15'$ and $80^{\circ}35'W$ and extended approximately from the south shore of Richards Bay or the north side of Igloolik Island to the south coast of Baffin Island (Figure 3). Survey transects were north-south and spaced about 6.5 km (10 min of longitude) apart (Table 1). The complete survey block was sampled on each of three days: 11, 13 and 15 August. The aircraft remained on transect at all times and did not break off from the flight path to examine individual groups. The entire survey block was sampled in 2 to 2.5 hours.

We used the same deHavilland Twin Otter for the strip surveys as was used for reconnaissance surveys and, again, flew at an altitude of 338 m at 204 to 222 km/h (110 to 120 knots). Aircraft position was monitored using the Global Positioning System in the plane; the observer in the co-pilot's seat recorded both time of day and GPS location at the beginning

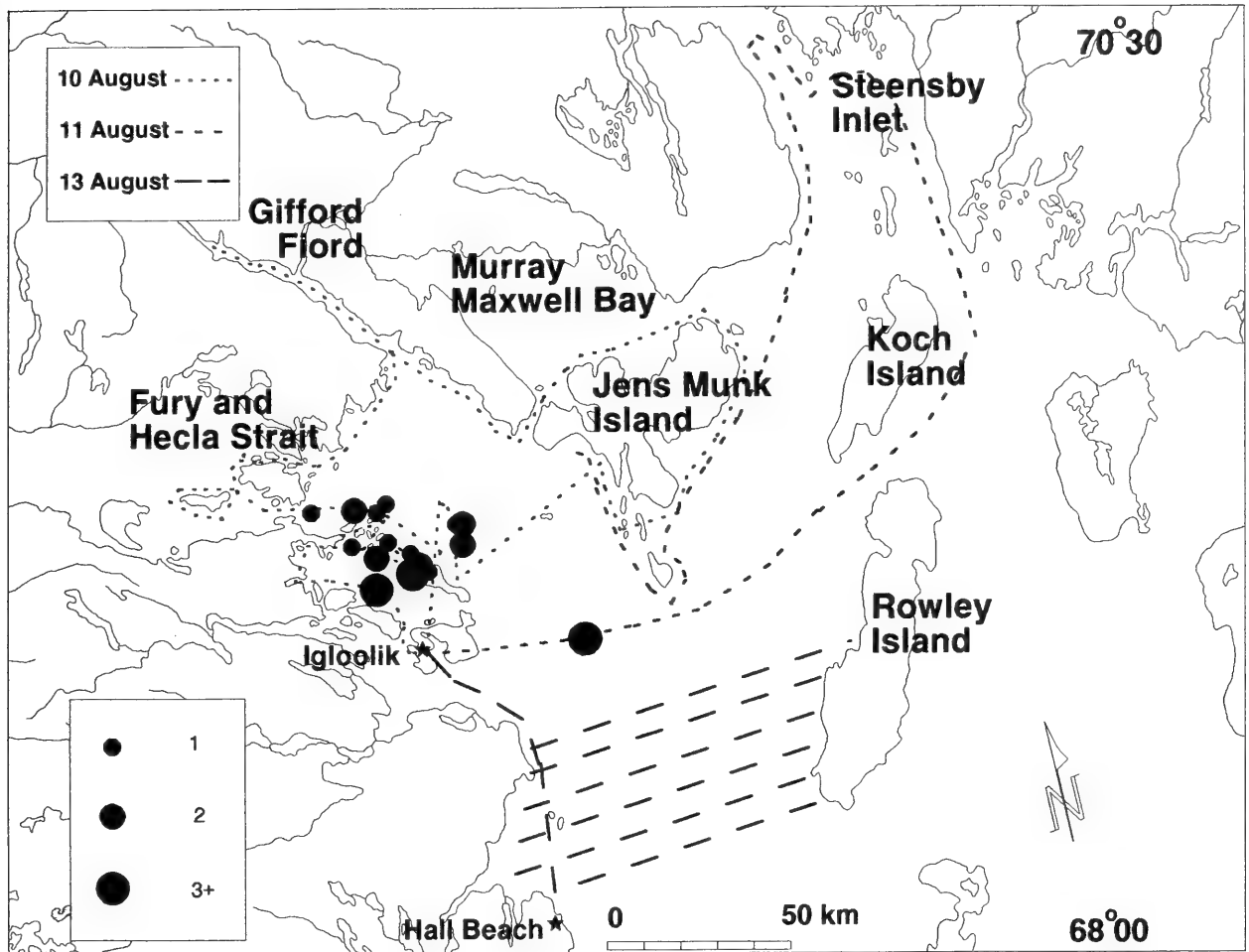


FIGURE 2. Aerial reconnaissance survey routes flown and Bowheads seen in August, 1994.

and end of each transect. This observer also recorded Bowhead and other marine mammal sightings along with their GPS locations. The two observers in the rear of the aircraft recorded the time of day, species and group size of each sighting. The location of these sightings was determined by matching time of day with the GPS data recorded by the observer in the co-pilot's seat.

All sightings, including those of the pilot, were used to tabulate numbers seen. Inclusion of the sightings made by the pilot and the observer in the co-pilot's seat resulted in sampling of the strip under the plane because animals seen ahead of the aircraft were counted. Data were checked for duplicate sightings to ensure that Bowheads seen by more than one observer were counted only once in the analysis. Observers remained in the same seats throughout the survey.

Using an inclinometer, the survey strip width was estimated to be 600 m on either side of the aircraft. Animals estimated to be within 600 m of the aircraft were counted. Identification of species and accurate estimation of group size was found to be

difficult for whales more than about 600 m from the aircraft; however, sightability of whales with distance from the aircraft was not systematically documented. Inclinometer readings were periodically taken during the survey to confirm that sightings were within 600 m.

Data from the 13 August survey were not used because Beaufort 4-5 wind conditions reduced visibility of the whales. The number of Bowhead sightings made in this survey was about half that made in the other two and most of these sightings were made along the flight line of the plane thus the strip width appeared to be reduced from what it was on calm days.

Using the method outlined by Kingsley (1993), the total number of whales sighted on each day was multiplied by an expansion factor k , calculated as

$$k = S / W \quad (1)$$

where S = transect spacing and W = strip width. Transect spacing averaged 6.54 on 11 August and 6.42 on 15 August. Slight differences in transect placement from one survey to the next resulted in

TABLE 1. Transect locations, transect lengths and Bowhead counts from systematic aerial surveys conducted on 11 and 15 August in northern Foxe Basin.

Transect Number	Longitude	Length km on 11 August	Count on 11 August	Length km on 15 August	Count on 15 August
1	82° 15'	27.4	0	22.4	0
2	82° 05'	34.1	2	27.6	0
3	81° 55'	35.9	10	34.1	0
4	81° 45'	46.3	3	41.9	3
5	81° 35'	52.0	21	44.8	3
6	81° 25'	49.6	5	49.4	12
7	81° 15'	40.0	6	43.0	35
8	81° 05'	43.3	0	32.0	0
9	80° 55'	32.6	0	23.7	0
10	80° 45'	27.4	0	22.0	0
11	80° 35'	25.4	0	20.7	0

variation in average transect spacing. Strip width was estimated to be 1200 m. The derived estimate of numbers

$$\hat{N} = k \sum_{j=1}^J x_j \quad (2)$$

where J = the number of transects and x_j = the number of whales counted on the j^{th} transect is applicable only to the survey block in northern Foxe Basin and cannot be applied to the whole geographic range of the stock.

The variance of the estimate of numbers was also calculated following the method used by Kingsley (1993) where

$$\hat{V} = \frac{k(k-1)J}{2(J-1)} \sum_{j=1}^{J-1} (x_j - x_{j+1})^2 \quad (3)$$

Standard errors of the estimates of Bowhead numbers are reported.

Results and Discussion

In June, Fury and Hecla Strait was blocked by land-fast ice (Figure 4). The northern portion of Foxe Basin was open and a shore lead extended south along the coast of Melville Peninsula. The southern portion of Foxe Basin was covered with unconsolidated ice. Cloud-free satellite images of Roes Welcome Sound and Frozen Strait were not available for the spring survey period, however, we saw from the aircraft that Frozen Strait was also blocked by land-fast ice. Land-fast ice was also present in Roes Welcome Sound from just south of Wager Bay at about 65°07'N to about 64°32'N. North of Wager Bay, a shore lead extended along the mainland coast to about 66°11'N. By August, ice in Fury and Hecla Strait had broken up and Foxe Basin was relatively ice-free.

Reconnaissance surveys flown on 22, 24 and 26 June found few Bowheads (Figure 1). We saw no

Bowheads along the coast of Melville Peninsula and only four in the vicinity of Southampton Island. Hunter reports of Bowheads at the Igloolik ice edge were received on 28 June and an aerial count, made the same day, indicated that at least 20 whales were present (Figure 1) but, on 29 June, we counted at least 30 whales from a boat. With the exception of two possible sub-adults, all whales seen appeared to be large adults. Observations from both the plane and boat indicated that the whales were probably feeding. They dived repeatedly, often raising their flukes out of the water and remained submerged for up to 20 min. Boat-based observations made during the break-up period indicated that the whales were seen in the same general location until the ice began to disintegrate. Whales then moved northward through the deteriorating ice, using melt holes for breathing.

Early whalers believed that Bowheads migrated from the high arctic through Fury and Hecla Strait into Foxe Basin (Reeves et al. 1983). Early whaling reports (Reeves et al. 1983) also indicated that bowheads in Roes Welcome Sound were thought to migrate through Frozen Strait into Foxe Basin. Both Frozen Strait and Fury and Hecla Strait were blocked with land-fast ice during the June reconnaissance surveys so whales found at the ice edge had to have arrived through Foxe Basin which was open. Up to three migration routes may, therefore, be used by bowheads to move into northern Foxe Basin.

Local hunters from both Igloolik and Hall Beach indicated that Bowheads are commonly seen in and around Fury and Hecla Strait after the ice has broken up. Two sightings of Bowheads (see Figures 1 and 3) were reported in the vicinity of Fury and Hecla Strait in 1994, although movement through the channels was not documented.

Bowheads were seen along the coast of Melville Peninsula, in the vicinity of Hall Beach, in July (Figure 5). Their distribution in August was centred in an area north of Igloolik Island (Figures 2 and 5)

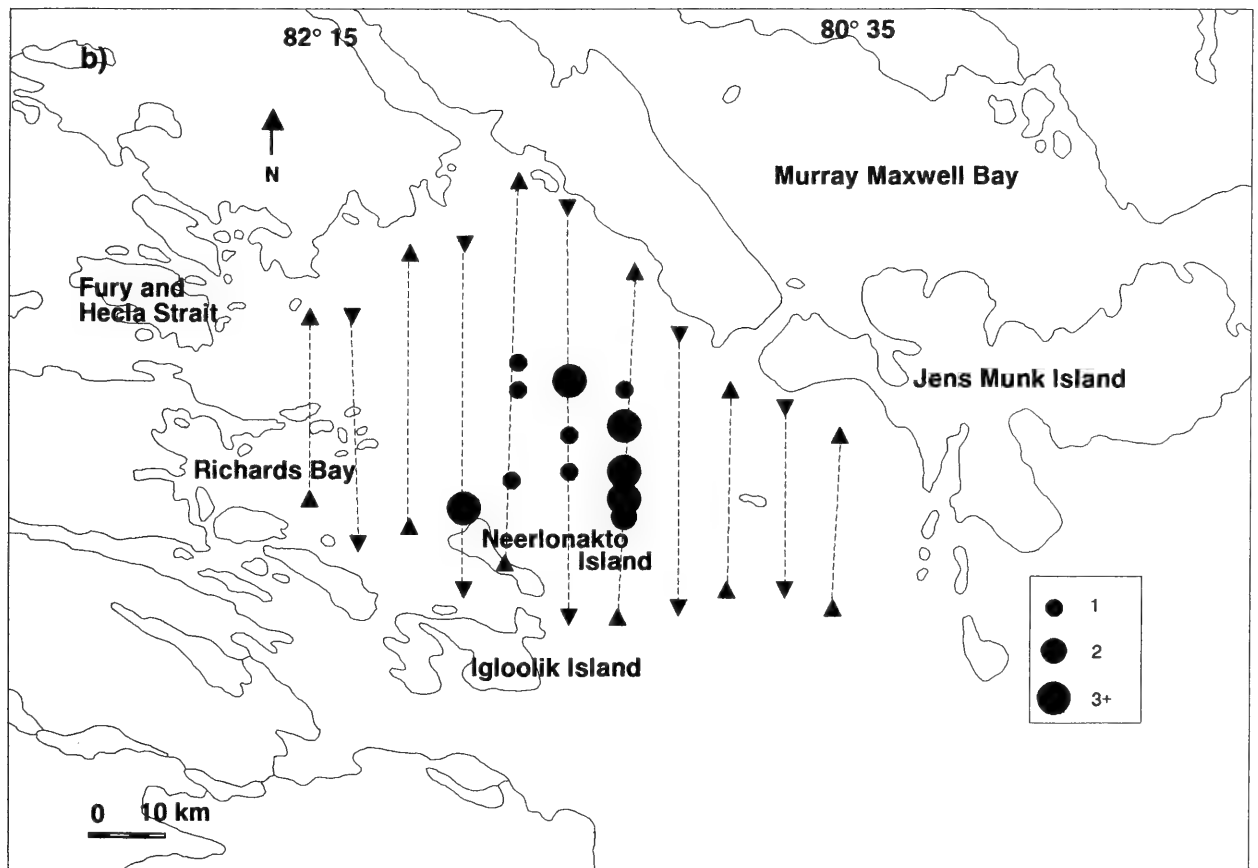
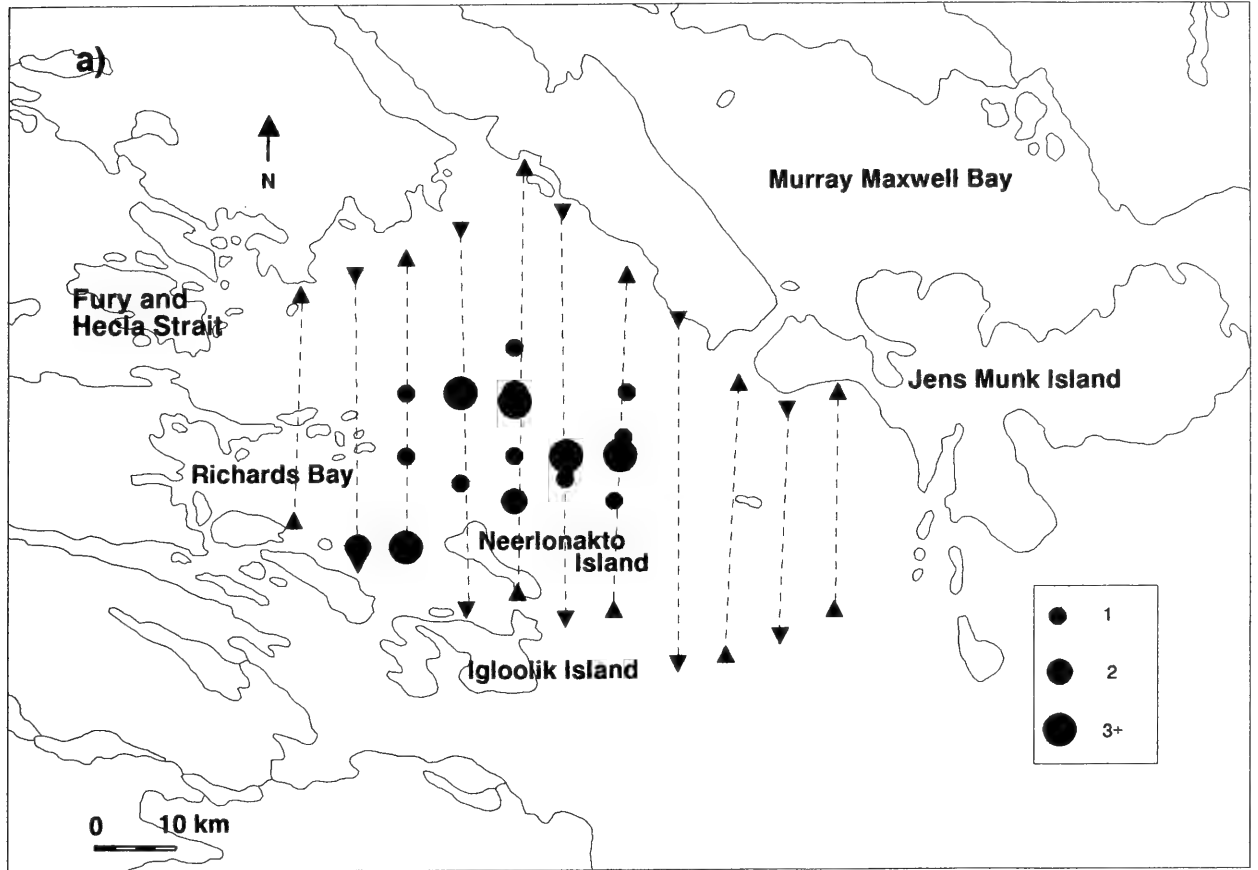


FIGURE 3. Locations of survey transects and Bowhead sightings during systematic strip surveys on (a) 11 August and (b) 15 August, 1994.



FIGURE 4. Satellite image of ice conditions during reconnaissance surveys in northern Foxe Basin, including Fury and Hecla Strait in June, 1994.

where they were consistently found throughout the summer, associated with loose pack ice. Both fluke-up diving and skim feeding (see Wursig et al. 1989) were observed in this area. Other behaviours such as tail-slapping, rolling and, apparently, sleeping were also observed. Two calves were seen from the boat and two were also seen from the aircraft. It is not known whether these were the same or different calves.

Based on observations from reconnaissance surveys, the area between $82^{\circ}15'$ and $80^{\circ}35'W$ was selected for systematic surveys. From these surveys, we estimated 256 ± 31.3 Bowheads in the survey block on 11 August and 284 ± 48.6 Bowheads on 15 August (Figure 5), based on sightings of 47 and 53 individuals respectively (Table 1). The distribution of whales was somewhat more clumped on 15 August, thus the Standard Error is wider than the one calculated for the survey on 11 August.

Underestimation of strip width would result in an overestimation of Bowhead numbers. Harwood and Borstad (1985), flying at an altitude of 305 m, used a 2 km wide strip for Bowhead whale surveys in the southeast Beaufort Sea. Their distribution of sighting

distances indicated that Bowheads were visible up to a distance of 1100 m. If a strip width of 2 km were to be assumed in the present study, estimates of surface Bowheads would reduce to 154 ± 17.3 (11 August) and 170 ± 26.8 (15 August).

The surveys conducted in 1994 were intended to provide a minimum estimate of visible Bowhead present in Foxe Basin. Future surveys would benefit from using line transect methods where sightability as a function of distance from the aircraft, group size and behaviour can be quantified and appropriate correction factors applied to the final estimate (Cooke 1985). Regardless of the inadequacies of the 1994 surveys, results indicate that the number of Bowheads present in northern Hudson Bay/Foxe Basin is larger than a few tens of animals. A more rigorous survey is needed to more accurately estimate numbers using this area during the summer.

Bowheads in northern Foxe Basin appear to aggregate in a relatively well defined area. Both aerial surveys and boat-based observations suggested that Bowheads of all age classes were present because calves as well as juveniles and adults were

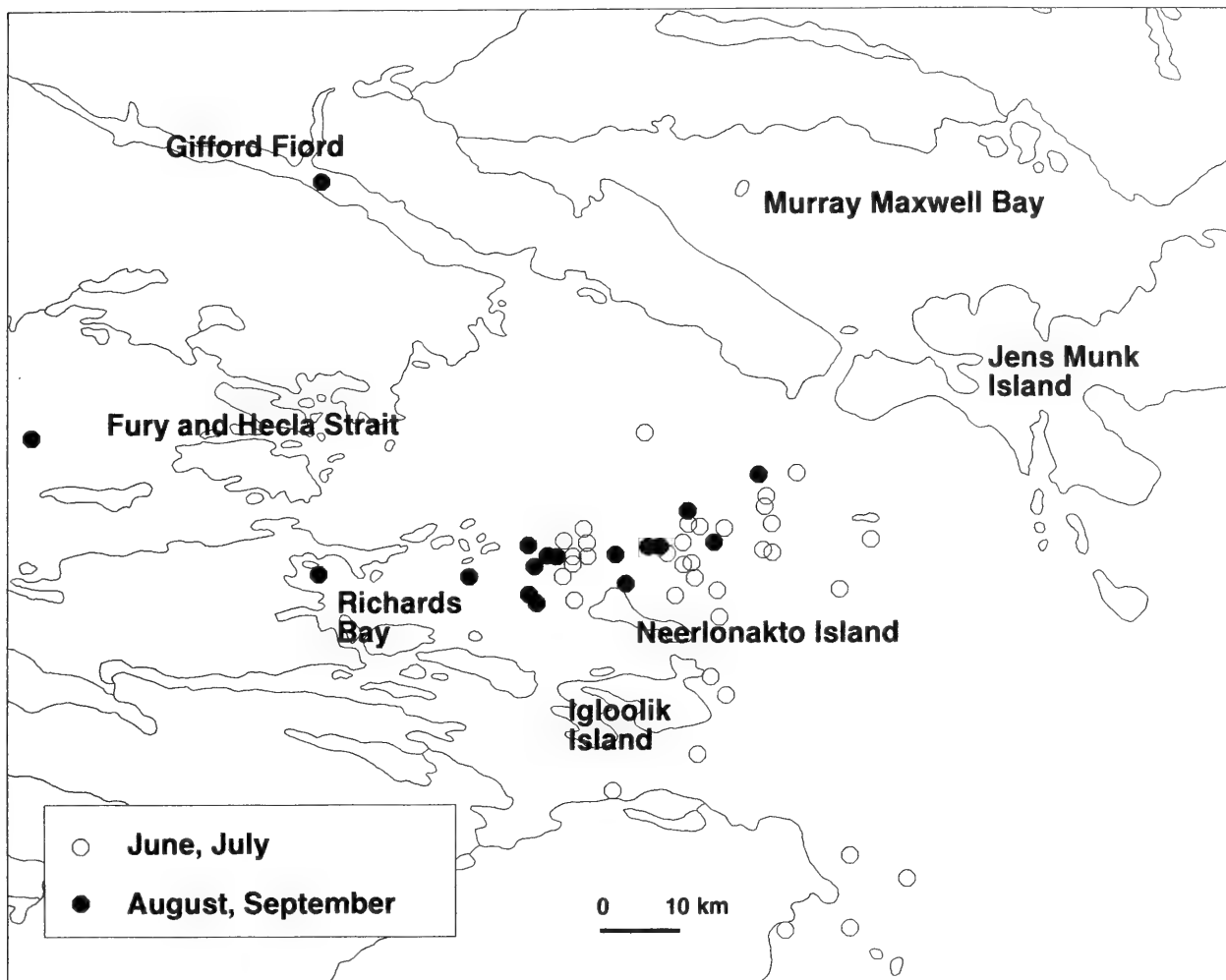


FIGURE 5. Boat-based sightings of Bowhead Whales made by local hunters and the authors. The Bowhead on the west side of Fury and Hecla Strait, at $69^{\circ}52'N$ $83^{\circ}18'W$, was seen by a helicopter crew en route to Igloolik.

seen. Information on the age structure of this stock should be collected to determine whether all components of the stock are present in northern Foxe Basin during the summer.

Bowheads were also present in northern Hudson Bay at the time of our surveys in Foxe Basin (Robert Luke, personal communication), thus our estimate did not include all animals present in northern Hudson Bay and Foxe Basin. Although northern Hudson Bay and Foxe Basin Bowheads are considered to be one stock, (see Reeves and Mitchell 1990), additional research is required to clarify stock relationships so that census results can be properly interpreted and management units identified.

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Wolf, *Canis lupus*, Predation and Maternal Defensive Behavior in Mountain Goats, *Oreamnos americanus*

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Four attacks by single Wolves on Mountain Goats were observed at Caw Ridge, Alberta, during July and August 1995. One Wolf killed a yearling female and an adult female successfully defended her kid against an adult Wolf. In 206 agonistic encounters between kids and older Goats, mothers defended their kids only five times. These results do not support the hypothesis that maternal defense against conspecifics is common in Mountain Goats but demonstrate that females can defend kids against predators.

Key Words: Wolf, *Canis lupus*, Mountain Goat, *Oreamnos americanus*, predation, maternal defensive behavior, Alberta.

Wolves (*Canis lupus*) and Mountain Goats (*Oreamnos americanus*) both inhabit the Rocky Mountains in Alberta, Canada (Mech 1970; Rideout 1978). Wolves are known to prey upon Mountain Goats opportunistically but goats are usually a rare prey (Smith 1986; Huggard 1993; Festa-Bianchet et al. 1994; but see Fox and Streveler 1986). Huggard (1993) observed that Mountain Goats represented <2% of the biomass consumed by two Wolf packs in summer and 0.2% in winter in Banff National Park, Alberta. Peterson et al. (1984) reported that, although Mountain Goats were present in their study area on the Kenai Peninsula (Alaska), they were absent from the Wolf diet. Inaccessibility of goat range (Rideout 1978) and the potential risk presented by the very sharp horns of Mountain Goats (Geist 1967; Nelson and Mech 1985) could explain the scarcity of reports of Wolf predation on goats.

Offspring maternal defense against predators has been reported for several large ungulate species [Bighorn Sheep (*Ovis canadensis*): Hornocker 1969, Berger 1978; Buffalo (*Syncerus caffer*): Schaller 1972; Chamois (*Rupicapra pyrenaica*): Locati 1990; Moose (*Alces alces*): Stephenson and Van Ballenberghe 1995; Mule Deer (*Odocoileus hemionus*): Hamlin and Schweitzer 1979; Muskoxen (*Ovibos moschatus*): Gray 1987; Pronghorn (*Antilocapra americana*): Lipetz and Bekoff 1980; Thomson's Gazelle (*Gazella thomsonii*): Estes 1991; White-tailed Deer (*Odocoileus virginianus*): Smith 1987; Wildebeest (*Connochaetes taurinus*): Kruuk 1972; Zebra (*Equus burchelli*): Schaller 1972]. For Mountain Goats, Brandborg (1955) first suggested that maternal defensive behavior was important in defense against conspecifics, and could also be against predators. To our knowledge, however, there are no direct reports of maternal defense against predators by Mountain Goats. Geist (1971, 1974) stated that maternal protection of kids against conspecifics is common and necessary in Mountain

Goats because of frequent juvenile and adult aggression but no study has presented quantitative evidence of such behavior. Here we examine maternal defensive behavior of Mountain Goats against conspecifics and against predators and report a direct observation of predation of a Wolf on a goat.

Interspecific observations

During a study of Mountain Goats in west-central Alberta, Canada, we observed a female goat defend her 4-month-old kid against an adult Wolf. We also observed a Wolf kill a 15-month-old female. The events reported here occurred on Caw Ridge (54°04'N, 119°25'W), a gently rolling mountain complex in the front range of the Rocky Mountains.

On 30 August 1995, we observed a group of 40 goats (38 were marked) and 12 kids foraging in an open slope at about 2010 m altitude. They were approximately 100 m from timberline when, at 12:55, two adult Wolves (one gray and one completely black) ran out of the forest and chased the goats uphill for 300 m to the closest rocky cliff. The Wolves did not get closer than 40–50 m from the goats before they reached the cliff. At 13:02, the gray Wolf approached the goats at the bottom of the cliff and, after a few attempts, grabbed goat Number 166, a 3-month-old male kid of 23 kg marked 2 weeks before. As soon as the Wolf pulled the kid down the rocky ledge, the kid's mother (Number 23, a 7-year-old first marked as a kid) jumped down and charged the Wolf. She hit it twice on the rump and missed it on an other attempt. The Wolf released Number 166 and both mother and kid fled to the cliff to join the other goats. Three other adult goats then charged the Wolf and forced it to retreat. Number 23 apparently did not injure the Wolf which returned to join the other Wolf about 150 m away. The goats then disappeared to the other side of the escape terrain followed at about 200 m by the two Wolves that skirted round the cliff.

At 16:15, the group of goats came back to feed on the same slope they had used in the early afternoon. At 17:16, the same gray Wolf (as determined by its coloration) appeared alone at the top of the ridge and started pursuing the goats that ran toward a rocky cliff. As the Wolf approached the base of the cliff, the last three goats changed direction and started to run toward the forest. The Wolf caught up to the goats and grabbed the smallest one (a marked yearling female) by a hindleg but the goat escaped and kept running towards the forest. The Wolf recaptured the goat by the same hindleg while running downhill and they rolled together 15 m downslope. The goat got up again but was quickly caught at the throat and knocked down by the Wolf. The goat managed to stand and escape once again but was again recaptured, bitten at the throat, and died in <3 min. The Wolf then disappeared in the forest (<20 m away) for 5 min. It came back to the carcass at 17:36 and dragged it into the forest out of sight. At 17:44, the other goats started to bed in the cliff. Goat Number 75 (the mother of the yearling which had been killed) looked for several minutes at the site where the Wolf had disappeared and was the last goat to bed. She had not attempted to defend the yearling.

We documented two other Wolf attacks on goats in 1995. On 11 July, an adult Wolf attacked a group of 63 goats including 16 kids feeding in an open forest at 1920 m but was unsuccessful. On 20 August, a juvenile Wolf chased a group of 84 goats including 20 kids that were foraging at about 400 m from a steep rock face but the goats ran to the cliff and the Wolf never got closer than 30 m to them.

Another case of antipredator defense behavior was observed on 9 June 1994 in the same goat population. M. Festa-Bianchet and S.D.C. observed a Wolverine (*Gulo luscus*) near a group of 15 goats feeding below a ledge close to timberline. At this time, kids were only 1 to 2-weeks-old and therefore vulnerable to predators. Number 35, a 5-year-old female, ran towards the Wolverine and drove it away. This female did not have a kid.

Intraspecific observations

We sampled agonistic encounters involving kids between May and September 1995 and 1996. In 249.9 h of focal observation periods (Altmann 1974), we observed kids 3591 times within <4 m of goats other than their mothers or other kids. Kids were displaced by older goats in 206 (5.7%) of these encounters. Adult females, subadult females (1 and 2-year-old), and subadult males (1 and 2-year-old) were responsible for 63.9%, 30.3%, and 5.8% of these agonistic interactions, respectively. The mother intervened and defended her kid only five times (once against an adult female, once against a 2-year-old female, once against a yearling female which was the kid's sister, and twice against unclassified

individuals), suggesting that defense against conspecifics is rare.

Discussion

Our observations suggest that female Mountain Goats can protect their young against large predators but that goats may be vulnerable when far from escape terrain (Geist 1971; Rideout 1978; Smith 1983). Since 1989, 19 marked goats were known to have been killed by predators at Caw Ridge, including six taken by Wolves (Festa-Bianchet et al. 1994; Côté et al., unpublished data). Even if, in general, Mountain Goats appear not to be a common prey of Wolves (Smith 1986; Huggard 1993), Fox and Strevler (1986) reported that 62% of 124 Wolf scats collected in southeastern Alaska contained goat remains. Most goat populations in west-central Alberta are small (40–50 individuals [\bar{x} = 44] inhabiting defined home range with very little immigration and emigration) and have a very slow rate of increase (Smith 1988). It may only takes one pack that specializes on goat predation to cause an important increase in the yearly mortality of a goat population. If a Wolf pack killed ten goats during a winter, it could reduce population numbers by as much as 20–25%, as has been suggested for Cougar (*Felis concolor*) predation on Bighorn Sheep (Wehausen 1996; Ross et al., submitted). Therefore, it appears important to consider the possibility of individual Wolf packs specializing on goat predation when managing Mountain Goat populations.

The role of maternal defensive behaviour against conspecifics appeared much less important in our study population of Mountain Goats than suggested by Geist (1971, 1974). During 206 encounters, the female defended her young only five times. We observed just four cases where older goats used horn contact to displace a kid and each time the goat pushed the kid harmlessly instead of rushing it, suggesting little need for maternal defense. Furthermore, other researchers observed that kids were less commonly attacked by other goats than adult females and juveniles (Chadwick 1977; Dane 1977). In a winter study of goats at a baiting site, Masteller and Bailey (1988) observed that an orphan kid received much aggression, while kids with their mothers received few threats. Therefore, it appears that kids may be sheltered from many interactions by their mother (Singer 1977). This suggests that, even if kids are rarely defended against aggressors, they receive some protection just by being close to their dam (Chadwick 1977).

In our study, subadult males performed only 5.8% of the agonistic interactions received by kids. Similarly, Chadwick (1977) found that interactions with 2-year-old males accounted for only 13% of the kids' total number of social interactions. These results do not support Geist's (1974) hypothesis that

female Mountain Goats protect their kids against conspecifics and especially against subadult males. Therefore, there appears to be little selective pressure for maternal defense against conspecifics in goats (*see* Maestriperi 1992 for a review of maternal defense in mammals). No maternal defense against conspecifics was observed in studies of Bighorn Sheep (Geist 1971), Apeninne Chamois (Locati and Lovari 1990) and Muskoxen (Gray 1987). However, all our observations were conducted in summer when resources were abundant, and we might have reached different conclusions if it would have been possible to observe the goats during winter. When snow is deep, resources are scarce, rates of aggression increase (Petocz 1973), and kids feed in craters dug by their mothers (Chadwick 1977). They may at this time receive more protection from their dam.

Maternal defense in Mountain Goats seems to be used only in extreme situations such as defense against predators (Holroyd 1967; this study). Such behavior has been reported in several species of large ungulates (Packer 1983) and is likely to be selected even if it prevents offspring predation only a few times during the lifetime of a female.

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New and Noteworthy Records from the Vascular Flora of Nova Scotia

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Eleven taxa, ten species and one hybrid, are reported new to the vascular flora of Nova Scotia. Three species are rare native plants (*Carex alopecoidea*, *Carex digitalis*, *Carex tinctoria*), two appear to be adventive from elsewhere in North America (*Bulbostylis capillaris*, *Hypericum gentianoides*), and five are introductions from Europe (*Cerastium pumilum*, *Cerastium semidecandrum*, *Erophila verna*, *Myosotis stricta*, *Veronica verna*). The hybrid sedge, *Carex flava* x *Carex viridula* ssp. *oedocarpa*, has not previously been reported from North America. Notes are provided on four other plants rarely reported from Nova Scotia (*Aira caryophyllea*, *Aira praecox*, *Carex wiegandii*, *Veronica peregrina*).

Key Words: Nova Scotia, vascular plants, floristics, new records.

We report ten species and one hybrid new to the vascular flora of Nova Scotia: *Bulbostylis capillaris*, *Carex alopecoidea*, *Carex digitalis*, *Carex flava* x *Carex viridula* ssp. *oedocarpa*, *Carex tinctoria*, *Cerastium pumilum*, *Cerastium semidecandrum*, *Erophila verna*, *Hypericum gentianoides*, *Myosotis stricta*, and *Veronica verna*. These taxa are not listed in the most recent flora of Nova Scotia (Roland and Smith 1969) nor are they listed for Nova Scotia in the most recent flora of Canada (Scoggan 1978-1979) or in the bibliography of Catling et al. (1995). Of the additions, the three *Carex* species appear to be overlooked rare native species. *Bulbostylis capillaris* and *Hypericum gentianoides* are probably adventive in Nova Scotia, although native to North America. The sedge hybrid *Carex flava* x *Carex viridula* ssp. *oedocarpa* has not previously been reported from North America. The remaining five species are European weeds found in campgrounds where they appear to be at least in part dispersed by camping equipment.

In addition, we present information on four species which are rare or infrequently reported in Nova Scotia: *Aira caryophyllea*, *Aira praecox*, *Carex wiegandii*, and *Veronica peregrina*. Following specimen citations we discuss the distribution, habitat and status of each species in Nova Scotia. Taxa are arranged alphabetically, with those new to Nova Scotia indicated by *. Herbarium acronyms follow Holmgren et al. (1981) and Boivin (1980), except where otherwise indicated.

Aira caryophyllea L. (Poaceae) Silvery Hairgrass
Annapolis County, Kejimikujik National Park, main campground, rare on campsites; 25 June 1992; M. J. Oldham 13868 (DAO, MICH, NSMP, mjo - personal herbarium of M. J. Oldham). Inverness County, Cape Breton Highlands National Park, Cheticamp Camp-

ground, rare in open gravel of campsites, with *Cerastium fontanum*; 21 June 1992; M. J. Oldham 13847 (DAO, MICH). Shelburne County, Islands Provincial Park, near Shelburne, rare campground weed, with *Aira praecox*; 26 June 1992; M. J. Oldham 13884 (DAO, MICH). Victoria County, Cape Breton Highlands National Park, Broad Cove Campground, campsites; 22 June 1992; M. J. Oldham 13855 (DAO, NSPM).

Catling et al. (1984) found Silvery Hairgrass on Seal Island, Nova Scotia, and reported it new to eastern Canada. This species and the related Early Hairgrass (*Aira praecox*) are tiny, annual grasses introduced into North America from Europe. *Aira caryophyllea* was previously known in Canada from Yukon and British Columbia (Boivin 1969; Scoggan 1978-1979). Elsewhere in eastern North America it is known from dry, open areas near the coast from Vermont and Massachusetts south to Texas and Florida (Gleason and Cronquist 1991).

Aira praecox L. (Poaceae) Early Hairgrass

Shelburne County, Islands Provincial Park, near Shelburne, uncommon campground weed, with *Aira caryophyllea*; 26 June 1992; M. J. Oldham 13883 (DAO, MICH, NSPM). Yarmouth County, Ellenwood Provincial Park, near Yarmouth, campground; 28 June 1992; M. J. Oldham 13896 (DAO, MICH, NSPM).

Early Hairgrass was previously reported in eastern Canada only from Seal Island and Mud Island, both in Yarmouth County, Nova Scotia (Erskine 1958; Roland and Smith 1969; Catling et al. 1984). Erskine (1958) speculated that its presence on Seal Island resulted from seeds coming ashore in the sand-ballast of ships driven up on the beach. Elsewhere in Canada *Aira praecox* is known from southern British Columbia (Hubbard 1969; Scoggan 1978-1979). In

the eastern United States it occurs from southern New York to Virginia in dry sandy soil near the coast (Gleason and Cronquist 1991). Both hairgrass species are small and inconspicuous, and their presence in widely separated park campgrounds in Nova Scotia suggests they should be looked for elsewhere in dry, sandy open areas in the Maritime provinces and New England. The two *Aira* species grew intermixed in campsites in Islands Provincial Park, Shelburne County.

**Bulbostylis capillaris* (L.) C. B. Clarke (Cyperaceae) sedge

Annapolis County, Jerry Lake, 44°43' North Latitude, 65°26' West Longitude; locally abundant on sandy roadside; 1 July 1993; M. J. Oldham 15113 (MICH, NSPM, mjo).

Bulbostylis capillaris is a small annual sedge which is widespread in eastern North America from Maine to Minnesota, south to Florida, Texas, and Arizona (Kral 1971; Gleason and Cronquist 1991). In Canada it was previously known from southwestern Quebec where it is doubtfully native (Bouchard et al. 1983), and southern Ontario where it occurs both as a rare native and as an introduction along railways and roadsides (Argus et al. 1982-1987; Oldham 1994). *Bulbostylis capillaris* is apparently adventive in Nova Scotia, where it grows along railway tracks and roadsides. This sedge was first collected in Nova Scotia at Halifax in 1967, but was not reported (Taschereau and Chute, NSPM). Subsequent collections exist from Wolfville, Kings County (Vanderkloet in 1972, ACAD); Annapolis Royal, Annapolis County (Johnson in 1971, ACAD); Shelburne County (Newell and Newell in 1981; ACAD); and near Bridgewater, Lunenburg County (Reznicek in 1990; MICH). At its most recent locality it was found with another annual, *Radiola linoides*, a European species known in northeastern North America only from Nova Scotia (Gleason and Cronquist 1991).

**Carex alopecoidea* Tuckerman (Cyperaceae) sedge
Antigonish County, St. Georges Bay, west of Antigonish, 45°38' North Latitude, 61°47' West Longitude; local in moist, overgrown clear-cut area near shore, with *Carex stipata*; 17 June 1992; M. J. Oldham 13813 (CAN, MICH, NSPM, mjo). 24 June 1993; M. J. Oldham 14984 (DAO, TRTE).

This northeastern North American sedge is distributed from Maine to Minnesota, south to New Jersey, Indiana, and Missouri (Gleason and Cronquist 1991). In Canada it occurs in southern Saskatchewan, Manitoba, Ontario, and Quebec, but

has not previously been reported from any of the Maritime Provinces (Scoggan 1978-1979; Boivin 1992). *Carex alopecoidea* is rare in New England (Seymour 1982), and is known in Maine only from Oxford and Kennebec Counties (Richards et al. 1983).

The Antigonish County colony grew in an open, moist, cut-over area with the superficially similar sedge, *Carex stipata*. *Carex alopecoidea* appears native to Nova Scotia and should be added to the province's rare plant list (Maher et al. 1978).

Carex digitalis Willd. (Cyperaceae) sedge

Annapolis County, Kejimikujik National Park, local in sandy woods adjacent to main campground; 25 June 1992; M. J. Oldham 13873 (MICH, NSPM, ctb - personal herbarium of C. T. Bryson, mjo).

Carex digitalis is a woodland sedge ranging from Maine to Florida, west to Wisconsin, Illinois, Missouri, and eastern Texas (Bryson 1980; Gleason and Cronquist 1991). Elsewhere in Canada it is known only from southern Ontario and southwestern Quebec (Scoggan 1978-1979; Boivin 1992). Bouchard et al. (1983) consider it rare in Quebec. Although considered frequent in New England by Seymour (1982), *C. digitalis* has not previously been reported from the Canadian Maritime Provinces. Nova Scotia material of *C. digitalis* belongs to var. *digitalis* (Fernald 1950; Bryson 1980). In Kejimikujik National Park *Carex digitalis* grows in dry, sandy woods where it is undoubtedly native.

**Carex flava* L. x *Carex viridula* Michx. ssp. *oedocarpa* (N. J. Andersson) B. Schmid (Cyperaceae) hybrid sedge

Cumberland County, Cape d'Or, north shore of Minas Channel, locally common in moist, open seepage on exposed headland; 25 June 1993; M. J. Oldham 15001 (MICH, NSPM, mjo).

One of the parents of this hybrid, *Carex flava*, is common and widespread in northeastern North America, while the other, *C. viridula* ssp. *oedocarpa* (= *C. demissa* of Roland and Smith 1969), is rare in North America and known from a few scattered sites along the east coast from Newfoundland south to New Jersey (Crins and Ball 1989). Crins and Ball (1989) suggest that *C. viridula* ssp. *oedocarpa*, a widespread European sedge, is most likely adventive in North America. The hybrid between these two sedges is known from Europe (Jermy et al. 1982), but has not previously been reported from North America (Cayouette and Catling 1992). There is one previous Nova Scotia collection from Digby County, "in a swale near the lake, west of Centreville". It was initially identified as *Carex flava* var. *fertilis*, and was annotated by W. J. Crins in 1985 as this hybrid (E. C. Smith et al. in 1954, ACAD).

At Cape d'Or in Nova Scotia, the hybrid was locally common in an open seepage slope with *Carex flava* and *Carex viridula* ssp. *oedocarpa*.

**Carex tincta* Fern. (Cyperaceae) sedge

Antigonish County, St. Georges Bay, Antigonish Harbour, west of Bayfield, 45°38' North Latitude, 61°47' West Longitude, common at edge of mixed woods along dirt road; 20 June 1992; M. J. Oldham 13835 (MICH, NSPM, mjo).

This poorly understood member of the difficult Ouales Section of *Carex* (Reznicek 1989) is rare throughout its range in Canada (Boivin 1992; A. A. Reznicek, personal communication). Although most recent authors recognize *Carex tincta* as a species (e.g., Scoggan 1978-1979; Seymour 1982; Boivin 1992), some mention the possibility of it being a hybrid (e.g., Scoggan 1978-1979; Gleason and Cronquist 1991; Boivin 1992). In Canada it ranges from southern Alberta (Fernald 1950; Scoggan 1978-1979; Boivin 1992), Ontario (A. A. Reznicek, personal communication), Quebec (Scoggan 1978-1979; Boivin 1992), New Brunswick (Scoggan 1978-1979; Hinds 1986; Boivin 1992), and Prince Edward Island (Scoggan 1978-1979; Erskine et al. 1985; Boivin 1992). Previous reports from British Columbia, Saskatchewan, and Newfoundland (e.g., Fernald 1913; Scoggan 1978-1979) have been more recently discounted (Taylor 1983; Boivin 1992). Hinds (1986) considers *Carex tincta* locally common in moist meadows, roadside ditches, woodland borders and clearings in New Brunswick, especially in the Saint John River drainage system, and it is locally frequent in large areas of Maine and New Hampshire (A. A. Reznicek, personal communication).

In Nova Scotia *Carex tincta* was found to be locally common at the edge of a mixed woodland where it is undoubtedly native.

Carex wiegandii Mackenzie (Cyperaceae) sedge

Shelburne County, Port la Tour bog, between Port la Tour and Cape Negro, uncommon and local at edges of extensive bog; 30 June 1993; M. J. Oldham 15054 (MICH, mjo).

Reznicek and Ball (1980) map this rare sedge only from Cape Breton Island in Nova Scotia. This collection extends its range to southern Nova Scotia. The range of *Carex wiegandii* is centred on the Gulf of St. Lawrence, extending inland to Ontario, and south, very sparingly to Maine, northern Massachusetts and Pennsylvania (Rothrock 1978; Reznicek and Ball 1980).

Cerastium pumilum Curtis (Caryophyllaceae) Curtis'

Mouse-ear Chickweed

Annapolis County, Kejimikujik National Park, uncommon weed on campsites in main camp-

ground; 25 June 1992; M. J. Oldham 13869 (CAN, MICH, mjo). Shelburne County, Islands Provincial Park, near Shelburne, uncommon campground weed; 26 June 1992; M. J. Oldham 13878 (MICH, mjo); 26 June 1992; M. J. Oldham 13885c (NSPM). Yarmouth County, Ellenwood Lake Provincial Park, rare on campsites with *Aira praecox* and *Cerastium fontanum*; 30 June 1993; M. J. Oldham 15079 (MICH).

This small, early flowering, annual European weed has been greatly overlooked in the North American flora. It has been found in most states in eastern North America, although many of these are very recent reports (Rabeler and Cusick 1994). *Cerastium pumilum* is not reported from Canada by Boivin (1969) or Scoggan (1978-1979), although it is now known from several southern Ontario sites (Morton and Venn 1984; Morton and Venn 1990; M. J. Oldham collections at MICH and WAT). Collections in 1992 from New Brunswick (Charlotte County, M. J. Oldham 13913, CAN, MICH, mjo) and Maine (Hancock County, M. J. Oldham 13920, MICH, NEBC, mjo) appear to be first records (Richards et al. 1983; Hinds 1986; Seymour 1982).

In Nova Scotia *Cerastium pumilum* was collected from campgrounds in three widely separated parks. This chickweed is part of a characteristic early spring weedy flora of open, usually sandy campsite tent-pads. Several other species discussed in this paper are also components of this flora: *Aira caryophyllea*, *A. praecox*, *Cerastium semidecandrum*, *Erophila verna*, *Myosotis stricta*, *Veronica peregrina*, and *Veronica verna*. In Nova Scotia, other species growing in this habitat include *Cerastium fontanum*, *Poa annua*, *Sagina procumbens*, and *Veronica arvensis*. This habitat is greatly overlooked by botanists, as evidenced by the fact that five species new to the Nova Scotia flora were discovered in park campgrounds in 1992 and 1993. These species are best sought in the early spring, since most are small, early flowering annuals, and they wither up and disappear later in the season. In addition, heavy trampling by humans makes them much more difficult to detect in summer. Some of these species may be dispersed by camping equipment, as was speculated for *Veronica verna* in Ontario (Crins et al. 1987).

Cerastium semidecandrum L. (Caryophyllaceae)

Small Mouse-ear Chickweed

Inverness County, Cape Breton Highlands National Park, Cheticamp Campground, locally common on campsites with *Cerastium fontanum*; 21 June 1992; M. J. Oldham 13848 (MICH, WAT, mjo). Inverness County, Cape Breton Highlands National Park, Corney Brook Campground, rare on campsites; 21 June 1992;

M. J. Oldham 13853 (CAN, MICH). Shelburne County, Islands Provincial Park, near Shelburne, rare campground weed; 26 June 1992; M. J. Oldham sight record. Victoria County, Cape Breton Highlands National Park, Broad Cove Campground, campsites; 22 June 1992; M. J. Oldham 13858 (CAN, MICH, NSPM, WAT, mjo). Yarmouth County, Ellenwood Provincial Park, near Yarmouth, campsites; 28 June 1992; M. J. Oldham sight record.

Scoggan (1978-1979) reports this small, European, weedy annual only from southwestern British Columbia and southern Ontario in Canada. It is not listed for New Brunswick by Hinds (1986) or Prince Edward Island by Erskine et al. (1985). The discovery of *Cerastium semidecandrum* in five different campgrounds suggests that this plant has been overlooked in Nova Scotia and probably other Maritime provinces, as it has been elsewhere in eastern North America (Rabeler and Cusick 1994).

Erophila verna (L.) Chevall. (Brassicaceae)
Whitlow-grass

Inverness County, Cape Breton Highlands National Park, Corney Brook Campground, rare on campsites; 21 June 1992; M. J. Oldham 13852 (CAN, MICH, NSPM). Shelburne County, Islands Provincial Park, near Shelburne, rare campground weed; 26 June 1992; M. J. Oldham 13885b (NSPM). Yarmouth County, Ellenwood Provincial Park, near Yarmouth, rare campground weed; 28 June 1992; M. J. Oldham 13989 (MICH, NSPM).

Whitlow-grass is a small annual or winter-annual European plant widely naturalized in North America. It is treated by some authors (e.g., Scoggan 1978-1979; Gleason and Cronquist 1991) as *Draba verna*. In Canada, Scoggan (1978-1979) reports it from British Columbia, Ontario, and Quebec. The only published report from the Canadian Maritime Provinces is from Albert County, New Brunswick, where it was found in a Fundy National Park campground (Hinds 1986). Specimens at NSPM show this early-spring ephemeral as being in Nova Scotia since at least 1983, when it was collected at Smiley's Provincial Park, Hants County (Butters and Moores, NSPM). Since that time, collections have been made from Annapolis Royal, Annapolis County (Wilson in 1989, NSPM) and Kentville Research Station, Kings County (Zinck in 1992; NSPM). At each site it is locally common in disturbed soil. This Whitlow-grass has been seen at Golden Arm Campground, near Sydney, Cape Breton County (Sullivan-Fraser, personal communication 1995); a documenting specimen was lost in transit.

Hypericum gentianoides (L.) Britton, Sterns & Pogg.
(Guttiferae) Orange-grass
Lunenburg County, southeast side of Hwy. 103

between the highway and Fancy Lake, along railtracks, ca. 5 km southwest of Bridgewater, dry sand and gravel along railway tracks, frequent in a very small area with *Bulbostylis capillaris*; 16 September 1990; A. A. Reznicek 8732 (MICH).

Orange-grass or pinweed is a diminutive St. John's-wort previously known in Canada only from the Windsor area of southwestern Ontario (Gillett and Robson 1981; Argus et al. 1982-1987). A published report from southwestern Quebec (Scoggan 1978-1979) is apparently based on a label error (National Museum of Canada Rare Plant Project file, copies on file at Natural Heritage Information Centre). Argus and Pryer (1990) consider the species a rare plant in Canada.

The Nova Scotia population is probably adventive since suitable habitat for the species was not present in the vicinity of the collection, which was made along a railway (A. A. Reznicek, personal communication). *Hypericum gentianoides* does however range into New England as a native plant (Seymour 1982; Richards et al. 1983). See addendum page 398.

Myosotis stricta Link (Boraginaceae) Blue Scorpion-grass

Shelburne County, Islands Provincial Park, near Shelburne, rare campground weed; 26 June 1992; M. J. Oldham 13882 (MICH, NSPM). Victoria County, Cape Breton Highlands National Park, Broad Cove Campground, campsites; 22 June 1992; M. J. Oldham 13857 (CAN, MICH, NSPM, mjo). Yarmouth County, Ellenwood Provincial Park, near Yarmouth, rare campground weed; 28 June 1992; M. J. Oldham 13897 (MICH).

Blue Scorpion-grass is another small European annual or winter-annual which is locally introduced in dry waste places in northeastern North America (Gleason and Cronquist 1991). Some authors call this plant *Myosotis micrantha* (e.g., Scoggan 1978-1979; Gleason and Cronquist 1991). Previous Canadian reports are from southern British Columbia, Alberta, Ontario, Quebec (Scoggan 1978-1979), and New Brunswick (Hinds 1986). In New England, Seymour (1982) reports it only from Massachusetts. A 1992 Maine collection (Hancock County, M. J. Oldham 13925, MICH) appears to be the first from that state (Seymour 1983; Richards et al. 1983).

Veronica peregrina L. (Scrophulariaceae) Purselane Speedwell

Victoria County, Cape Breton Highlands National Park, Broad Cove Campground, campsites; 22 June 1992; M. J. Oldham 13861 (CAN, MICH).

Roland and Smith (1969) mention only a single

Nova Scotia record of Purslane Speedwell from Nova Scotia, citing the report of Smith and Erskine (1954) from Point Pleasant Park in Halifax. The specimen cited above extends the known Nova Scotia range north to Cape Breton Island. *Veronica peregrina* is widespread in North America. It is known throughout the southern part of Canada, from coast to coast (Scoglan 1978-1979).

Veronica verna L. (Scrophulariaceae) Spring Speedwell

Shelburne County, Islands Provincial Park, near Shelburne, rare campground weed; 26 June 1992; M. J. Oldham 13881 (MICH, NSPM).
Victoria County, Cape Breton Highlands National Park, campsites; 22 June 1992; M. J. Oldham 13856 (CAN, MICH, NSPM).

Gleason and Cronquist (1991) mention the occurrence of this small European weed only from southern Ontario and Michigan in northeastern North America. Hinds (1986) has reported it from roadsides in New Brunswick, and it was collected in 1992 from a New Brunswick campground (Charlotte County, M. J. Oldham 13914, CAN, MICH). A 1992 Lewis County, New York collection (M. J. Oldham 13787, MICH, NYSM) appears to be the first from New York State (Mitchell 1986). Crins et al. (1987) found *Veronica verna* to be quite common and widespread in southern Ontario, particularly in provincial park campgrounds.

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Addendum

We recently became aware of the following two additional Nova Scotia records of *Hypericum gentianoides*. Lunenburg County, railway path at Italy Cross; 25 September 1996; M. Zinck (NSPM). Shelburne County, west side of Hwy. 103, 1.6 km southwest of Granite, roadside ditch with *Hypericum canadense* and *Radiola linoides*, 27 September 1979, D. F. Brunton 2093 and H. L. Dickson (MICH, mixed collection with *Hypericum canadense*).

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Vegetative Concealment, Proximity to Trails, and Predator Activity as Relative Factors Affecting Nest Success and Egg Loss in Spruce Grouse, *Dendragapus canadensis*

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Sixty-seven nests of Spruce Grouse (*Dendragapus canadensis*) were located during five nesting seasons in north-central Ontario. There was no difference in success of nests > 25 m from a trail than those < 25 m away. Nests with high predator activity indices had lower success than those with low indices. There was no correlation between nest concealment and success. I suggest that the importance of concealment to nest predation diminishes as vegetative cover increases from patchy and open to uniformly dense. Further, I submit different types of predators attracted to varying cover types, specializing in either visual or olfactory cues, as the proximal cause.

Key Words: Spruce Grouse, *Dendragapus canadensis*, nest success, predator activity.

Nest destruction by predators is the primary source of production loss in grouse (Tetraoninae) (Johnsgard 1973; Zwickel 1975; Boag et al. 1979; Bergerud and Gratson 1988). Further, Boag et al. (1979) indicated that most deaths of young Spruce Grouse (*Dendragapus canadensis*) occur at the egg state and are caused primarily by predators. Some believe that breeding success and fledging survival determine spring population numbers (Bergerud 1970; Myrberget 1972). Despite this, the relative importance of factors influencing nest vulnerability is not well understood.

Boag et al. (1979) suggested that productivity loss due to predation in Spruce Grouse was inversely related to population density. Several studies have since refuted this hypothesis by showing no relationship between egg loss and female density (Redmond et al. 1982; Smyth and Boag 1984; Boag et al. 1984). Compelling evidence has shown nest success to be directly proportional to vegetative concealment of nests (Wallestad and Pyrah 1974; Keppie and Herzog 1978; Redmond et al. 1982). However, owing to inconsistencies in their own data (i.e., eggs in well-concealed nests that did not hatch and vice-versa), Redmond et al. (1982) concluded that some factor(s) other than concealment alone affects nest success. Boag et al. (1984) used artificial nests to investigate egg loss among Spruce Grouse; Red Squirrels (*Tamiasciurus hudsonicus*) were the principal predator destroying clutches. The authors hypothesized that the probability of nest destruction is a function of nest placement relative to activity centers of predators.

These studies concentrated largely on either nest concealment or predator activity as a factor affecting egg loss, neglecting the possibility of a combined effect varying with habitat conditions. Furthermore, the validity of conclusions based on studies using

artificial nests has been questioned (Roper 1992). The objectives of my study were to identify the relative importance of vegetative concealment, predator activity in the immediate vicinity of nests, and proximity of nests to trails, to nest success and egg loss among natural nests of Spruce Grouse.

Study Area

Spruce Grouse nests were located in a 266-ha area approximately 148 km northwest of Sudbury, Ontario (47°36'N, 82°45'W). The area consisted primarily of 11 to 23 year-old Jack Pine (*Pinus banksiana*) hand-planted or aerially-seeded plantations. Jack Pine heights varied from 2-3 to 7-9 m in the younger and older plantations, respectively. Ground vegetation in high-density Jack Pine areas was primarily uniformly dense blueberry (*Vaccinium* spp.), Sweet-Fern (*Comptonia peregrina*), Trailing Arbutus (*Epigaea repens*), Wintergreen (*Gaultheria procumbens*), and lichens (*Cladina* spp.). In clearings and low-density Jack Pine areas, ground vegetation was primarily dense grasses, sedges (*Carex* spp.), raspberry (*Rubus* spp.), and lichens. There were numerous natural and human-made trails varying in prominence and width from 0.5 to 3.0 m. Topography was flat with a total elevational range of approximately 10 m.

Methods

Sixty-seven nests were located with the aid of pointing dogs during five nesting seasons (1985-1988, 1990) prior to and during incubation and post-hatch. Nests were found in the course of on-going Spruce Grouse population studies (e.g., Keppie 1992). Field procedures were similar to those used earlier in New Brunswick and Alberta (e.g., Keppie 1987), with 2-4 people searching for grouse daily with trained dogs from April through to at least October. The study area was searched repeatedly on

a sectional rotation basis. Population counts were considered complete (Keppie 1992).

Nests were monitored (usually visited every second day) until empty (i.e., eggs hatched, nest abandoned by female, or destroyed by predator). At each nest, vegetative concealment of the nest was measured, using a systematized visual estimate (Keppie and Herzog 1978) once the nest was empty, to reduce site disturbance during incubation. Concealment was measured horizontally and vertically. For horizontal concealment, the nest was viewed in each cardinal direction from 10 m at 0.5 m above ground level. From each vantage, an estimate of horizontal concealment was scored to a maximum of 25. If a nest was directly at the base of a tree, it was automatically scored 25 points for the effect of the tree bole. The four scores were summed to a maximum of 100. Vertical concealment was estimated from 1.8 m directly above the nest for a single score to a maximum of 100. Horizontal and vertical scores were combined for a concealment index to a maximum of 200. Redmond et al. (1982) used several objective and subjective methods to estimate nest concealment and concluded that this visual technique is of similar accuracy to any other method they evaluated.

An index of mammalian activity around each of 13 nests was obtained in 1986. A pair of sand transects was established, once nests were empty, radiating north and west from the nests. Transects were constructed by cutting out existing ground vegetation and scraping out 2-3 cm of soil within a rectangular area of 30 cm by 6 m. Sand was imported and placed within the transect until flush with ground level. Care was taken to minimize disturbance of vegetation around the nest and transects. The number and species of mammalian tracks (Murie 1974) were recorded every second day for one month, and transects were swept clear on each visit. In 1985 and 1986, distances from nests to the nearest natural or man-made trail were recorded.

The fate of each nest was determined by examining egg shell fragments and other evidence in and around the nest. A successfully hatched egg was one which had one half of the egg shell cupped inside the other half in a relatively symmetrical fashion; thus allowing an accurate count of eggs hatched. Abandoned nests were identified by the presence of cold eggs at consecutive visits without sighting the female on or near the nest, and were treated as unsuccessful nests. For depredated nests, the type of predator was determined by evidence of shell breakage and nest disturbance (Bump et al. 1947; Boag et al. 1984).

Both nest success (defined as ≥ 1 egg hatched [Keppie 1982]) and egg loss (individual eggs that fail to hatch) were used as measures of nest success. This was done to account for Red Squirrels, a major nest predator on the study area, which tend to prey on individual eggs rather than entire nests (Boag et al. 1984), thus accounting in the analysis for depre-

dated eggs that belonged to successful nests. Statistical tests of independence for comparing rates of egg and nest success were made with log-likelihood non-parametric tests using William's correction (G_{adj}) (Zar 1984). Student's-t parametric tests were used to compare average values of nest parameters (all tests of homogeneity $P > 0.05$).

Results

A total of 67 nests was found over the five years. In 37 (55%) of these, eggs were depredated; in 27 (40%), eggs were not depredated; in 2 (3%), eggs were destroyed by research dogs; and in 1 (2%), the nest contained eggs of undetermined fate. Of nests containing depredated eggs, 16/37 (43%) were preyed upon by a large mammal (e.g., Red Fox [*Vulpes vulpes*], Black Bear [*Ursus americanus*], Striped Skunk [*Mephitis mephitis*]), 9 (24%) by Red Squirrels, 2 (5%) by another rodent, 1 (3%) by a bird, and 9 (24%) by unknown animals. For those nests where the outcome (successful or not) was known, 51% (33/65) were successful.

Concealment

The average nest concealment rating was 104 ($n = 67$, $SD = 41.2$, range = 35-191). In nests rated ≤ 104 (low concealment) 44% (74/169) of eggs laid hatched; in nests rated > 104 , 59% (90/153) of eggs hatched, a similar proportion in both concealment ratings ($G_{adj} = 2.4$, $df = 1$, $P = 0.13$). Nest success was also similar between low and high concealment ratings ($\leq 104 = 54%$ [19/35 nests], $> 104 = 57%$ [17/30 nests]; $G_{adj} = 0.3$, $df = 1$, $P = 0.62$). There was also no difference between average concealment ratings for successful nests ($x = 109$, $n = 33$, $SD = 39.7$) and unsuccessful nests ($x = 102$, $n = 32$, $SD = 43.0$) ($t = 0.73$, $df = 62$, $P = 0.47$). Further, when classed by concealment ratings (Table 1), there were no differences between proportions of successful and unsuccessful nests in each category (all $G_{adj} < 0.44$, $df = 1$, $P > 0.25$).

Predator Activity Around Nests

Mammalian tracks ($n = 208$) were recorded in 12 visits to each nest; of these, 191 (92%) were attributed to Red Squirrels, 10 (5%) to other small rodents, 4 (2%) to skunks, and 3 (1%) to Red Fox. The average total track count per nest was 17.3 tracks ($n = 12$, $SD = 16.8$, range = 2-37). This value was used to differentiate between low and high predator-activity nests. In nests with ≤ 17.3 track counts (i.e., low activity), 82% (31/38) of eggs laid hatched, significantly more than the 23% (6/26) that hatched in nests with > 17.3 track counts ($G_{adj} = 6.8$, $df = 1$, $P = 0.01$). Similarly, 6 of 7 nests with low predator activity were successful, whereas 3 of 5 nests with high predator activity were successful ($G_{adj} = 0.6$, $df = 1$, $P = 0.46$).

Proximity to Trails

In nests < 25 m from a trail, 63% (26/41) of eggs hatched, similar to nests > 25 m from a trail (42%

TABLE 1. Concealment and success for 166 Spruce Grouse nests of *Dendragapus canadensis canadensis* and *D.c. franklinii* from New Brunswick (N.B.), Ontario (Ont.), and Alberta (Alta.), 1970-1990, using a subjective visual concealment method after Keppie and Herzog (1978)^a.

Concealment rating (200 points maximum)	<i>D.c. canadensis</i> (N.B.) ^b (n = 36)		<i>D.c. canadensis</i> (Ont.) ^c (n = 66)		<i>D.c. franklinii</i> (Alta.) ^d (n = 64)	
	Successful	Unsuccessful	Successful	Unsuccessful	Successful	Unsuccessful
Very good (>100)	21	5	18	13	8	4
Good (51 - 100)	7	2	11	14	4	11
Poor (26 - 50)	1	0	4	5	0	10
Very poor (≤25)	0	0	0	0	7	20
Totals	29	7	33	32	19	45

^aN.B. and Alta. data from Redmond et al. (1982)

^bOne additional nest in N.B. had "very good" concealment but success was unknown; three unsuccessful nests that had "very good" concealment were deserted just after discovery, prior to start of incubation.

^cOne additional nest in Ont. had "poor" concealment, another had "good" concealment, but both were destroyed by a dog.

^dOne additional nest in Alta. had "good" concealment and two had "very poor" concealment but success was unknown.

[39/92]) ($G_{adj} = 1.60$, $df = 1$, $P = 0.21$). Nor was there any difference in success rates between nests ≤ 25 m from a trail (6/9 [67%]) and > 25 m from a trail (7/16 [44%]) ($G_{adj} = 0.35$, $df = 1$, $P = 0.55$). The average distance from a trail for depredated nests (66 m, $n = 10$, $SD = 65.0$) was greater than that for other nests (26.8 m, $n = 16$, $SD = 24.60$) ($t = 2.18$, $df = 25$, $P = 0.04$).

Discussion

Proximity of nests to trails did not increase the chance of a nest being depredated, contrary to the intuitive assumption that mammals that use trails would more likely discover nests close to trails. Scat collections confirmed that mammals used trails on the study area during the nesting season (D. M. Keppie, unpublished data), supporting the hypothesis that predators often use trails for reasons other than foraging for prey as suggested by Boag et al. (1984).

Sand transects were an easy and effective way to index mammalian activity around nests and warrant further use. Results of sand-transect experiments indicated that high predator activity in the vicinity of nests increases the probability of nest failure and egg loss, supporting Boag et al.'s (1984) hypothesis. Red Squirrels accounted for the majority of tracks, are probably opportunistic predators, and will revisit a nest once they have discovered it (R. D'Eon and D. Keppie, personal observations). This behaviour pattern would likely compound the effects of nest placement in a Red Squirrel activity centre by increasing the probability of all eggs in a nest being preyed upon once discovered. Therefore, in these situations, predator abundance (i.e., Red Squirrels) and dispersion of activity centers would likely be the most important factors influencing nest success.

A regional comparison (Table 1) reveals a convincing correlation between magnitude of visual concealment and nest success of Spruce Grouse among studies. New Brunswick (N.B.) had the highest proportion of nests rated >100 points for concealment (72%, $n = 36$) and proportion of successful nests (81%, $n = 36$), followed by Ontario (48% and 51% respectively, $n = 65$), and Alberta (19% and 30% respectively, $n = 64$). Despite this correlation however, concealment of nests in Ontario was unrelated to nest success and egg loss. The disparity between these results and past studies is likely due to area differences in vegetative cover. All nests found by Keppie and Herzog (1978) in Alberta were in Lodgepole Pine (*Pinus contorta*) forests characterized by sparse, low ground vegetation, whereas Redmond et al. (1982) found most nests in open spruce-pine forests with moderately dense and patchy ground cover. However, the Young Jack Pine forests of the present study typically had dense, uniform ground vegetation and contrasted greatly with the earlier studies.

Redmond et al. (1982) suggested that differences in mechanisms of locating prey by predators, a func-

tion of habitat structure, could result in different success rates for Spruce Grouse nests. Most nests in the present study were depredated by large mammals (Red Fox, Black Bear, Striped Skunk) that likely primarily use auditory and olfactory (in this case primarily olfactory) senses to locate prey (Banfield 1974), and Red Squirrels, a predator that appears to be largely opportunistic in its search pattern. The presence of these types of predators is likely a function of the uniformly dense ground vegetation, that tends to conceal nests well but does little to deter predators using non-visual cues. I suggest, that although concealment generally contributes to nest success, concealment in uniformly dense vegetative cover is not as important in determining egg loss and nest success as in areas of sparse and/or patchy ground vegetation where predators may be primarily using visual cues to locate nests (e.g., Keppie and Herzog 1978). Further, I submit the importance of nest concealment in relation to nest predation diminishes as the overall vegetative ground cover of an area increases from patchy and open to uniformly dense, by attracting different types of predators that hunt either visually (as in patchy and open areas) or by olfactory cues (as in uniformly dense areas).

The findings in this study rest on assumptions that require validation. I urge caution in their interpretation. Activities of field workers and dogs around nests may be a cause of unrepresentative nest information in studies of this kind. Some have suggested field workers at nests could be a partial cause of high nest failure in birds (e.g., Dwernychuk and Boag 1972; Zwickel 1975). Keppie and Herzog (1978) investigated this concern and concluded that dogs did not promote a greater rate of Spruce Grouse nest failure, nor was there conclusive evidence that finding a nest by any means lessened its chances of being successful.

Despite some advancement, a particularly persistent question remains: how does a female grouse choose her nest site? Bergerud and Gratson (1988) stated that the most important reproductive decision a female must make is where to locate her nest. This decision should relate primarily to locating a nest that will best avoid detection by predators. Further work should attempt to determine the influence of vegetative cover on the types of predators preying on nests and how these factors influence a female's choice of nest sites.

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Cadmium, Copper, and Lead in Fish from the Lower Nelson River System in Northern Manitoba

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Pip, Eva, and Jeffray Stepaniuk. 1997. Cadmium, copper, and lead in fish from the Lower Nelson River system in northern Manitoba. *Canadian Field-Naturalist* 111(3): 403–406.

Cadmium, copper and lead were examined in a catch of fishes from the Lower Nelson River system. In Lake Whitefish, (*Coregonus clupeaformis*) cadmium and copper concentrations in skeletal muscle decreased in larger fish. In Northern Pike, (*Esox lucius*), lead concentrations in muscle were inversely correlated with fish weight, and fish downstream of the Limestone Dam showed higher copper concentrations than those upstream, reflecting a parallel difference in environmental copper levels. Interspecific differences in metal concentrations were not significant. In Brook Trout (*Salvelinus fontinalis*), heart tissue showed the highest cadmium concentrations, while lead was highest in the liver and ovary.

Key Words: Cadmium, copper, lead, fishes, Lake Whitefish, *Stizostedion vitreum*, Northern Pike, *Esox lucius*, Lake Whitefish, *Coregonus clupeaformis*, *Salvelinus fontinalis*, Goldeye, *Hiodon alosoides*, Longnose Sucker, *Catostomus catostomus*, Nelson River, Manitoba.

Heavy metal contamination of aquatic environments is of continually increasing concern as anthropogenic loadings are becoming more widespread. Since fish are the trophic components of the greatest economic significance, published research has concentrated on them. While species such as Walleye (*Stizostedion vitreum*), Northern Pike (*Esox lucius*) and Lake Whitefish (*Coregonus clupeaformis*) can survive in rather high environmental concentrations of heavy metals (van Loon and Beamish 1977), fish may bioaccumulate metals even at low levels through long-term exposure via the gills and food chain. The Nelson River system in northern Manitoba has been intensively developed for hydroelectric power, and many local residents, as well as tourists, consume fish from this waterway. The objective of the present study was to examine levels of cadmium, copper and lead in a sample catch of fishes from the study area.

Study Area

Sampling was conducted on the Nelson River at two sites: above (56° 24' 57"N, 94° 11' 11"W) and below (56° 31' 59"N, 94° 03' 22"W) the Limestone Dam. Brook Trout (*Salvelinus fontinalis*) were obtained at McMillan Creek (56° 39' 56"N, 94° 31' 03"W), a tributary of the Limestone River which drains into the Nelson River. In addition to the Limestone Dam, two additional major hydroelectric developments are located nearby on the Nelson River: Long Spruce, 23 km upriver from the Limestone Dam, and Kettle Generating Station, 16 km upstream of Long Spruce. A map of the study area and description of the developments are given by Pip and Stepaniuk (1992).

Materials and Methods

Walleye, Northern Pike, Lake Whitefish, Goldeye (*Hiodon alosoides*) and Longnose Sucker (*Catostomus catostomus*) were obtained from the last week of May to the first week of August, 1988, using a series of three gillnets, of stretched-mesh size ranging from 3.9–12.7 cm. Each series was set 2–4 m deep and allowed to remain overnight. Brook Trout were obtained by angling. The total harvest consisted of: 28 Northern Pike, 14 Lake Whitefish, 3 Goldeye, 2 Brook Trout, and 1 each of Longnose Sucker and Walleye. All of these individuals were analyzed.

Fresh weight (nearest g) and fork length (nearest mm) were recorded. Samples of skeletal muscle were removed below the dorsal fin (first dorsal fin in the case of Walleye), and frozen. Otoliths, cleithra, and scales were collected as appropriate for age determinations. The age of the oldest fish in the sample (18 y) coincided with the start of construction of Limestone Dam (1975), although the generating station was still not in full operation at the time of sampling.

Water samples were collected 10–20 cm below the surface in acid-washed polypropylene bottles. Surface sediments were obtained with a plastic shovel. All samples were frozen within 5 h of collection.

Frozen tissue and sediment samples were freeze-dried. Particles larger than 4 mm were excluded from sediment samples. Each sample was extracted as three separate 1 g replicates. Extraction was carried out by heating for 1 h at 60°C. with 7.5 mL concentrated nitric acid and 1.5 mL 70% perchloric acid. After cooling to room temperature, 10 mL of 1% nitric acid were added, followed by filtration through Whatman #541 hardened ashless filter paper. The filtrate and two 2 mL rinses of 1% nitric acid were

TABLE 1. Weight, length, age, and metal concentrations in muscle tissue of fish at the study sites. Values in parentheses are standard errors.

Parameter	Northern Pike	Lake Whitefish	Goldeye	Brook Trout	Longnose Sucker	Walleye
Wet weight (g)						
\bar{x}	996 (77)	995 (129)	253 (23)	1210 (240)	400	570
range	400–1900	400–2100	230–300	971–1450	–	–
Fork length (mm)						
\bar{x}	516 (9)	392 (17)	259 (5)	440 (10)	390	370
range	442–610	292–500	252–268	430–450	–	–
Age (yr)						
\bar{x}	8.3 (0.5)	10.2 (1.0)	–	9.5 (1.5)	6	9
range	5–13	5–18	–	8–11	–	–
Cd ($\mu\text{g/g}$ dry wt)						
\bar{x}	2.9 (0.2)	2.5 (0.3)	3.7 (0.7)	3.0 (0.2)	1.7	2.6
range	0.4–5.0	0.4–4.2	2.8–5.1	2.8–3.1	–	–
Cu ($\mu\text{g/g}$ dry wt)						
\bar{x}	1.7 (0.3)	1.2 (0.3)	1.4 (1.1)	3.0 (0.2)	0.4	0.5
range	<0.1–4.9	<0.1–2.8	0.3–3.7	2.8–3.1	–	–
Pb ($\mu\text{g/g}$ dry wt)						
\bar{x}	4.8 (1.2)	4.2 (1.2)	6.5 (2.4)	1.3 (1.2)	8.7	0.1
range	<0.1–20.5	<0.1–16.4	1.9–10.2	<0.1–2.4	–	–
N	28	14	3	2	1	1

pooled and diluted to 30 mL with 1% nitric acid. This extract was aspirated into an IL-151 atomic absorption spectrophotometer (Instrumentation Laboratory Inc., Wilmington, Massachusetts).

Water samples were acidified and treated with ammonium pyrrolidinedithiocarbamate and methyl isobutyl ketone (American Public Health Association 1985), and the organic extract was aspirated for spectrophotometry as above.

All glassware was acid-leached prior to use. Blanks consisted of all reagents and steps in the procedure, less sample material. The standard additions method was used to compensate for matrix absorption effects, using certified atomic absorption standards (Fisher Scientific Co., Fairlawn, New Jersey).

Statistical tests were carried out using SPSS (SPSS, Inc., Chicago, Illinois). The critical significance level was $p = 0.05$.

Results

Metal levels in whole water samples were low, with concentrations of approximately 0.01 $\mu\text{g/L}$ for cadmium, and up to maxima of 7 $\mu\text{g/L}$ for copper and lead. Bottom sediment concentrations were higher, with mean values (\pm S.E.) of 1.85 (0.25), 6.3 (0.8) and 30 (3) $\mu\text{g/g}$ dry weight for cadmium ($n=23$), copper ($n=23$) and lead ($n=13$) respectively.

All metals showed great variation within individual species (Table 1), and ANOVA showed no significant interspecific differences in skeletal muscle concentration among Northern Pike, Lake Whitefish and Goldeye. Unpaired T-tests showed that concentrations in muscle tissue were significantly ($p<0.001$)

higher than in sediments for cadmium, but consistently ($p<0.001$) lower than in sediments for copper and lead. In Northern Pike, cadmium and copper concentrations were linearly correlated with each other ($p = 0.018$).

Northern Pike and Lake Whitefish were examined in greater detail. Lead in muscle was inversely correlated with body wet weight in Northern Pike ($p = 0.007$). In Lake Whitefish, copper was inversely correlated with weight, fork length ($p = 0.02$) and age (0.005), while cadmium was inversely correlated with fork length (0.001). Correlations for lead and copper were most pronounced when age, weight and length were log transformed.

T-tests comparing Northern Pike upstream and downstream of Limestone Dam showed no significant differences with respect to weight, length or age of fish in the samples, and no significant differences for cadmium or lead concentrations in muscle. However copper concentrations were significantly greater in the downstream catch ($p<0.001$). Lake Whitefish could not be compared, as this species was present only in samples taken downstream of the dam.

The two Brook Trout from McMillan Creek were dissected and individual organs were examined (Table 2). In both specimens, heart tissue showed the highest cadmium levels, but the greatest lead concentrations were observed in liver and ovaries; copper was also high in these organs in the old female.

Discussion

Intraspecific variation of metal concentrations in muscle tissue was quite large; similar variability has

TABLE 2. Metal concentrations in organs of Brook Trout, as $\mu\text{g/g}$ dry weight of tissue. A = Female, 11 years old, 1450 g wet weight, 45 cm fork length. B = Male, 8 years old, 971 g wet weight, 43 cm fork length.

Tissue	Individual	Cd	Cu	Pb
Skeletal muscle	A	2.8	3.1	2.4
	B	3.1	2.8	<0.1
Bone	A	5.1	3.3	30
	B	6.6	2.2	27
Scales	A	1.6	9.9	69
	B	2.2	7.1	33
Brain	A	5.5	6.3	30
	B	2.9	2.6	2.4
Liver	A	3.0	107	203
	B	2.7	7.9	137
Gills	A	3.0	4.7	24
	B	3.9	6.6	28
Heart	A	6.7	23.5	52
	B	12.7	18.1	<0.1
Reproductive organs	A	2.1	71	123
	B	4.3	14.4	39

been observed by Pagenkopf and Neuman (1974), Mathis et al. (1979) and Wren et al. (1983). Concentration factors compared to sediment were greatest for cadmium, and least for lead. Similar trends have been reported by Enk and Mathis (1977) for a stream ecosystem. Johnson (1987) found that lead showed the lowest biomagnification potential of nine trace metals examined in whole fish.

No significant differences in muscle metal levels were seen between carnivorous Northern Pike and omnivorous Lake Whitefish. This is consistent with the results of other workers (e.g., Mathis and Cummings 1973; Hutchinson et al. 1975; Johnson, 1987) who reported that cadmium, copper and lead levels in muscle are not greater in carnivorous fishes.

In Lake Whitefish, copper concentrations per unit muscle weight decreased in older, heavier and larger fish, and cadmium decreased with size as well. In Northern Pike, lead decreased with body weight, but copper showed no significant relationship with age or weight in this species. This finding supported that of Wren et al. (1983) for Northern Pike. In other species, Mathis and Kevern (1975) and Mathis et al. (1979) found no correlation between muscle cadmium or lead and fish length and weight. Thus relationships between metal uptake and growth appear to vary greatly with species. Cadmium and lead concentrations have been shown to decrease with increasing age in aquatic arthropods (Jop and Wojtan 1982) and freshwater gastropods (Pip 1992) and mussels (Pip 1995).

Northern Pike muscle tissue showed a substantial difference for copper above and below Limestone Dam, and appeared to reflect differences in environmental copper concentrations. Pip and Stepaniuk

(1992) found significantly higher copper levels in sediments downstream, compared to upstream, of Limestone Dam. Macrophytes also showed higher copper concentrations downstream of the dam. The reason for this effect is not known and was not related to differences in sediment particle size distribution.

In Brook Trout, muscle tissue showed comparatively low levels of copper and lead, compared to other organs. Mathis et al. (1979) have reported large variation in lead concentrations for the same organs among individual fish. High levels of cadmium and copper have been found in liver and kidney tissue of some species (Hutchinson et al. 1975; Badsha and Goldspink 1982; Bendell-Young et al. 1986), but cadmium and lead have been reported to be greatest in heart tissue in fish studied by Mathis et al. (1979). Heart tissue showed the highest cadmium concentrations in the Brook Trout in the present study.

Concentrations of cadmium and copper in the liver have been reported to increase with age (McFarlane and Franzin 1980), and accumulation is proportional to rate of fish growth (Bendell-Young et al. 1986). McFarlane and Franzin (1980) suggested that accumulation in the liver may be associated with metallothioneins, metal-binding proteins that act as sequestering agents. These workers also reported high copper levels in female gonads, which was observed in the present study as well.

In many pollution monitoring programs, skeletal muscle is the only fish tissue examined, but this tissue contains the lowest metal levels. Whole fish in turn tend to have much lower metal body burdens than plankton or bottom dwelling organisms (Mathis and Cummings 1973; Namminga et al. 1974). Fish skeletal muscle, therefore, may not be a good indica-

tor of ecosystem health. Similarly, prediction of metal concentrations in fish is difficult because of the large number of variables which may influence metal uptake, for example growth rates, environmental calcium concentrations (McFarlane and Franzin 1980), and possible effects of stress conditions such as parasites, disturbance, competition, and presence of other pollutants.

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Comparison of Plant and Animal Diversity on New Reservoir Islands and Established Lake Islands in the Northern Boreal Forest of Québec

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We determined species diversity of passerines, small mammals, and woody plants on new islands of the La Grande-3 hydroelectric reservoir, in the northern boreal forest of Québec, and compared it with that on natural islands of two large neighbouring lakes. We predicted that species diversity on reservoir islands would be greater than that on lake islands because relaxation (progressive loss of species caused by an excess of extinction over immigration) had not fully operated on reservoir islands due to their relatively recent creation, only 11 years before the study. Animal diversity, richness and species composition were similar in both island groups. Exceptions were a greater abundance of Northern Waterthrush (*Seiurus noveboracensis*) and Meadow Vole (*Microtus pennsylvanicus*) on lake islands. However, richness of woody plants on reservoir islands exceeded that on lake islands. We did not find four shrub species in our samples on lake islands which were recorded on reservoir islands. The mean age of trees on lake islands (192 y) significantly exceeded that of trees on reservoir islands (112 yr). In contrast to the mainland, where young stands regenerating following fire abounded, mature forest stands strongly dominated on lake islands. We speculated that fire cycles might be longer on natural islands than on the mainland, and that reservoir islands could become similar to lake islands with time. Difference in plant diversity between island groups may have resulted from differences in fire cycle rather than from time since isolation alone. We discuss the future of reservoir islands with respect to plant and animal diversity.

Nous avons déterminé la diversité spécifique des passereaux, des petits mammifères et des plantes ligneuses sur de nouvelles îles du réservoir hydroélectrique La Grande-3, au nord de la forêt boréale québécoise, et nous l'avons comparée à celle d'îles naturelles de deux grands lacs voisins. Nous avons prédit que la diversité en espèces des îles du réservoir dépasserait celle des îles naturelles parce que la relaxation (perte progressive d'espèces résultant d'un surplus d'extinctions par rapport aux immigrations) des espèces ne se serait pas encore totalement manifestée sur les îles du réservoir, compte tenu de leur création récente, 11 ans avant l'étude. La diversité animale, la richesse et la composition en espèces étaient semblables pour les deux groupes d'îles, sauf pour la Paruline des ruisseaux (*Seiurus noveboracensis*) et le Campagnol des champs (*Microtus pennsylvanicus*) qui étaient tous deux plus abondants sur les îles des lacs. Cependant, la richesse des plantes ligneuses des îles du réservoir surpassait celle des îles des lacs. Nous n'avons pas détecté la présence de quatre espèces d'arbuste sur les îles des lacs, qui furent rencontrées sur les îles du réservoir. Nous avons observé que l'âge moyen des arbres était plus grand sur les îles des lacs (192 ans) que sur celles du réservoir (112 ans). De plus, les peuplements forestiers matures dominaient fortement sur les îles des lacs, contrairement à la terre ferme entourant le réservoir. Il se pourrait que le cycle des feux ait été plus long sur les îles naturelles que sur la terre ferme, et que les îles du réservoir puissent ressembler à celles des lacs avec le temps. Les différences de diversité végétale entre les deux groupes d'îles pourraient donc avoir résulté d'un cycle des feux différent plutôt que du temps d'isolement en soi. Nous discutons du futur des îles du réservoir du point de vue de la diversité animale et végétale.

Key Words: Small mammals, passerines, woody plants, boreal forest, diversity, islands, isolation, Québec.

Island biogeography was initially developed in an effort to explain species richness on oceanic islands (Darlington 1957; MacArthur and Wilson 1967). There has been a renewed interest in the subject given the accelerated rate of extinction of species due to ecosystem fragmentation (Saunders et al. 1991). Species extinction related to loss of wilderness areas, most notably due to agriculture and urbanization, is not a novel problem for ecologists (Curtis 1956) but the desire to maintain biodiversity, despite an increasing number of fragmented habitats, is a more recent concern (McNeely et al. 1990).

Scandinavian countries have become increasingly concerned about changes to forest composition by intensive forestry and consequent habitat simplification (Enoksson et al. 1995; Angelstam 1996). However, the boreal forest of North America has not been yet subjected to such intensive silviculture, and many parts still remain relatively natural (Haila and Jarvinen 1990). In northern boreal forests, logging has not been introduced and forest fires are uncontrolled. In northern Québec, natural fires often destroy large areas of forest (Payette et al. 1989; Hunter 1993) which can become vast homogeneous

TABLE 1. Number of passerines observed or heard per census point, richness indices and diversity indices ($\bar{x} \pm \text{S.E.}$) in mature forest stands of 10 lake islands and 10 reservoir islands in the northern boreal forest of Québec, 17 to 24 June, 1993. Variables from both island groups were compared using the Kruskal-Wallis test.

	Islands		K-W
	Lakes	Reservoir	
Species			
Yellow-rumped Warbler, <i>Dendroica coronata</i>	2.0 ± 0.2	2.3 ± 0.3	
Ruby-crowned Kinglet, <i>Regulus calendula</i>	1.6 ± 0.3	2.0 ± 0.3	
Dark-eyed Junco, <i>Junco hyemalis</i>	1.3 ± 0.2	1.1 ± 0.2	
Northern Waterthrush, <i>Seiurus noveboracensis</i>	0.9 ± 0.2	0.3 ± 0.2	*
Boreal Chickadee, <i>Parus hudsonicus</i>	0.3 ± 0.2	0.4 ± 0.2	
Blackpoll Warbler, <i>Dendroica striata</i>	0.3 ± 0.2	0.3 ± 0.2	
Gray Jay, <i>Perisoreus canadensis</i>	0.4 ± 0.3	0.2 ± 0.1	
Fox Sparrow, <i>Passerculus iliacea</i>	0.1 ± 0.1	0.1 ± 0.1	
Hermit Thrush, <i>Catharus guttatus</i>	-	0.3 ± 0.2	
White-winged Crossbill, <i>Loxia leucoptera</i>	0.5 ± 0.3	-	
Swainson's Thrush, <i>Catharus ustulatus</i>	0.2 ± 0.1	-	
Pine Grosbeak, <i>Pinicola enucleator</i>	0.2 ± 0.1	-	
White-crowned Sparrow, <i>Zonotrichia leucophrys</i>	-	0.2 ± 0.1	
White-throated Sparrow, <i>Zonotrichia albicollis</i>	-	0.1 ± 0.1	
Lincoln's Sparrow, <i>Melospiza lincolnii</i>	-	0.1 ± 0.1	
Common Redpoll, <i>Carduelis flammea</i>	0.1 ± 0.1	-	
Yellow Warbler, <i>Dendroica petechia</i>	-	0.1 ± 0.1	
Cape May Warbler, <i>Dendroica tigrina</i>	-	0.1 ± 0.1	
Winter Wren, <i>Troglodytes troglodytes</i>	-	0.1 ± 0.1	
Richness			
Total species	12	15	
Mean richness/census point	4.9 ± 0.5	4.9 ± 0.6	
Diversity			
Log-Alpha index	4.918 ± 0.584	5.347 ± 0.830	
Shannon index	1.496 ± 0.115	1.488 ± 0.087	
Berger-Parker index	0.283 ± 0.028	0.345 ± 0.025	
Simpson Index	0.246 ± 0.033	0.251 ± 0.020	

* $P \leq 0.05$

stands (Heinselman 1981). Natural fire periodicity covers about 100 years around the James Bay area in eastern Canada. The interval between fire disturbance lengthens progressively towards the Atlantic coast to the east, and towards the forest-tundra and tundra to the north (Foster 1983; Payette et al. 1989). In southern boreal forests, Bergeron (1991) observed that fire cycles covered similar period on lakeshore and island stands; i.e., 99 vs. 112 years during the last century. Fires on islands occurred more frequently but were smaller than fires on the mainland. In southern boreal forests, fires are suppressed because logging is an important economic activity; large clearcuts are common. There, the preservation of biodiversity is becoming a major concern for wildlife managers, in particular locally in remnant mature stands surrounded by young cutovers.

We studied an extreme case of isolation: conversion of hilltops to islands after flooding of the La Grande-3 hydroelectric reservoir (LG-3). We measured plant and animal diversity on these newly created islands and compared them with those on natural islands of two large adjacent lakes. We predicted

that species diversity on reservoir islands would be greater than that on lake islands because relaxation (progressive loss of species caused by an excess of extinction over immigration: Diamond 1975) had not fully operated on reservoir islands due to their recent creation, 11 years before the study. We selected only mature stands as defined by Morneau and Payette (1988) in order to eliminate the effect of stand age that influences species composition in northern boreal forests (Morneau and Payette 1988; Crête et al. 1995); we expected identical fire cycles on islands and on the mainland (Bergeron 1991). We wanted to predict the future of reservoir islands in terms of biodiversity and we expected that our findings might be extended to exploited boreal forests for remnant uncut patches of comparable size.

Study area

The study area was in northwestern Québec, approximately 200 km east of James Bay, near the LG-3 hydroelectric reservoir (53°-54°N, 75°-76°W) (Figure 1). The area belongs to the Canadian Precambrian Shield dominated by Archean granitic and

gneissic rock, and covered with glacial deposits (Rowe 1972). The annual temperature averages 2.5°C and precipitation reaches 650 mm, with 40% falling as snow. The growing season lasts 130 days, with a frost-free period of 60-80 days (Wilson 1971; Environment Canada 1986).

Vegetation is typical of the northern boreal forest and consists of open woodlands, dominated by Black Spruce (*Picea mariana*) and Jack Pine (*Pinus banksiana*), with a lichen carpet (Gérardin 1980). Natural fires have occurred, on average, at 100-year intervals during recent centuries (Payette et al. 1989). In well drained areas on the mainland around the LG-3 reservoir, 17 species of woody plants, 8 species of small mammals and 26 species of nesting passerines were found in forest stands of varying ages (Crête et al. 1995). However, when considering

only mature stands, richness decreased to 14 species of woody plants, 5 of small mammals and 10 of nesting passerines.

Only islands covered with mature forests were chosen to eliminate variability from fire succession. We selected 10 reservoir islands and matched them to 10 comparable islands within two large natural lakes: six in Lac de la Montagne du Pin and four in Lac Patukami (Figure 1). Islands selected in LG-3 reservoir were former hilltops isolated from the mainland when the reservoir was flooded in 1982. Reservoir islands were chosen so that their size and distance from the mainland could be matched with those of lake islands. Reservoir islands covered from 9 to 82 ha (average (\bar{x}) = 28 ha \pm standard error (S.E.) = 7) as compared to 10 to 62 ha (\bar{x} = 28 \pm 6) for lake islands. Minimum distance from the shore

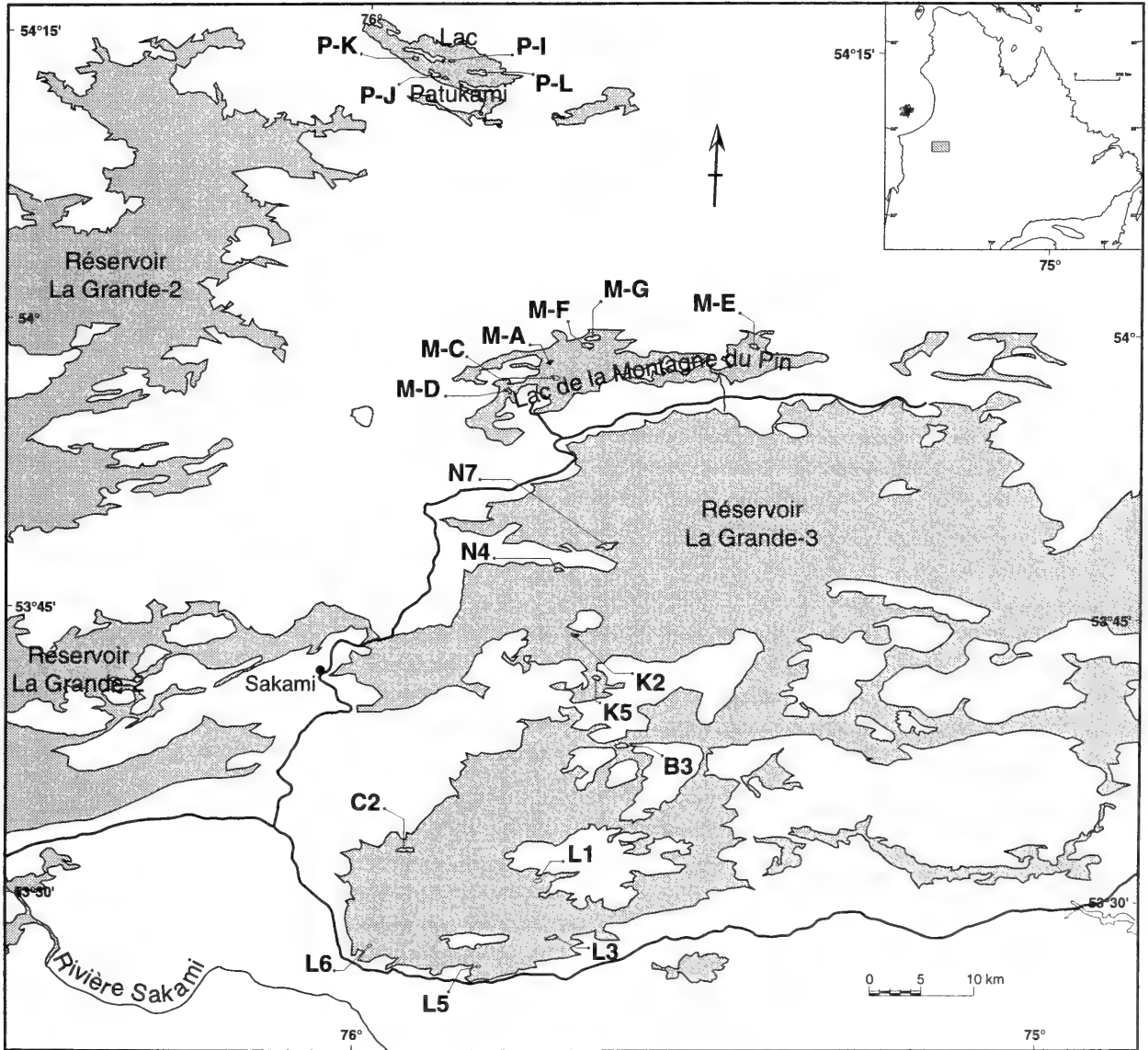


FIGURE 1. Location of the study area in northwestern Québec and of the 20 islands where passerines, small mammals and woody plants were censused.

TABLE 2. Number of small mammals captured per 100 trap-nights, richness indices and diversity indices ($\bar{x} \pm \text{S.E.}$) in mature forest stands of 10 lake islands and 10 reservoir islands in the northern boreal forest of Québec, 4 to 17 August 1993. Variables from both island groups were compared using the Kruskal-Wallis test.

	Islands		K-W
	Lakes	Reservoir	
Rodents			
Southern Red-backed Vole, <i>Clethrionomys gapperi</i>	11.56 \pm 2.72	11.01 \pm 2.91	*
Meadow Vole, <i>Microtus pennsylvanicus</i>	0.52 \pm 0.29	0.14 \pm 0.12	
Heather Vole, <i>Phenacomys intermedius</i>	0.10 \pm 0.05	0.32 \pm 0.29	
Northern Bog Lemming, <i>Synaptomys borealis</i>	0.10 \pm 0.06	0.02 \pm 0.02	
Meadow Jumping Mouse, <i>Zapus hudsonius</i>	-	0.02 \pm 0.03	
Insectivores			
Masked Shrew, <i>Sorex cinereus</i>	0.60 \pm 0.30	0.36 \pm 0.20	
Richness			
Total species	5	6	
Mean richness/census grid	2.7 \pm 0.3	2.0 \pm 0.3	
Diversity			
Log-Alpha index	0.736 \pm 0.111	0.478 \pm 0.103	
Shannon index	0.425 \pm 0.083	0.258 \pm 0.119	
Berger-Parker index	0.840 \pm 0.046	0.895 \pm 0.056	
Simpson index	0.759 \pm 0.057	0.855 \pm 0.072	

* $P \leq 0.05$

ranged from 100 to 1130 m ($\bar{x} = 548 \pm 125$) for lake islands, and from 180 to 1950 m ($\bar{x} = 530 \pm 164$) for reservoir islands. Distance between islands varied from 90 to 2400 m ($\bar{x} = 956 \pm 192$) on Lac de la Montagne du Pin, from 170 to 620 m ($\bar{x} = 347 \pm 61$) on Lac Patukami, and from 460 to 4500 m ($\bar{x} = 2220 \pm 172$) on the LG-3 reservoir. Elevation ranged from 8 to 23 m ($\bar{x} = 14 \pm 2$) on lake islands and from 8 to 38 m ($\bar{x} = 15 \pm 3$) on reservoir islands.

Annual variations in water level (± 12 m) create a "tidal" range on reservoir islands, which has been subjected to strong disturbances (flooding, ice erosion and forest debris accumulation). During periods of low water level, a beach of variable width (5-175 m) is created, which separates the treeline from the water's edge and where some herbaceous plants grow; this is less pronounced on lake islands. Forest stands on selected islands were exclusively mature woodlands (> 75 years) with relatively homogeneous structure and plant composition, and without wetlands or anthropogenic disturbances. Areas surrounding the LG-3 reservoir and the study lakes were covered by forest stands of varying ages (Crête et al. 1995).

Methods

Species census

Three groups of organisms were selected to estimate species diversity: nesting birds of the order Passeriformes, small mammals of the orders Rodentia and Insectivora, and woody plants; nomenclature follows Peterson (1980), Banfield (1977) and Marie-Victorin (1964). Breeding passerines were counted from June 17 to 24, 1993, using the fixed-

radius point-count method (Ralph et al. 1993). A census point was located in the middle of each island and the circular plot had a radius of 50 m. The perimeter of each plot was at least 50 m away from the shore to minimize edge effect. Each census point was visited twice on different days by different observers; the census, which lasted 15 minutes, was conducted between 04:30 and 09:30 on clear calm days (no rain and winds < 20 km/h). Abundance of individual species was determined from the maximum number of birds observed or heard during both visits for each census point.

On each island, 12 50-m transects, running parallel to the shore and covering the bird census plot, were used to sample small mammals. Trapping was carried out from 4 to 17 August 1993. One "Victor" number 0 mousetrap and one "Museum Special" trap (both Ekco Canada Inc., Niagara Falls, Ontario) were set side-by-side at every 10 m along each transect; in all, 72 traps of each type were used per island. For three consecutive nights, traps were baited with apple cubes and peanut butter. Dental structure [based on Van Zyll de Jong (1983) for insectivores and on Banfield (1977) for rodents] was used to identify all captured specimens. Abundance was expressed as the number of trapped specimens per 100 trap-nights per island. The number of captured specimens was divided by the number of functional traps, which was the number of traps set minus the number of traps accidentally triggered. That number was then multiplied by 100.

Forest characteristics

Nine transects served to determine forest structure

TABLE 3. Frequency occurrence of woody plant species per height stratum, richness indices and diversity indices ($\bar{x} \pm S.E.$) in mature forest stands of 10 lake islands and 10 reservoir islands in the northern boreal forest of Québec. Fisher's exact test was used to compare qualitative variables, whereas the Kruskal-Wallis test was used to compare quantitative variables of both groups.

	Islands		Fisher
	Lakes	Reservoir	
Low shrubs			
Labrador Tea, <i>Ledum groenlandicum</i>	1.0 \pm 0	1.0 \pm 0	
Sour-top Blueberry, <i>Vaccinium myrtilloides</i>	0.7 \pm 0.2	1.0 \pm 0	
Leather Leaf, <i>Chamaedaphne calyculata</i>	0.7 \pm 0.2	0.7 \pm 0.5	
Sheep Laurel, <i>Kalmia angustifolia</i>	0.3 \pm 0.2	1.0 \pm 0	**
Swamp Laurel, <i>Kalmia polifolia</i>	-	0.2 \pm 0.1	
High shrubs			
Willows, <i>Salix</i> spp.	0.3 \pm 0.2	0.5 \pm 0.2	
Speckled Alder, <i>Alnus rugosa</i>	-	0.7 \pm 0.2	**
Dwarf Birch, <i>Betula glandulosa</i>	-	0.5 \pm 0.2	*
Bartram's Serviceberry, <i>Amelanchier batramiana</i>	-	0.2 \pm 0.1	
Pin Cherry, <i>Prunus pensylvanica</i>	0.1 \pm 0.1	-	
Trees			
Black Spruce, <i>Picea mariana</i>	1.0 \pm 0	1.0 \pm 0	
Jack Pine, <i>Pinus banksiana</i>	0.6 \pm 0.2	0.7 \pm 0.2	
Tamarack, <i>Larix laricina</i>	0.5 \pm 0.2	0.1 \pm 0.1	
			K-W
Richness			
Total species	9	12	
Mean richness/quadrat	5.2 \pm 1.8	7.5 \pm 1.1	**
Diversity ^a			
Shannon Index	2.054	2.336	
Simpson Index	0.139	0.425	

* $P \leq 0.05$; ** $P \leq 0.01$

^aDiversity indices were calculated using presence-absence data.

and abundance of woody plants on each island. Eight of them, whose projection crossed the centre of the bird census plot, started on the perimeter of a 40-m square, one transect on each corner and one in the middle of each side; transects followed the cardinal directions. The 40-m square was centered on the bird census point where was located the last transect. Transect length varied according to plant stratum: 1 m for the ground stratum, 2 m for herbaceous and low shrub (≤ 0.5 m) strata and 10 m for high shrub (0.5 m $<$ height ≤ 2 m) and tree (> 2 m) strata. Coverage of woody plants was recorded by species only over 10-m transects.

Density and basal area of trees were estimated with a point-centered quarter method (Cottam and Curtis 1956) at one end of all nine transects; two classes of diameter at breast height (d.b.h.) were selected: 2.5 cm \leq d.b.h. $<$ 6 cm, and d.b.h. ≥ 6.0 cm. Abundance of fallen dead trees was estimated using the number of trunks bisecting 10-m transects. Density of standing dead trees was determined by counting the number of trunks in a 2×10 -m sampling plot, which was parallel to the central 10-m

transect. A clinometer served to determine canopy height in the centre of the quadrat. The age of the five largest trees found around each plot was determined by counting growth annuli.

Age distribution of forest stands

We observed, during reconnaissance flights, that mature forest stands were very common on lake islands and we estimated their ages to compare with those on the mainland. Forest stands growing on mesic sites were divided into four post-fire successional stages, according to composition and distribution of lichens (Morneau and Payette 1988): (1) recent burns (0-20 y) with dead lichens or bare soil; (2) shrubs (21-40 y), characterized by a discontinuous cover of *Cladonia* species; (3) young forests (41-60 y), distinguished by a continuous cover of *Cladonia mitis* and *C. rangiferina*; and (4) mature woodlands (> 60 y), with a ground stratum dominated by *C. stellaris*. The frequency distribution of forest stands per post-fire successional stage was computed for all islands on Lac de la Montagne du Pin and Lac Patukami, and compared with that of the mainland, along the road surrounding the LG-3

TABLE 4. Age of dominant trees, percentage of plant cover per height stratum and dendrometric characteristics ($\bar{x} \pm \text{S.E.}$) of mature forest stands of 10 lake islands and 10 reservoir islands in the northern boreal forest of Québec. Variables from both island groups were compared using the Kruskal-Wallis test.

	Islands		K-W
	Lakes	Reservoir	
Age of trees (y)	192 ± 19	112 ± 14	*
Cover(%)			
Ground stratum			
Lichens	47 ± 7	53 ± 7	
Bryophytes	45 ± 28	36 ± 6	
Bare ground and litter	7 ± 2	10 ± 2	
Herbaceous stratum	10 ± 2	1 ± 1	***
Shrub stratum			
Low shrubs (≤ 0.5 m)	43 ± 3	40 ± 3	
High shrubs ($0.5 > m \leq 2$)	7 ± 1	12 ± 1	*
Tree stratum			
Small timber ($2 < m \leq 5$)	9 ± 1	5 ± 1	
Large timber (> 5 m)	22 ± 2	21 ± 3	
Dendrometric characteristics			
Basal area (m^2/ha)			
Small timber ($2.5 \text{ cm} \leq \text{d.b.h} < 6.0 \text{ cm}$)	1.14 ± 0.25	0.63 ± 0.12	
Large timber ($\text{d.b.h.} \geq 6.0 \text{ cm}$)	7.52 ± 0.84	5.02 ± 0.83	*
Tree density (trees/ha)			
Small timber ($2.5 \text{ cm} \leq \text{d.b.h} < 6.0 \text{ cm}$)	843 ± 178	620 ± 114	
Large timber ($\text{d.b.h.} \geq 6.0 \text{ cm}$)	868 ± 118	712 ± 75	
Standing dead trees (trunks/ m^2)	0.07 ± 0.02	0.07 ± 0.02	
Fallen dead trees (trunks/10 m)	0.8 ± 0.2	0.8 ± 0.2	
Canopy height (m)	10 ± 0.3	10 ± 0.3	

* $P \leq 0.05$; *** $P \leq 0.001$

reservoir (Figure 1; Crête et al. 1995). Forest stands on islands were homogeneous, and each island was considered as one sample. On the mainland, a forest stand was defined as a homogeneous vegetation unit located on either side of the road surrounding the LG-3 reservoir. Forest stands on islands and the mainland were mapped from a helicopter. We did not map forest stands according to post-fire successional stage on reservoir islands due to budget constraint, but their frequency distribution appeared comparable to that of the mainland. The chi-square test was used to compare the age structure of forest stands on lake islands with that of the mainland.

Effects of isolation

The effects of time since isolation were evaluated by comparing plant and animal communities on reservoir islands, created in 1982, to those of natural islands. We first determined an abundance index for each of the three groups of organisms: number of woody plant species surveyed per island, number of small mammals captured per 100 trap-nights and maximum number of passerines per observation point. We also determined two richness indices

[Log-Alpha (Krebs 1989) and Shannon (Shannon and Weaver 1949)] and two dominance indices [Berger and Parker (1970); Simpson (1949)]. Finally, we compared mean age of sampled trees, coverage per height stratum, basal area and density of trees. The Kruskal-Wallis test (SAS Institute Inc. 1985) was used to compare the two sets of islands, because of small sample size. The Fisher's exact test was used to compare frequency occurrence of woody plant species; standard deviation of means was estimated with the binomial distribution.

Results

Abundance and diversity

PASSERINES: Nineteen species of passerines were recorded as present on both island groups combined (Table 1). However, only four species were common: the Yellow-rumped Warbler (*Dendroica coronata*), the Ruby-crowned Kinglet (*Regulus calendula*), the Dark-eyed Junco (*Junco hyemalis*) and the Northern Waterthrush (*Seiurus noveboracensis*). Northern Waterthrush abundance was significantly greater on lake islands than on reservoir islands. Although the cumulative richness per island

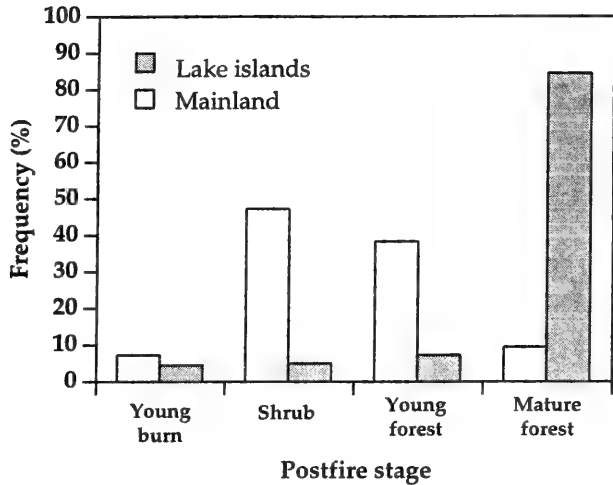


FIGURE 2. Frequency distribution per post-fire successional stage of forest stands covering islands of two natural lakes (n = 70), compared to that of forest stands growing on the mainland (n = 90), along the road surrounding the La Grande-3 reservoir. These two distributions are statistically different (Chi square = 745; 1 d.f.; p ≤ 0.001).

group was lower on lake islands (12 species) than on reservoir islands (15 species), mean richness per census point was more or less the same (4.9 species) for both island groups. As for species diversity, none of the selected indices showed a significant difference from one island group to the other.

SMALL MAMMALS: Six species of small mammals were captured on both island groups combined (Table 2). The Southern Red-backed Vole (*Clethrionomys gapperi*), by far the commonest species, comprised 91% of captured specimens. There was no significant difference in the abundance of this vole from one island group to the other, with an average of ≈ 11 captures/100 trap-nights. Meadow Voles (*Microtus pennsylvanicus*) were commoner on lake islands than on reservoir islands. The abundance of other species was low and did not differ significantly between island groups. Species richness reached five species on lake islands and six on reservoir islands. Communities were made up of the same species, except for the Meadow Jumping Mouse (*Zapus hudsonius*), captured only on reservoir islands. Mean richness per census grid varied from 2,0 to 2,7 species and did not differ significantly between island groups. There were no significant differences in species diversity indices from one island group to the other.

WOODY PLANTS: Thirteen species of woody plants were tallied on all islands together (Table 3). Except for Sheep Laurel (*Kalmia angustifolia*), Speckled Alder (*Alnus rugosa*) and Dwarf Birch (*Betula glandulosa*), there was no significant difference in percent ground cover of woody plants between island groups. Species richness was lower on lake islands than on reservoir islands. The mean richness per quadrat was also significantly lower on lake islands

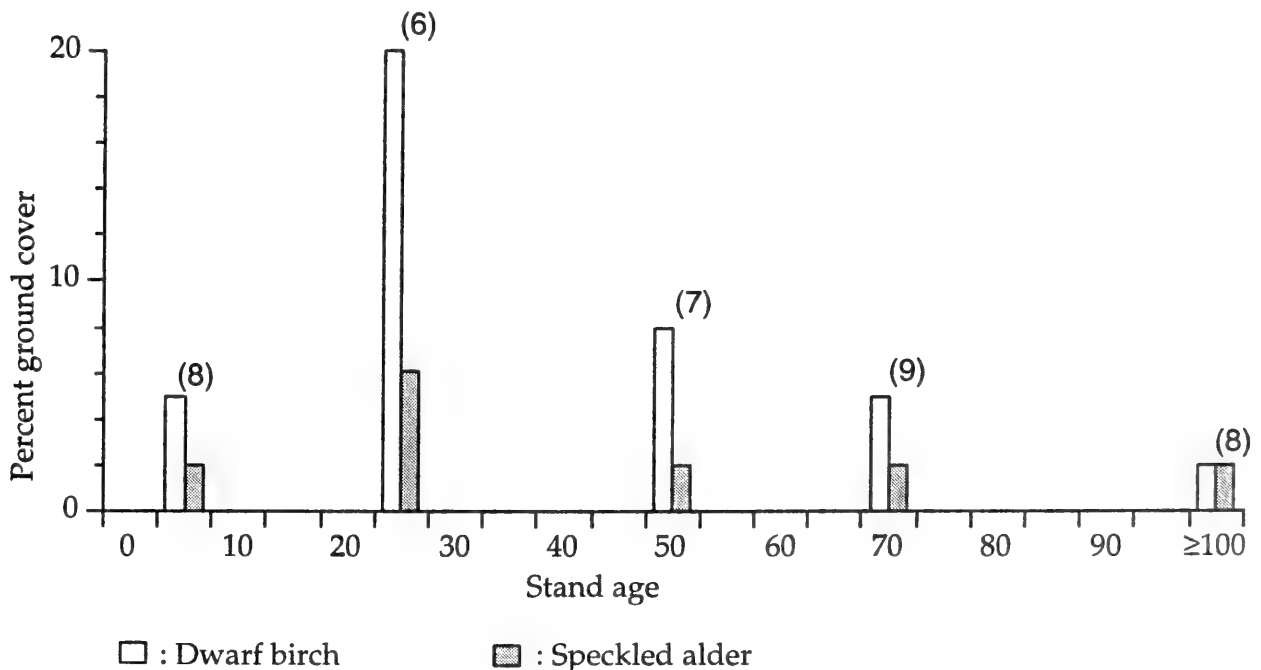


FIGURE 3. Percent ground cover for Dwarf Birch (*Betula glandulosa* Michx) and Speckled Alder (*Alnus rugosa* (DuRoi) Spreng) according to the age of forest stands originating from fire and growing on mesic sites in the northern boreal forest of Québec. Numbers in parentheses indicate the number of sampled stands. Data taken from mainland stands (Crête et al. 1995) and from islands of the La Grande-3 reservoir (this study).

than on reservoir islands, due mainly to the absence of Dwarf Birch, Speckled Alder, Bartram's Serviceberry and Swamp Laurel in lake island surveys. Shannon's diversity Index and Simpson's dominance Index were both lower on lake islands than on reservoir islands. However, because indices were based on frequency of occurrence, we could not perform any statistical comparisons. For the same reason, the Log-Alpha and Berger-Parker Indices were not computed.

Permutation tests (Mantel 1967) did not reveal any significant influence of the distance to other islands or to the shore on species composition for the two sets of islands (unpublished).

Characteristics of mature forest stands on reservoir and lake islands

Forests of the two island groups did not differ significantly ($P > 0.05$) with respect to coverage of lichens, bryophytes, litter, low shrubs and trees (Table 4). However, mean age of dominant trees on lake islands (192 yr) significantly exceeded that of trees on reservoir islands (112 y). Coverage by high shrubs was lower on lake islands (7%) than on reservoir islands (12%), an opposite trend to that measured for the herbaceous stratum. Although the coverage of trees was similar for the two sets of islands, large trees (d.b.h. > 6 cm) covered a greater basal area on lake islands (7.52 m²/ha) than on reservoir islands (5.02 m²/ha). Density of standing dead trees and number of fallen dead trees across the 10-m transect were low, with similar numbers on the two island groups.

Age of forest stands: lake islands vs mainland

The frequency distribution of forest stands per post-fire successional stage on lake islands was significantly different ($P < 0.05$) than that found on the mainland (Figure 2). Mature woodlands made up 84% of island stands but only 9% of stands in mainland forests.

Discussion

Relaxation after isolation

Contrary to our prediction, overall characteristics of animal populations on reservoir islands, measured 11 years after flooding, were similar to those on lake islands. All common species were present on both island groups, but the abundance of the Northern Waterthrush and the Meadow Vole was greater on lake islands. As the Northern Waterthrush usually occupies habitats in close proximity to water (Godfrey 1986), this species may avoid reservoir islands because of the large exposed area created by drawdown. But this "tidal" range might be suitable for those passerines which prefer open habitats bordering forests. This added feature to the landscape of reservoir islands, which does not exist on lake islands, might explain the presence there of the White-crowned Sparrow, the White-throated Sparrow and the Lincoln's Sparrow. A greater abun-

dance of the Meadow Vole on lake islands might depend on the greater coverage of the herbaceous stratum there (Grant 1971, 1975).

Small mammal and bird populations on reservoir islands showed no major decline in species richness after flooding isolation, when compared to surveys done the previous year on the mainland (Crête et al. 1995). Eleven years after flooding, cumulative richness was slightly greater on reservoir islands than on the mainland. However, the Deer Mouse (*Peromyscus maniculatus*), usually found in young forest stands (Fox 1983; Crête et al. 1995), and the Yellow-bellied Flycatcher (*Empidonax flaviventris*) were absent from reservoir islands. Although this comparison is based on surveys from different years, results suggest that animal communities established on reservoir islands were similar to those observed on the mainland. The greater number of bird species surveyed on islands compared to the mainland was likely the result of the greater proximity of census points to the shoreline on islands.

In contrast to mammals and birds, plant communities showed a greater species richness on reservoir islands than those on lake islands. This may have been due to a lower occurrence of Sheep Laurel, and the absence of Speckled Alder, Dwarf Birch, Swamp Laurel (*Kalmia polifolia*) and Bartram's Serviceberry (*Amelanchier bartramiana*) on lake islands. Although these species may have been present on lake islands, they were certainly rare because none were found along the sampled transects. Bartram's Serviceberry and Swamp Laurel were rare everywhere, and their absence on lake islands could simply result from chance. However, the absence of Dwarf Birch and Speckled Alder could be linked to their difficulties of persisting in old forests. Distribution of these two species was quite variable in the study area; they generally reached maximum coverage about 20 years after fire, and declined afterwards (Figure 3). This suggests that the observed differences in species richness of woody plants might result from differences in fire regimes rather than from length of isolation.

Because fire periodicity averages only 100 years in the boreal forest of eastern North America (Payette et al. 1989; Bergeron 1991), most stands are young. Over large areas of boreal forests with frequent fire disturbance, the distribution of stand ages follows a steep exponential decrease (Van Wagner 1978), and approximately two thirds of the stands are in regeneration (Rowe 1983). Forests on the mainland around the LG-3 reservoir (and most likely on reservoir islands which were connected to the mainland until 1982) were dominated by regenerating stands but stand distribution on lake islands deviated substantially from the expected distribution, with only 16% of regenerating stands. In addition, the mean age of dominant trees indicated a longer

life expectancy on lake islands than on reservoir islands. The age structure of forest stands and the age of dominant trees may indicate that the fire regime in our study area could differ on islands and the mainland, contrary to what Bergeron (1991) found in southern boreal forests.

Future of reservoir islands and implications for exploited boreal forests

This study was limited to two large natural lakes and one reservoir. Although it precludes extensive conclusions, our data set allows some predictions for the LG-3 reservoir. The creation of reservoir islands may change insular patterns of wild fires. With time, forest structure may become dominated by old-growth forest stands, similar to lake islands. Among small mammals, the Meadow Vole would benefit the most from such changes. Older forest stands on reservoir islands would also benefit species which prefer mature forests, such as the Southern Red-backed Vole, the Caribou (*Rangifer tarandus*) and the Ruby-crowned Kinglet (Crête et al. 1995). As well, the degree of isolation of reservoir islands might also influence composition of plant and animal communities, especially after a fire, because the colonizing capacity of plant and animal species is variable (Hanski 1993; Kadmon and Pulliam 1993). The larger size of the reservoir, compared to the two lakes, may create a harsher microclimate on islands, which could influence tree survival, regeneration and primary production on reservoir islands (Y. Bégin, personal communication).

With respect to exploited boreal forests, our results suggest that studied bird and mammal species should persist in remnant patches of mature forests of similar size (9-82 ha). However, predation pressure might differ between islands and the mainland; recent studies done in mixed forests indicated that patch size did not affect bird richness in mature forests bordering clearcuts (Rudnicki and Hunter 1993).

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Estimating the Accuracy of Counting Eastern Wild Turkeys, *Meleagris gallopavo silvestris*, Using Helicopters in Wisconsin

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Forty-three flocks of Eastern Wild Turkeys (*Meleagris gallopavo silvestris*), 26 of which contained ≥ 1 bird with a functional radio, were used to compare the number of flocks and number of birds counted in winter by aerial observers with known numbers on the ground. Research was conducted in an experimental turkey hunting zone (THZ) where Turkeys were intensively monitored as part of a population dynamics study. Helicopter-based counts (H) of total flocks and total birds averaged 86% and 80%, respectively, of ground-based (G) counts in the THZ where H/G comparisons were made in 1989, 1991, and 1993. Turkey densities adjusted by the 0.80 H/G ratio based on the total number of birds counted by helicopter- and ground-based observers in the experimental THZ, varied from 0.9 to 11.0/km² during 12 helicopter counts in 5 THZs during 1989–1994. Turkey densities were correlated ($P = 0.025$) with the spring harvest density derived from the number of gobblers killed/km² of forest from mandatory registration. Helicopter surveys of Wild Turkeys are most applicable in areas dominated by deciduous woodlands and agricultural crop fields where snow depths ≥ 15 cm occur.

Key Words: Eastern Wild Turkey *Meleagris gallopavo silvestris*, aerial survey, count, density, helicopter, Wisconsin

Helicopters have been successfully used for population surveys and censuses of Wild Turkeys, *Meleagris gallopavo*, and other wildlife in the United States and Canada (Thompson and Baker 1981). Although Thompson and Baker (1981) reported helicopters were used to count Wild Turkeys, we are unaware of any published reports that indicate the relative accuracy of counting Wild Turkeys using helicopters in areas where snow can provide a contrasting background. Stoll et al. (1991) reported that 100% of White-tailed Deer (*Odocoileus virginianus*) were counted where small deciduous woodlots comprised about 10% of an intensively farmed area in western Ohio. Comparison of helicopter and ground surveys of the number of Prairie Chicken (*Tympanuchus cupido*) leks in Colorado (Schroeder et al. 1992) indicated that ground surveys were more accurate.

To complement various population indices and capitalize on a unique situation where large numbers of radio-marked birds were present, helicopter-based counts were initiated in 1989 to test their validity for obtaining independent estimates of turkey densities in Wisconsin. The objectives were to: (1) determine an air-to-ground detection rate by comparing helicopter- (H) and ground-based (G) counts of Wild Turkey flocks and total birds during winter; and (2) apply the H/G ratio of total birds seen to helicopter-based counts in 5 THZs to determine the correlation with spring harvest densities.

Study Area

We conducted helicopter-to-ground comparisons

in THZ 1A, an experimental area designated for research on Wild Turkeys and turkey hunting in southwestern Wisconsin (Figure 1). Helicopter-based counts without ground-based comparisons were conducted in THZs 2, 4, and 6 in southwestern Wisconsin, and THZ 17 in east-central Wisconsin.

In southwestern Wisconsin, topography was characterized by steep slopes and deep valleys. Forests occupied 39% of the land area. Oak/hickory (*Quercus* spp./*Carya* spp.) occupied 63% of the forest land, other deciduous trees 36%, and conifers only 1%. THZ 17 had gently rolling terrain interspersed with wetlands that comprised 14% of the surface area. About 20% of the land area was forested, with oak occupying 60% of the forest land, other deciduous trees 27%, and conifers 13%. Most woodlands occurred in small blocks <40 ha. Dairy farming was the primary land use, and agricultural cropfields dominated the landscape in the areas surveyed.

Methods

Ground-Based Counts of Wild Turkeys in THZ 1A

To estimate H/G ratios for the number of flocks and number of birds/flock, ground-based counts were conducted during winter in 1989, 1991, and 1993 when snow depths were ≥ 15 cm. Counts were made by two wildlife biologists and two technicians who had monitored movements and survival of radio-marked Wild Turkeys throughout the winter.

Ground-based observers used radio-telemetry procedures, binoculars, and spotting scopes to verify

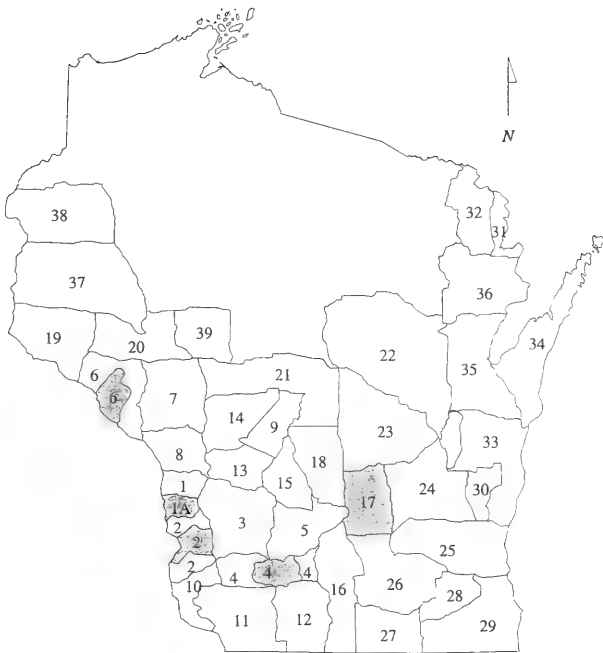


FIGURE 1. Location of helicopter-based counts of Wild Turkeys in harvest management zones in Wisconsin, 1989–1994.

flock size, composition, location, and time of observations on the day of helicopter-based counts. Data were recorded on U. S. Geological Survey (USGS) 7.5-minute topographic maps.

Helicopter-Based Counts of Wild Turkeys

Each THZ surveyed was divided into survey blocks delineated on USGS topographic maps using roads, power lines, streams, or woodland/open field edges as boundaries. Most blocks were ≤ 5 km² of land area to minimize navigational error and ensure greater accuracy of turkey locations, particularly where woodlands occupied $> 50\%$ of the land area.

Aerial observers searched an average of 45 randomly-selected (SAS Institute Incorporated 1990) survey blocks during each of three winters in THZ 1A (Figure 1). This represented an average of 36% of the entire land area within 125 survey blocks in THZ 1A. We designated randomly-selected survey blocks ($n = 89$ –124) in the approximate geographic center of THZs 2, 4, and 6. Fiscal limitations kept survey time to about 15 hours/THZ, and the level of sampling required to survey the entire portion of THZ 2, 4, and 6 to further improve the accuracy of results would have been too costly. Attempts to further replicate H/G comparisons in THZ 1A were complicated by insufficient snow cover in 1992, and by inadequate numbers of radio-marked birds present in 1994 as the research concentrated on gobblers.

Given nearly similar landscape composition within the portions of THZs 2, 4, and 6 that were sampled and in the remainder of THZs, we assumed Turkey distribution and density were not appreciably

different. Aerial observers searched 29–38 survey blocks (range = 23–38%), resulting in 6–9% of the land area searched in THZ 2, 4, and 6. In THZ 17, we searched 51 (14%) of 356 survey blocks that covered 14% of the land area. Snow depth varied from 20–30 cm, except on steep south-facing slopes in the southwestern unglaciated “Driftless Region”, where snow depths < 15 cm and some bare patches occurred.

Conditions were considered suitable for flying if wind velocity was < 24 km/hr and ≥ 15 cm of snow was present. Counts were made by a pilot and two biologists using three-seat helicopters (Hughes 300C in 1989, Engstrom F28A in 1991, and Bell 47 during 1992–1994. Helicopter rental ranged from \$210–240/hr, and total aerial survey cost varied from \$4100–4600.

We searched each block systematically using 100–200 m wide transects flown 30–60 m above ground at airspeeds of 35–70 km/hr. Transect width, altitude, and airspeed were modified to maximize ground visibility, particularly where dense conifer stands might conceal birds. Upon encountering turkeys, we circled and hovered to scatter the flocks and increase counting efficiency. We plotted on topographic maps the locations, size, and sex-age composition of flocks encountered. Habitat type (predominant overstory and understory species), estimated distance to the nearest woodland edge, and time of day were also recorded.

Comparison of Helicopter- and Ground-Based Counts in THZ 1A

A somewhat greater number of survey blocks were searched by aerial observers to ensure that more “known” flocks counted by ground-based observers were encountered to increase the validity of the H/G ratio. To avoid biasing the H/G ratio, aerial observers were unaware which survey blocks contained flocks counted by ground-based observers.

The H/G ratio observed in THZ 1A was applied to 12 helicopter-based counts (4 replications in THZ 1A and 8 in 4 other THZs) to determine the numbers of birds/km² of land area for correlation with spring harvest densities (the number of gobblers killed/km² derived from mandatory registration).

Data Analyses

Ground- and helicopter-based data were compared to determine the number of ground-based flocks and birds that were detected by aerial observers. Data were analyzed using the Statistical Analysis System (SAS Institute Incorporated 1990). We tested whether the percentage of known flocks counted on the ground that were seen from the air differed among years with Chi-square tests in THZ 1A. Additionally, we used analysis of variance (ANOVA) to test whether the difference between helicopter- and ground-based counts of flocks seen from the air varied among years. We further tested whether the dif-

ference between helicopter- and ground-based counts of flocks seen from the air, pooling data from the three years, differed from 0 with a paired T-test. We also assessed whether the difference between helicopter- and ground-based counts was correlated with flock size. Because survey blocks were of unequal size, the ratio method (Jolly 1969) was used to estimate density/km². Pearson correlations measured the strength of comparisons between the winter density estimated from helicopter-based counts and the spring harvest density.

Results

Helicopter-based counts were conducted 6–7 March 1989, 28–29 January 1991, 25–26 January 1993, in THZ 1A, and between 27 December and 15 March 1989–1994 in the remaining 4 THZs. Ground-based estimates were obtained from 43 flocks that had 1–50 birds (26 contained ≥ 1 turkey with a functional radio) (Table 1). By comparison, 21 of 26 (81%) flocks containing ≥ 1 radio-marked bird and 16 of 17 (94%) unmarked flocks were counted by aerial observers. We detected no difference among years for the percentage of known flocks (0.86; range = 0.83–0.89; $\chi^2 = 5.05$, 2df, $P = 0.08$) and the percentage of birds (0.80; range = 0.78–0.86; $\chi^2 = 0.211$, 2df, $P = 0.900$) that were counted by aerial observers.

The difference between paired helicopter- and ground-based counts of the 37 flocks seen from the air did not vary ($F = 0.11$, 2df, $P = 0.90$) among years and was not significantly different from 0 ($t = -1.43$, $P = 0.16$). Mean (\pm SE) flock size was 17.7 (± 2.1) from the air and 19.3 (± 2.3) from the ground. The difference between air and ground counts was negatively correlated with flock size for both all known flocks counted on the ground ($r = -0.39$, $n = 43$, $P = 0.01$) and those flocks that were only seen from the air ($r = -0.37$, $n = 37$, $P = 0.02$), suggesting the degree of undercounting by aerial observers increased with flock size.

Helicopter-based counts of flock size were within five birds of ground-based counts for 23 of 43 (53%) flocks. Seventeen and 10 flocks were under-

counted and overcounted respectively, by aerial observers. Six flocks known to be present in a searched block were not seen by aerial observers. Two flocks containing 32 and 40 birds were concealed by dense conifer cover, while four flocks containing from 5 to 16 birds occupied deciduous woodlands.

Ninety-nine percent of the turkeys encountered during helicopter-based counts in THZ 1A were ≤ 100 m of woodland edges or in agricultural crop-fields where corn (picked or standing) or spread manure provided food. Turkeys were rarely seen in the interior of woodlands by aerial observers, particularly where large contiguous blocks occurred.

Aerial counts of turkeys were more difficult where Eastern Red Cedar (*Juniperus virginiana*) or plantations of Red and White pine (*Pinus resinosa* and *P. strobus*) provided concealment. However, Eastern Red Cedar occurred as small (<2 ha) patchy areas on south-facing slopes, and nearly all pine plantations were <2 ha.

Turkey densities adjusted by the H/G ratio of birds counted in THZ 1A varied from 0.9 to 11.0 birds/km² of land area, and were highest in THZ 4 and lowest in THZ 6 (Table 2). Turkey densities calculated from helicopter-based counts were correlated ($r = 0.64$, 11df, $P = 0.025$) with the gobble harvest density (Wisconsin Department of Natural Resources, unpublished data) in the spring of the same year in those THZs where helicopter-based counts were made.

Discussion

We believe our ground-based counts were reliable because turkey flocks with and without radio-marked birds in THZ 1A were intensively monitored throughout the winter. The combined experience of both aerial observers who had considerable experience using helicopters or fixed-wing aircraft to count deer and waterfowl also were important factors affecting the reliability of this technique.

The accuracy of helicopter-based counts was affected by several factors: (1) the size of the flock; (2) nature of the flush (direction and distance relative to the helicopter); and (3) whether or not all the

TABLE 1. Comparison of helicopter-based (H) counts of Wild Turkeys and known number of flocks and total birds counted by ground-based (G) observers in Turkey Hunting Zone 1A in Vernon County, Wisconsin, 1989–1993.

Year	Number of flocks ^a		Number of turkeys		H/G Ratio	
	H	G	H	G	Total flocks	Total birds
1989	5 (3)	6 (4)	134	155	0.833	0.865
1991	16 (14)	19 (17)	266	337	0.842	0.789
1993	16 (4)	18 (5)	256	328	0.889	0.780
Total	37 (21)	43 (26)	656	820	0.855	0.800 ^b

^aNumber of flocks with ≥ 1 radio-marked turkey in parentheses.

^bBased on total birds because H/G ratio did not differ ($P = 0.900$) between years.

TABLE 2. Turkey densities estimated during helicopter-based counts in southwestern and east-central Wisconsin, 1989–1994.

Zone	Land Area (km ²)	Mean (SE) turkeys/km ² land area ^a				
		1989	1991	1992	1993	1994
1A	455	2.7 (0.6)	4.7 (0.7)	-	3.7 (0.8)	3.4 (0.7)
2	1411	3.8 (0.9)	6.4 (1.2)	-	3.6 (0.8)	6.3 (1.2)
4	1520	-	10.7 (1.7)	-	11.0 (2.7)	-
6	2062	-	-	1.4 (0.6)	0.9 (0.6)	-
17	1798	-	-	-	-	1.4 (0.7)

^aEstimates calculated using the ratio method because survey blocks were of unequal size, and the helicopter-to-ground (H/G) ratio (0.80) observed in an Experimental Turkey Hunting Zone.

turkeys flushed at once. Visibility of birds also appeared to be affected by the amount of concealment provided by conifers or residual oak leaves. Once flushed, it was more difficult to obtain a complete count if specific birds could not be verified on the second counting attempt. Aerial observers may have missed flocks close to the boundary of a survey block if birds moved to an adjoining area between the time ground- and helicopter-based counts were made. This did not occur with the 26 flocks with ≥ 1 radio-marked bird used for comparison of H/G counts.

In THZ 1A, most turkey flocks had little incentive to move any appreciable distance from day-to-day, having waste grain, principally corn or spread manure nearby, usually within 800 m, throughout the winter. In Massachusetts (Vander Haegen et al. 1989), turkey movements were restricted to < 20 ha as birds spent 54% of the diurnal period in cropland and pasture concentrating on corn stubble and spread manure during periods of deep snow (> 24 cm) during January-February. In Minnesota, where standing corn was the principal food, the average home range of turkeys was < 25 ha for most birds as snow depths exceeded 32 cm during January-March, compared to 288 ha during December (Porter 1977).

We believe that the accuracy of aerial counts for turkeys would be compromised in areas where conifer cover occupies $> 10\%$ of the forest land. Lone birds or small flocks of < 10 birds that occupy the interior of large woodland tracts also could be missed. Other factors that can contribute to undercounting turkeys include pilot inexperience in conducting wildlife surveys and obstructed view for the navigator who occupies the center seat in a three-seat helicopter. In addition, unfamiliarity with the area, few ground references, and resolution of topographic maps versus aerial photos may cause difficulties in maintaining proper orientation.

Because of the inherent difficulty in obtaining accurate ground-based counts, application of this technique to other areas would require independent verification of the H/G ratio, even in areas with similar habitat and terrain. This technique was tested on

an area where considerable independent effort was devoted to obtaining reliable ground-based counts.

Ground-based count costs were about \$1500 for the three-day period that encompassed aerial counts in THZ 1A. Actual costs were about \$6000, since about two weeks were required prior to helicopter-based counts to facilitate verification of flock size and location on the day helicopter-based counts were made. Without radio-marked birds present, the cost of locating flocks would have been greater.

We believe a three-seat ≥ 250 hp helicopter is optimal for conducting wildlife surveys, and appears to be effective whether steep or flat terrain is present. Although the center seat of a three-seat helicopter has a partially obstructed view, both observers have greater visibility than in larger machines where only the forward observer has an unobstructed view.

Helicopter-based counts of Wild Turkeys are most applicable where snow depths ≥ 15 cm can be expected in areas dominated by deciduous woodlands. In addition, helicopters provide considerable flexibility (moderate flight speed, optimum maneuverability, and good observer visibility at reduced heights above ground) to count turkeys with a high degree of confidence.

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The Distribution, Habitat, and Conservation Status of the Pacific Water Shrew, *Sorex bendirii*, in British Columbia

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Galindo-Leal, Carlos, and Gustavo Zuleta. 1997. The distribution, habitat, and conservation status of the Pacific Water Shrew, *Sorex bendirii*, in British Columbia. *Canadian Field-Naturalist* 111(3): 422–428.

During an intensive survey of small mammals in the Lower Mainland of British Columbia, we recorded Pacific Water Shrews (*Sorex bendirii*) in three sites. We documented habitat and microhabitat characteristics of the sites. Pacific Water Shrews are riparian habitat specialists with a relatively small geographical range in Canada, which overlaps with one of the main urban centres in the country. Although there is little information on *S. bendirii* abundance and population trends, suitable habitat has disappeared at a rapid rate and most remaining habitat is highly modified, fragmented, and isolated. Recently the Pacific Water Shrew has been designated as threatened in Canada. Factors influencing *S. bendirii* populations are largely the result of rapid and unplanned urbanization and agricultural development.

Key Words: Pacific Water Shrew, *Sorex bendirii*, British Columbia, COSEWIC.

The Pacific Water Shrew, Marsh Shrew, or Bendire's Shrew (*Sorex bendirii*) is restricted to the western part of North America from northern California to southern British Columbia (Hall 1981; Van Zyll de Jong 1983; Galindo-Leal and Runciman 1994; Nagorsen 1996). In Canada *S. bendirii* is restricted to the Lower Mainland of southwestern British Columbia (Figure 1). Its distribution overlaps with one of the main urban centers of the country. It has been recorded as far west as Point Grey, as far east as Chilliwack River, and from the North Shore Mountains in the north to the U.S. border in the south. Only fifteen individuals have been caught in the last 40 years.

The Pacific Water Shrew was designated in 1993 as threatened in Canada by COSEWIC (Galindo-Leal and Runciman 1994). Several sources of information indicate that suitable habitat for Pacific Water Shrews is disappearing rapidly. Historically, *S. bendirii* had likely a wide distribution in southwestern British Columbia. They were probably absent from areas like Richmond and Delta where habitats such as grasslands and shrublands predominated (North et al. 1979). A recent Landsat satellite image of the Lower Mainland shows that a substantial proportion of the lowland forest in the distributional range of the *S. bendirii* has been replaced by agriculture and urban development (MacDonald Dettwiler and Associates 1984). The aggregate channel length of the small rivers and streams in Vancouver has been reduced from over 120 kilometers to less than 20 kilometers (Oke et al. 1992). In many agricultural areas riparian forest has been greatly reduced or has been completely eliminated. The remaining habitat is highly modified, fragmented and isolated. Remaining forest patches may not be adequate for the requirements of *S. bendirii*.

Human activities in these areas have modified the composition and structure of the vegetation, and have modified the structure of streams. For example, 90% of forest fragments in Langley are either deciduous or mixed forest. The prevalence of these forest types is most likely due to previous human disturbances.

The objectives of this study were (1) to assess the current status of the Pacific Water Shrews in southwestern British Columbia and (2) to document habitat and microhabitat characteristics of sites inhabited by *S. bendirii*.

Study Area and Methods

The study was based on historical records and recent field surveys. We used a total of 108 specimens from 23 historical locations where *S. bendirii* had been collected from the databases of the Royal Provincial Museum, the University of British Columbia Vertebrate Museum, the Royal Ontario Museum, and the Conservation Data Centre. Two records were not confirmed with Voucher specimens: Orr Creek, Coquitlam, and Seymour River, North Vancouver (Galindo-Leal and Runciman 1994).

Seven more specimens were recorded in recent field surveys. We obtained three Pacific Water Shrews in three different localities (North Hoy Creek, Coquitlam, Davis Creek, Dewdney-Alouette, and Fergus Creek, Surrey). Four more specimens were captured recently in Sumas Mountain (Nagorsen 1996).

We sampled 55 sites distributed in 39 locations (Figure 1), in southwestern British Columbia during late July-October, 1992. Sites were selected using the presence of slow-moving watercourses as a requirement in topographic (1:50 000), and Forest

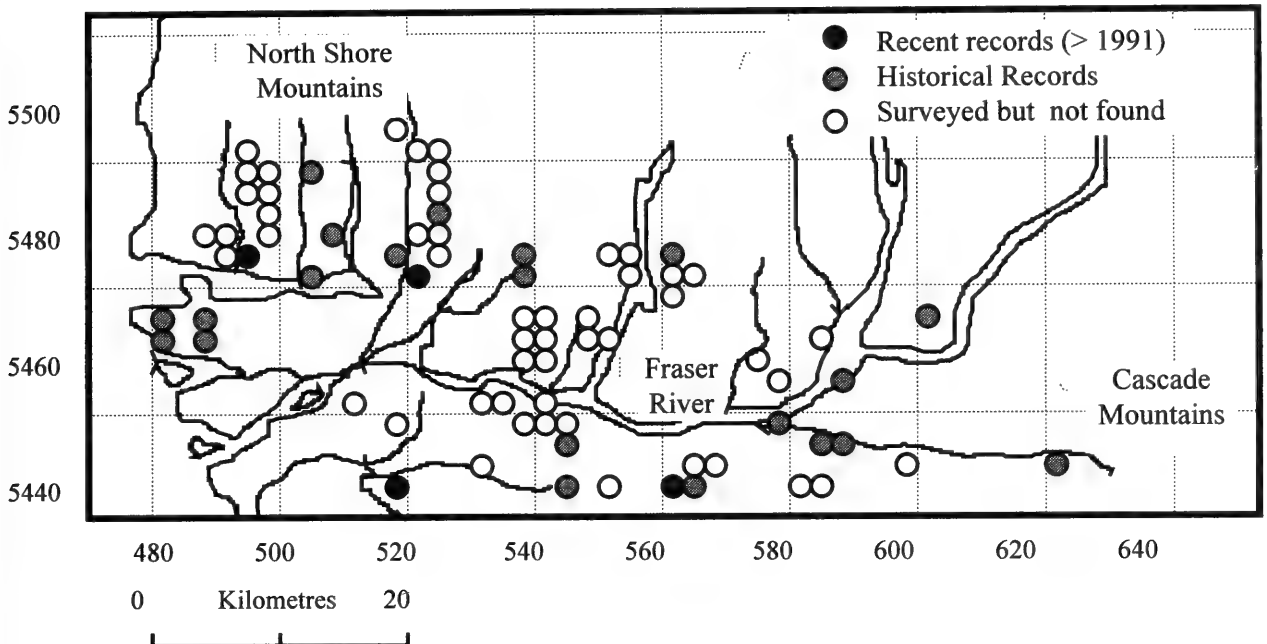


FIGURE 1. Distribution of *Sorex bendirii* in British Columbia derived from all known museum records (from Nagorsen 1996) and recent field surveys. UTM coordinates on both axis ($\times 10^3$).

cover maps (1:20 000). Site selection was restricted to locations at elevations below 600 m. Some locations were particularly selected to confirm historical records (50-100 years ago), such as Sumas Mountain or Harrison Lake. In every location, one to three sites were established; one site was set alongside a watercourse and one to two sites were set 50-100 m away into the forest. Every site had a trapline with 15 stations separated 15 m from each other with one pitfall trap per station. Pitfall traps (2-litre plastic buckets) contained 0.5-1 litres of 20% alcohol to preserve specimens. They had two small holes at mid-height to reduce flooding. Corn oil was added (5 ml) on top of the alcohol to minimize evaporation. A total of 55 traplines were installed and the total trapping effort was 19 810 trap-nights (TN). Traps were checked weekly during two to five weeks and specimens were collected. Traps were rarely disturbed by wildlife or humans. Only two traplines, in Stave Lake, were eliminated due to continuous disturbance by bears (Zuleta and Galindo-Leal 1994).

Shrews were identified following van Zyll de Jong (1983) and Nagorsen (1996). Voucher specimens were deposited in the Royal British Columbia Museum, Victoria, and in the University of British Columbia Vertebrate Museum, Vancouver.

The study area included only one biogeoclimatic zone: the coastal Western Hemlock ecosystem (Meidinger and Pojar 1991). Dominant tree species were: Western Hemlock (*Tsuga heterophylla*), Red Cedar (*Thuja plicata*), Douglas Fir (*Pseudotsuga menziesii*), Pacific Silver Fir (*Abies amabilis*), Sitka Spruce (*Picea sitchensis*), Pacific Yew (*Taxus brevifolia*), Lodgepole Pine (*Pinus* cf. *contorta*), Red

Alder (*Alnus rubra*), Big-leaf Maple (*Acer macrophyllum*), Black Cottonwood (*Populus balsamifera* ssp. *trichocarpa*), and Vine Maple (*Acer circinatum*).

To sample habitat and microhabitat we established four plots on each of the riparian and upland transects. Each plot consisted of two concentric circles that were centred on a trap station and adjacent plots were separated by 45 metres. Within a large circle of 15 metres radius (707 m²) we counted the number of live and dead coniferous trees of large (> 50 cm d.b.h.), medium (10-50 cm d.b.h.), and small (< 10 cm d.b.h.) diameter ranges as well as percentage cover of coniferous and deciduous canopy. Within the smaller circle of 5 metres radius (79 m²) we counted the number of live and dead coniferous and deciduous shrubs, mid-canopy shrubs, and coarse woody debris in three decomposition classes and two size classes. Percentage cover was recorded for ferns, grasses, forbs, mosses, exposed soil, and rocks.

Successional stages were classified as young forest, mature forest, and old growth forest. Young forest was defined as lacking trees with > 50 cm d.b.h. Mature forest was defined as having some trees with > 50 cm, d.b.h. Old growth was defined as having most trees with > 50 cm, d.b.h., but there were usually several trees with > 150 cm d.b.h.

Results

Pacific Water Shrews are extremely restricted and rare. Since 1888 only 115 specimens have been collected. Almost half of them were caught before 1900. Less than twenty individuals have been caught in the last 40 years (Table 1). They occupy an area of

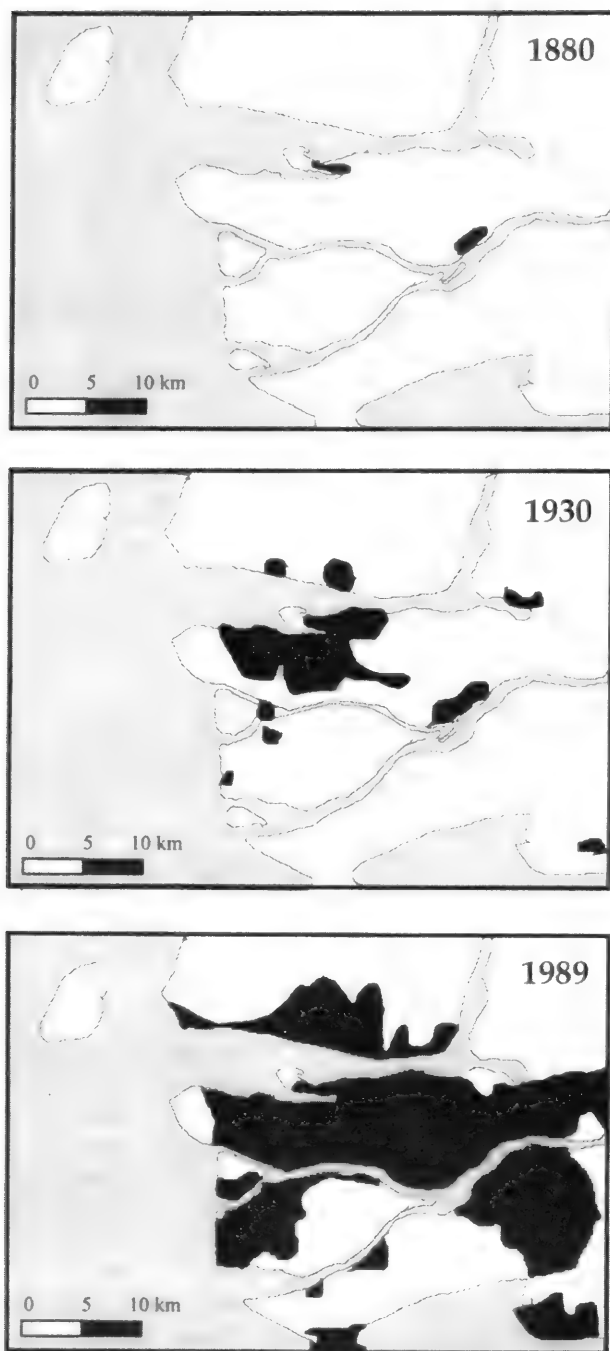


FIGURE 2. Historical progression of habitat loss in southwestern British Columbia (from Oke et al. 1992).

less than 6250 km² in southwestern British Columbia.

In our field survey, we caught only three individuals in three different sites from a total of 55 sites and 19 810 trap-nights. The three sites were more than 35 km apart from each other with no continuous habitat between them. All sites were within the historical distribution of the species (Figure 1). Two sites were north of the Fraser River: North Hoy Creek in Coquitlam (85 m.a.s.l. [metres above sea

level]), and Davis creek in Dewdney-Allouette (130 m.a.s.l.). The third site, Fergus Creek, was in White Rock (10 m.a.s.l.), near the U.S. border. All sites were near suburban areas. Pacific Water Shrews were trapped 5, 20, and 120 m away from public ways in Davis Creek, North Hoy Creek, and Fergus Creek sites, respectively.

We did not find Pacific Water Shrews in sites where they had been trapped before such as Chilliwack, Sumas, Aldergrove, Blaney Lake, Loon Lake, and Orr Creek. North Hoy Creek was the nearest site to locations with previous records. However, the previous record is about 100 years old: eight Pacific Water Shrews were caught in Port Moody between 1894-1897 (Nagorsen, D. 1996. British Columbia Mammal Database. Computer data base. Royal British Columbia Museum; Figure 1). Recently, four more specimens were collected from Sumas Mountain during environmental surveys (Nagorsen 1996).

Since we have detailed habitat data from only three sites where Pacific Water Shrews have been caught it is difficult to infer habitat use patterns. The main characteristics of these sites were as follows: All of the sites had creeks. Habitats were dominated by both conifers (Western Hemlock-Red Cedar) and mixed forests (Red Alder-Big-leaf Maple, Douglas Fir-Big-leaf Maple). All sites had mature forest with canopy cover greater than 50% (Table 2). They were captured alone, with Red-backed Voles (*Clethrionomys gapperi*), and with both Trowbridge's Shrews (*Sorex trowbridgii*) and Shrew-moles (*Neurotrichus gibbsii*).

The microhabitat in the three capture sites had very low percentage of exposed soil and grasses, moderate percentage of ferns, mosses and rocks and high percentage of fine litter. Sites differed widely in the amount of forbs (Table 3). The amount of ground cover by woody debris was similar in the three sites (15 to 19%). The percentage cover of old debris was higher than that of recent debris, particularly in Hoy Creek. There were more medium sized logs than large logs. However, large logs (> 50 cm width) were recorded in all three sites (Table 3).

The three capture sites had more coniferous than deciduous trees. Canopy was well developed both at medium and high levels. High canopy cover was similar for deciduous and conifers and medium canopy cover was slightly higher for deciduous trees (Table 3).

Discussion

A century ago (1889-1901), 50 Pacific Water Shrews were recorded in locations such as Port Moody (6 specimens in July, 1894), Sumas (16 specimens in April-June, 1895; 15 specimens in May-July, 1896) and Chilliwack (Nagorsen 1996). During our study only one specimen was recorded in Coquitlam, adjacent to Port Moody, and none in

TABLE 1. List of locations from west to east, municipality, year and number of *Sorex bendirii* collected in Canada (from Galindo-Leal and Runciman 1994).

Number	Location, Municipality	Year	Number of specimens
1	Vancouver, Vancouver	1950	2
2	Vancouver, Vancouver	1945, 1950, 1951, 1962, 1973	10
3	Vancouver, Vancouver	1933	1
4	Vancouver, Vancouver	1935	2
5	Vancouver, North Vancouver	1955	1
6	Seymour River, North Vancouver	1991	1*
7	Dollarton, North Vancouver	1977	1
8	Mount Seymour, North Vancouver	1933	2
9	Port Moody, Port Moody	1894, 1895, 1897	8
10	North Hoy Creek, Coquitlam	1992	1
11	Or Creek, Coquitlam	1991	1*
12	Fergus Creek, Surrey	1992	1
13	Loon Lake, Maple Ridge	1974	1
14	Blaney Lake, Maple Ridge	1973	1
15	Peardonville, Langley	1929, 1930	8
16	Aldergrove, Langley	1930	1
17	Huntingdon, Abbotsford	1927, 1932, 1934, 1935, 1941, 1943	10
18	Davis Creek, Dewdney-Alouette	1992	1
19	Sumas, Chilliwack	1895, 1896, 1897, 1995	44
20	Cultus Lake, Chilliwack	1927, 1942	2
21	Vedder Crossing, Chilliwack	1901, 1935	7
22	Chilliwack, Chilliwack	1888, 1889, 1891, 1926	4
23	Agassiz, Kent	1896	1
24	Chilliwack River, Chilliwack	1981	2
Total			115

*These records have not been confirmed with Voucher specimens.

Sumas and Chilliwack (Figure 1). We have insufficient information on habitat availability and trapping effort for the 100-year old surveys, to compare them with our information. However, we were unable to obtain similar numbers in our survey of 37 riparian habitats, even using the most efficient technique (pit-fall trapping; Williams and Braun 1983).

Over the last 20 years, only 9 specimens with positive identification have been recorded in British Columbia (Nagorsen 1996). Two of those were collected in non-riparian habitats in two locations of the University of British Columbia Research Forest (Maple Ridge), by Sullivan in 1973-1974. We sampled the same locations in both riparian and non-

TABLE 2. Habitat characteristics of sites where *Sorex bendirii* was caught in the Lower Mainland.

Creek		North Hoy	Davis	Fergus
Overstorey (Trees / ha)				
	< 50 cm dbh	Coniferous	59.40	292.79
		Deciduous	82.03	131.54
	> 50 cm dbh	Coniferous	22.63	52.33
		Deciduous	2.83	24.05
Percent canopy cover	High	Coniferous	24.0	31.7
		Deciduous	16.0	18.3
	Medium	Coniferous	4.0	20.0
		Deciduous	52.0	6.7
Dominant		Alder,	Hemlock,	Alder,
		Bigleaf Maple	Red Cedar	Red Cedar
Other spp.		Vine Maple,	Alder	Bigleaf Maple,
		Hemlock,		Sitka Spruce,
		Red Cedar		Hemlock
Creek width		2 m	50 cm	5 m
Substrate		Rocky	Large boulders	Sandy

TABLE 3. Microhabitat characteristics of sites in the Lower Mainland where *Sorex bendirii* were trapped.

Creek		North Hoy	Davis	Fergus
Ground cover (Mean percentage cover)	Exposed soil	14.0	3.3	2.5
	Ferns	31.0	13.0	15.0
	Fine Litter	92.0	43.0	78.0
	Forbs	6.0	27.0	58.0
	Grasses	0.0	10.0	0
	Mosses	16.0	10.0	20.0
	Rocks	8.0	28.0	13.0
Woody debris (Mean percentage)	Young (1-2)	0.0	6.7	2.5
	Decomposition state Med (3-4)	1.0	3.3	5.0
	Old (5-6)	19.0	6.7	7.5
Average number of logs/ha	Medium (10-50 cm wide)	79.21	94.77	124.47
	Large (> 50 cm wide)	33.95	4.24	25.46

riparian habitats, but no Pacific Water Shrews were trapped. More recently, the presence of four Water Shrews was reported in the Greater Vancouver watersheds (D. Seip and J. P. Savard. 1992. Wildlife diversity in old-growth forests and managed stands. B.C. Ministry of Forests, Vancouver Forest District. Unpublished draft report). Since no voucher specimens are available, there are some doubts whether these specimens were *S. bendirii* or Water Shrews (*S. palustris*) (Nagorsen personal communication.). We surveyed 14 sites in Capilano and Coquitlam watersheds, but no Water Shrews were found. Unlike the Water Shrew, the Pacific Water Shrew seems to be restricted to low altitude sites. The three sites where they were recorded during our survey were all below 150 m. The highest altitude documented was 850 m (Nagorsen 1996).

In the United States, *S. bendirii* habitat has been characterized as forested riparian areas with a prevalence of coniferous trees. *S. bendirii* has been captured in moist and wet young, mature and old-growth Douglas Fir forest in the Coast and Cascade Range of Oregon (Corn and Bury 1991; Gilbert and Allwine 1991; Gomez 1992) and in Douglas Fir forest of the Southern Cascades Range of Washington (West 1991). In these study areas they were captured in stands with relatively low conifer canopy cover (41.3%) and high density of logs of decay class 1 (Gilbert and Allwine 1991). They were absent from clearcuts (Corn and Bury 1991; Gilbert and Allwine 1991). In Oregon, they were more abundant in mature and old growth stands of Douglas Fir than in young stands (Corn and Bury 1991; Gilbert and Allwine 1991) whereas in Washington they were as or more abundant in young stands (Aubry et al. 1991; West 1991).

S. bendirii are most commonly associated with riparian and marshy habitats (Galindo-Leal et al. 1994; Nagorsen 1996). Most *S. bendirii* are caught within 25 m of streams, and their abundance is sig-

nificantly lower at 200 m away from streams (Gomez 1992; McComb et al. 1993; Zuleta and Galindo-Leal 1994). *S. bendirii* abundance has been found to be positively correlated with stream aspect, conifer basal area (m^2ha^{-1}), and mostly Western Red Cedar cover in Oregon (Gomez 1992). Capture locations of *S. bendirii* were characterized by evergreen tree cover, evergreen shrub cover, distance to stand edge, higher number of large logs, litter depth, percent slope and higher basal area of deciduous trees (Gomez 1992).

In riparian zones of the western Oregon Cascade Range they were caught in old growth, in mature, and in young coniferous forests (Anthony et al. 1987). However, they were more abundant in riparian areas with trees more than 80 years old than in riparian areas with younger stands (W. C. McComb and J. Hagar. 1993. Riparian wildlife habitat literature review. Department of Forest Sciences, Oregon State University. Unpublished manuscript. 63 pages). McComb and Hagar (1993) listed *S. bendirii* among the species associated with mature and old-growth forests.

S. bendirii uses streams for foraging. As their food habits seem more specialized than those of other shrews because of the inclusion of aquatic insects in their diet (Pattie 1973; Nagorsen 1996), changes in water quality may directly or indirectly detrimentally affect *S. bendirii*. Streams in urban areas are influenced by residential septic fields, runoff from urban areas and agricultural fields, industrial waste and erosion (Cook et al. 1993). Unfortunately, industrial and urban development in the Lower Mainland are happening at an unprecedented rate. For example, according to the latest topographic map (Map G/7 Port Coquitlam, scale 1:50 000), one of the sites (North Hoy Creek in Coquitlam) where we found *S. bendirii*, was a natural area in 1986. It was also 500 m away from the nearest housing area. Today, this site is almost enclosed by urbanization. One Pacific

Water Shrew was caught there only 20 m away from a public street.

There are a number of measures that must be taken to ensure the long-term persistence of *S. bendirii* populations in Canada. Most of these actions involve the maintenance, protection, and restoration of forested riparian habitats in the Lower Mainland of British Columbia. Maintenance of these systems has many other benefits that have been already considered in other contexts (i.e., fisheries). For *S. bendirii*, questions of habitat quality, connectivity, and width of riparian zones are most important. There is a strong need to protect relatively large fragments and their connectivity with other fragments. In many cases, habitat connectivity has been lost and it will be necessary to restore riparian habitats. Within fragments, maintenance of large trees, canopy cover, woody debris, fine litter, and stream structure are priorities.

An important consideration for the management of this species is the width of riparian habitats. *S. bendirii* is considered to be among the species sensitive to forest harvest along streamsides (McComb and Hagar 1993). Suggested buffer widths for riparian zones range from 10 m to more than 200 m (British Columbia Ministry of Forests 1992; Gomez 1992; McComb and Hagar 1993; Zuleta, G. 1993. Analysis of habitat fragmentation effects with emphasis on small mammals at risk. Ministry of Environment, Lands and Parks, Victoria, British Columbia Unpublished. 24 pages.; Galindo-Leal et al. 1994). Draft guidelines for this species under the Forest Practices Code of British Columbia Act call for 30 m riparian reserve zones plus 20 m riparian management zones (50 m total) on each side of occupied and historic watercourses (Province of British Columbia, *in preparation*, Managing Identified Wildlife Guidebook, Forestry Practices Code of British Columbia Ministry of Environment, Lands, and Parks, Victoria, British Columbia). However, these guidelines only apply to Pacific Water Shrew habitat on provincial crown lands. Urban development on private lands is considered a greater threat to species persistence.

Conservation of Pacific Water Shrew habitat on private lands will require a coordinated effort on the part of landowners and all levels of government. Private land stewardship and outright acquisition of critical habitats will be required. We recommend to implement a monitoring program to assess the efficacy of different riparian buffer widths.

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David Nagorsen of the Royal Provincial Museum provided the database with both historical and recent records where *S. bendirii* have been collected. Dick Cannings provided laboratory facilities and records from the University of British Columbia Vertebrate Museum. Mark Engstrom authorized the use of the

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Diets of Wolves, *Canis lupus*, in Logged and Unlogged Forests of Southeastern Alaska

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Diets of Alexander Archipelago Wolves (*Canis lupus ligoni*) on Prince of Wales and adjacent islands, southeastern Alaska, were investigated from November 1992 to July 1994 to evaluate the effects of logging on the predator-prey communities. Of 182 feces analyzed, 90% of them contained remains of Sitka Black-tailed Deer (*Odocoileus hemionus sitkensis*), 31% contained remains of Beaver (*Castor canadensis*), followed by remains of River Otter (*Lutra canadensis*), Black Bear (*Ursus americanus*), small mustelids, and fish. Remains of deer occurred homogeneously throughout the year and over space. Remains of River Otter and small mustelids occurred exclusively in feces from Wolves inhabiting logged areas, whereas fish remains were more common in feces from Wolves inhabiting undisturbed areas. Small sample size and the effects of logging were suspected for the source of heterogeneity.

Key Words: Wolves, *Canis lupus ligoni*, diet, forest, Alexander Archipelago, Prince of Wales Island, Alaska.

Populations of Sitka Black-tailed Deer (*Odocoileus hemionus sitkensis*) in southeastern Alaska have been predicted to decline because of harvest of old-growth forests (Wallmo and Schoen 1980; Schoen et al. 1988). A reduction in deer abundance would change diets of Alexander Archipelago Wolf (*Canis lupus ligoni*), especially on Prince of Wales and adjacent islands where the only ungulate is the Sitka Black-tailed Deer.

Large-scale clearcutting is the common practice in the region. Although the open clear-cut areas provide forage to deer in summer, the second growth of coniferous trees outcompete shrubs and forbs, and finally eliminate understory vegetation as its forest canopy closes. The closed second-growth forests will not produce forage for > 100 years (*see* Wallmo and Schoen 1980; Alaback 1982; Kirchoff et al. 1983 for detail). Not surprisingly, deer seem to feed in open clear-cuts during summer (Yeo and Peek 1992), but prefer old-growth forests during winters with deep snow (Schoen and Kirchoff 1990), and avoid second-growth forests with closed canopies throughout the year (Wallmo and Schoen 1980).

Similarly, relevant literature leads us to assume that abundance of prey other than deer (alternate prey) are lower in the closed second growth than in the unlogged. Researchers have indicated that unlogged areas are important for Marten (*Martes americana*) (Thompson 1994; Thompson and Colgan 1994), River Otter (*Lutra canadensis*) (Newman and Griffin 1994; Bowyer et al. 1995), and Coho Salmon (*Oncorhynchus kisutch*) (Tschaplinski and Hartman 1983; McMahon and Holtby 1992). Mammals with short life cycles such as small

rodents may increase in the open second growth (Van Horne 1982; Walters 1991; but *see* Van Horne 1983).

If these alternate prey are as sensitive as deer to changes in habitats caused by logging, density of both deer and alternate prey would decrease in the closed second growth. In that instance, Wolves may not change their preference for deer despite the reduction in deer abundance. Instead, Wolves might increase predation pressure on deer to compensate for the reduction in total biomass of prey in the closed second growth.

The objectives of our study were to evaluate the degree of dependence of Wolves on deer and alternate prey, and to investigate the difference in Wolf diets between logged and unlogged forests. We define the area covered by the closed second-growth forests as “logged” in this study. We tested the hypothesis that deer remains occurred less frequently in feces of Wolves inhabiting logged areas than in feces of Wolves inhabiting unlogged areas. The null hypothesis was that deer remains occurred equally in feces of Wolves inhabiting logged and unlogged areas.

Study Area

The study was conducted on central Prince of Wales Island and on adjacent Kosciusko, Dall, Tuxekan, Marble, and Orr islands in the Alexander Archipelago of southeastern Alaska (Figure 1). Southeastern Alaska has a cool, moist maritime climate. Mean monthly temperatures range from 13°C in July to 1°C in January. Annual precipitation varies from 200 to 600 cm. The topography consists of

Table 1. Temporal occurrence (%) of food items identified in 182 Wolf feces collected on Prince of Wales and adjacent islands, Alaska, from November 1992 through July 1994. Items of infrequent occurrence (e.g., voles, birds) were excluded. Small mustelids include Martens, Short-tailed Weasel, and Mink. Data from autumn 1993 were removed from comparisons between years. OF is occurrence/feces, and OI is occurrence/item indices.

Scale	Number of feces	Number of items	Deer		Beaver		River Otter		Black Bear		Small mustelids		Fish	
			% OF	% OI	% OF	% OI	% OF	% OI	% OF	% OI	% OF	% OI	% OF	% OI
(a) Combined	182	274	90	59	31	21	8	5	8	5	9	6	5	3
(b) Year														
Jan 93-Jul 93	46	70	89	56	37	24	2	1	9	6	13	9	0	0
Jan 94-Jul 94	72	115	96	60	42	26	3	2	11	7	6	3	0	0
Nov 92-Jul 93	53	81	91	59	36	23	4	2	9	6	11	7	0	0
Nov 93-Jul 94	76	121	96	60	41	26	3	2	11	7	7	4	0	0
(c) 4 seasons														
Winter (Dec-Feb)	49	81	94	57	47	28	12	7	4	2	8	5	0	0
Spring (Mar-May)	52	85	94	58	38	24	8	5	17	11	6	4	0	0
Summer (Jun-Aug)	39	50	92	72	18	14	3	2	5	4	10	8	0	0
Autumn (Sep-Nov)	42	58	76	55	17	12	10	7	2	2	12	9	21	16
(d) 2 seasons														
Snow-free (May-Oct)	89	126	82	58	21	15	9	6	9	6	10	7	10	7
Snow-covered (Nov-Apr)	93	148	97	61	41	26	8	5	6	4	7	5	0	10

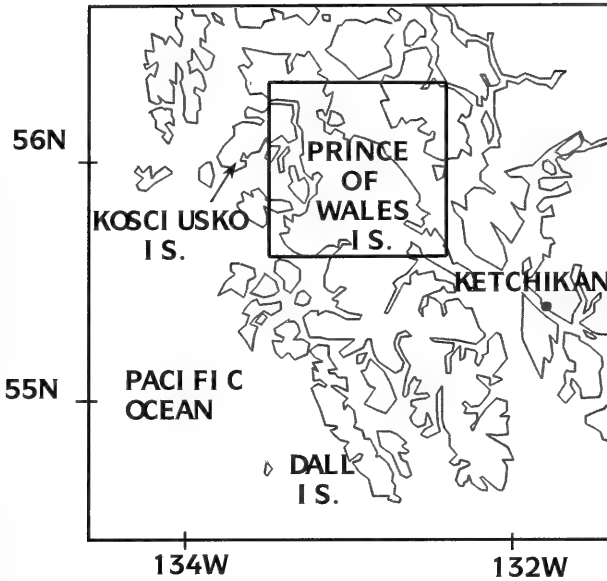


FIGURE 1. Prince of Wales Island in southeastern Alaska. Box indicates location of study area. Tuxekan, Marble, and Orr Islands are located between Prince of Wales and Kosciusko Islands.

steep, glaciated mountains, deep fjords and many islands. Because the mainland of southeastern Alaska consists of high mountains, glaciers, and ice-fields, the Alexander Archipelago includes the major portion of forests in southeastern Alaska. Due to its glacial history, isolation caused by glaciers, and island geography, the Alexander Archipelago supports many endemic species of flora and fauna (MacDonald and Cook 1996).

The Alexander Archipelago is within the Tongass National Forest (approximately 70 000 km²), the largest national forest in the United States. The area from sea level to about 600 m (approximately 60% of the Tongass National Forest) is covered with well-developed temperate rainforests (Schoen et al. 1988), primarily Sitka Spruce (*Picea sitchensis*) and

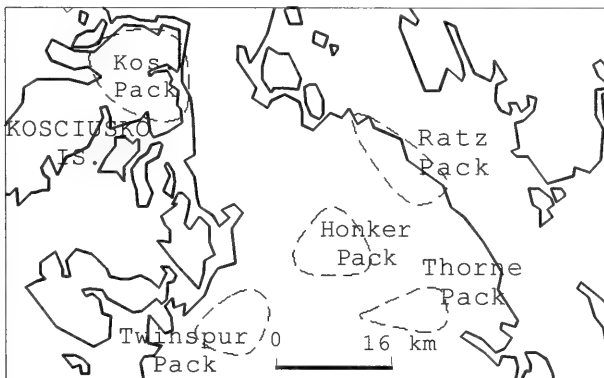


FIGURE 2. Study area and general locations of Wolf pack home ranges for categorizing collection locations of feces.

Western Hemlock (*Tsuga heterophylla*). Other common trees are Mountain Hemlock (*Tsuga mertensiana*), Alaska Cedar (*Chamaecyparis nootkatensis*), Western Redcedar (*Thuja plicata*), Red Alder (*Alnus rubra*), and Black Cottonwood (*Populus trichocarpa*) (Viereck and Little 1972). The remaining area is alpine tundra, riparian, or scattered muskeg. Of the forested area, 75% was old-growth forest in the early 1980s (Alaback 1982). Old-growth forests have multilayered canopies with numerous gaps, and the age of dominant trees exceeds 150 years (Alaback 1982; Schoen et al. 1988). The understory of old-growth forests is covered by coarse woody debris and vegetation such as ferns, mosses, lichens, fungi, herbs, and shrubs (Alaback 1982; Spies and Franklin 1988), and provides a mosaic of unique habitats for many species of plants and animals.

Although Prince of Wales Island (POW; 6700 km²) and adjacent islands support larger populations of terrestrial vertebrates than smaller islands in the region, the number of species is limited (e.g., no lagomorphs occur on POW or adjacent islands). Terrestrial mammals relevant to our study include the Wolf, Black Bear, River Otter, Mink (*Mustela vison*), Marten, Short-tailed Weasel (*Mustela erminea*), Sitka Black-tailed Deer, Beaver, and small rodents (*Microtus* spp. and *Peromyscus* spp.).

The natural landscapes of southeastern Alaska have been markedly altered by human activities such as timber harvesting. Clear-cut logging has been practiced on old-growth forests in the region for the past several decades. Since the early 1900s, and more intensively in the last 30 years, > 400 km² of high-volume old-growth forests on POW (6% of the island) have been logged (Schoen et al. 1988; Yeo and Peek 1992).

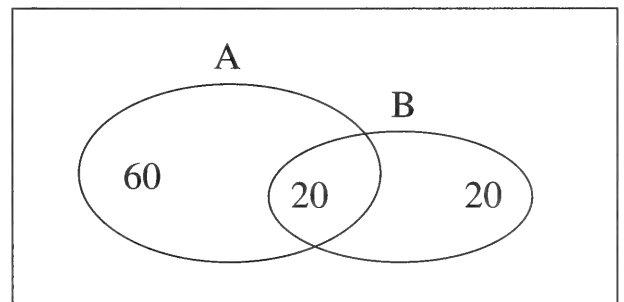


FIGURE 3. Calculation of two indices describing occurrence of food items in Wolf feces. Where the total number of feces, $n(A \cup B) = 100$; number of feces containing item A, $n(A) = 80$; number of feces containing item B, $n(B) = 40$; and number of feces containing both items A and B, $n(A \cap B) = 20$. Indices for item A are calculated as follows:

$$\text{Occurrence/feces}(A) = n(A) / n(A \cup B) = 80 / 100 = 0.8$$

$$\text{Occurrence/item}(A) = n(A) / [n(A) + n(B)] = 80 / 120 = 0.67.$$

TABLE 2. Pairwise Z-test results for fish occurrence in Wolf feces across four seasons using two indices, Prince of Wales and adjacent islands, Alaska, 1993 and 1994.

	Occurrence/feces index			Occurrence/item index		
	Spring	Summer	Autumn	Spring	Summer	Autumn
Winter	0	0	4.70**	0	0	5.06**
Spring		0	4.76**		0	5.11**
Summer			4.44**			4.51**

* $P < 0.0083$ ** $P < 0.0017$

Methods

As part of a wider study of Wolf ecology in Tongass National Forest, 182 fresh feces of Wolves were collected mainly along roads, occasionally at dens and rendezvous sites on POW and adjacent islands (Kosciusko, Marble, Orr, and Tuxekan Islands) from November 1992 to July 1994 equally across seasons (Figure 2). Location and date were recorded, and feces were stored frozen in plastic bags.

The procedure in the laboratory generally followed the method described by Bowyer et al. (1983). Feces were transferred to paper bags and autoclaved at 120°C for 20 minutes as a precaution to kill Hydatid Tapeworms (*Echinococcus granulosus*) that might be present. Sterilized feces were placed in nylon stockings (mesh size < 0.25 mm²) and thoroughly washed in lukewarm water. The remaining contents were spread on a metal tray and visually inspected for prey remains. Four or five random points in the tray were further examined by dissection and compound microscopes. Mammal remains were identified by comparison with hair samples and with descriptions of hair characteristics (Mayer 1952). Fish in feces were identified by the occurrence of teeth and vertebrae. Further identification beyond the family (Muridae) level was not attempted for voles; fish and birds were not identified beyond class. Plant identification was not attempted.

Feces were assigned to one of five general home ranges of Wolf packs or an undefined area according to the collection locations (Figure 2). Home ranges were defined from field observation and telemetry data of pack members (unpublished data) for the Kosciusko Island (Kos) pack, Honker pack, Ratz pack, Thorne pack, and Twin Spur pack. Feces collected outside areas defined in Figure 2 were categorized as undefined.

From the average percentage of the closed second growth area within home ranges (95% adaptive kernel; Kie et al. 1994) of individual pack members (unpublished data), the Ratz pack (average percent of closed second growth within home ranges = 26%, number of home ranges = 3) and the Twin Spur pack (16%, $n = 3$) were categorized as logged areas, and the Thorne pack (1%, $n = 1$) and the Honker pack (2%, $n = 1$) were regarded as unlogged areas. The

undefined area was categorized as logged although habitat composition was not measured, because of the generally high proportion of clear-cut areas outside home ranges of Wolf packs. Similarly, the Kos pack was assigned to unlogged area without data on habitat composition because its home range on eastern Kosciusko Island was not logged except small portions along the coastline.

Collection locations for feces were sufficiently discrete to be ascribed to home ranges of Wolf packs. Although some feces could have been deposited by dispersers or neighboring pack members, we considered that number of such feces were negligible. Feces occurring within the defined areas were assumed to be deposited by members of the corresponding pack.

Prey remains in feces are biased representations of food consumed by animals because of different digestibility among prey species, and among parts of prey (Mech 1970; Weaver 1993). Although none of the conventional indices is free of these biases, we used two indices to describe diets of Wolves; the occurrence/feces index (Pederson and Tuckfield 1983; Dibello et al. 1990; Reichel 1991) and the occurrence/item index (Voigt et al. 1976; Theberge et al. 1978; Bowyer et al. 1983) (Figure 3). Because a summation of the occurrence/feces index often exceeds unity when grouped, statistical analyses were conducted only using the occurrence/item index.

The occurrence of food item of Wolves was compared across seasons, years, and pack home ranges using Chi-square tests (White and Garrott 1990: 196), and pairwise Z-tests (Remington and Schork 1970: 217). Seasons were defined in two ways. One was spring (1 March-31 May), summer (1 June-31 August), autumn (1 September-31 November), and winter (1 December-28 February). The other was snow-free (1 May-31 October) and snow-covered (1 November - 30 April). A Yates correction for continuity (Zar 1984: 48) was applied for Chi-square tests with 1 degree of freedom. A Bonferroni correction was applied to multiple comparisons. The significance level was set at 0.05.

Results

Of 274 food items identified from 182 feces, the most common item, regardless of season and space,

TABLE 3. Spatial occurrence (%) of food items identified in Wolf feces, Price of Wales and adjacent islands, Alaska, 1993 and 1994. Proportions of closed second growth for Kos pack home ranges and Undefined were not measured. OF is occurrence/feces, and OI is occurrence/item indices.

Location	Closed Second Growth	Number of feces	Number of items	Deer		Beaver		River Otter		Black Bear		Small mustelids		Fish	
				% OF	% OI	% OF	% OI	% OF	% OI	% OF	% OI	% OF	% OI		
Unlogged areas															
Kos	—	28	39	93	67	18	13	0	0	4	3	0	0	25	18
Honker	2	28	47	100	60	46	28	0	0	21	13	0	0	0	0
Thorne	1	22	31	100	71	36	26	0	0	5	3	0	0	0	0
Combined		78	117	97	65	33	22	0	0	10	7	0	0	9	6
Logged areas															
Twin Spur	16	43	70	95	59	28	17	14	9	5	3	19	11	2	1
Ratz	26	35	45	83	64	29	22	3	2	3	2	9	7	3	2
Undefined	—	26	42	65	40	35	21	31	19	12	7	19	12	0	0
Combined		104	157	84	55	30	20	14	10	6	4	15	10	2	1

was Sitka Black-tailed Deer in both occurrence/feces and occurrence/item indices (90% and 59%, respectively), followed by Beaver (31%, 21%), River Otter (8%, 5%), Black Bear (8%, 5%), small mustelids (9%, 6%), and fish (5%, 3%) (Table 1a). Wolf hairs occurred in seven feces, and five feces consisted almost entirely of plants. Due to infrequent occurrence, three species of mustelids (Marten, Short-tailed Weasel, and Mink) were combined as small mustelids, and four items (voles, birds, Wolves, and plants) were excluded from analysis.

Because of the lack of data in autumn 1992, comparisons between years were calculated in two ways without data from autumn (January-July 1993 vs. January-July 1994, November 1992 - July 1993 vs. November 1993-July 1994) (Table 1b). No significant difference in occurrence of food items was revealed in either analysis ($\chi^2_5 = 2.31, P = 0.80$ and $\chi^2_5 = 1.29, P = 0.94$, respectively). Therefore, data were pooled over years.

Temporal differences in Wolf diets were significant among four seasons (Table 1c; $\chi^2_{15} = 52.58, P < 0.0001$) and between two seasons (Table 1d; $\chi^2_5 = 16.05, P = 0.0067$) due to use of fish in autumn and snow-free season (Table 2). Proportions of other five items did not show any detectable differences in season.

Diets of Wolves differed significantly among six areas (five home ranges and one undefined area) (Table 3; $\chi^2_{25} = 81.05, P < 0.0001$), and between logged and unlogged areas (Table 3; $\chi^2_5 = 30.05, P < 0.0001$). Fish remains occurred more often in Kos pack home range (Table 4), which belongs to unlogged area, whereas remains of River Otter occurred only in logged areas (Table 3, 4). Occurrences of other four items (Deer, Beaver, Black Bear, and small mustelids) were not statistically different over space.

Discussion

In spite of temporal and spatial changes in Wolf diets, the dependence of Wolves on deer was clearly demonstrated by the analysis. Occurrence of deer remains did not differ seasonally (snowfalls were normal during two winters of the study period) or spatially. Deer comprise the major portion of Wolf diet in the study area.

Temporal difference in Wolf diets was not detected except high use of fish in autumn. Frequent occurrence of Beaver throughout the year (Table 1c, d) agreed with studies on Vancouver Island of Canada (Scott and Shackleton 1980; Milne et al. 1989), in contrast with studies in other parts of North America, where Beaver remains did not occur in winter (Mech 1970; Voigt et al. 1976). Milne et al. (1989) attributed the results to the mild winter of the region that seems to make Beaver available to Wolves all the year round.

TABLE 4. Pairwise spatial comparisons of selected food items of Wolves using Z-values, Prince of Wales and adjacent islands, Alaska, 1993 and 1994. Twin. is Twin Spur, and Undef. is Undefined.

Item		Occurrence/feces index					Occurrence/item index				
		Honker	Thorne	Twin.	Ratz	Undef.	Honker	Thorne	Twin.	Ratz	Undef.
River Otter	Kos	0	0	2.09	0.41	4.11**	0	0	1.89	0.45	3.77**
	Honker		0	2.09	0.41	4.11**		0	2.00	0.47	3.94**
	Thorne			1.94	0.38	3.86**			1.75	0.42	3.54**
	Twin.				1.77	2.46				1.46	2.36
	Ratz					3.92**					3.45**
Fish	Kos	4.31**	4.05**	4.31**	4.03**	4.23**	4.65**	4.19**	4.64**	4.03**	4.53**
	Honker		0	0.44	0.52	0		0	0.43	0.60	0
	Thorne			0.41	0.48	0			0.37	0.53	0
	Twin.				0.11	0.43				0.23	0.41
	Ratz					0.51					0.58

* $P < 0.0033$ ** $P < 0.0007$

Although not significant, remains of Black Bear seemed to occur more often in spring (Table 1c). Wolf predation on bear cubs, scavenging of Wolves on bear carcass, and harassment of bears at Wolf dens are the possible source of this outcome. Conflicts between Wolves and Bears were documented previously by Murie (1944) and Mech (1970). On 15 April 1994, one radio-collared Wolf on POW died from wounds in the lower abdomen, which probably were inflicted by bear claws.

Compared spatially, occurrence of deer remains in Wolf feces did not differ significantly. This study failed to reject the null hypothesis of homogeneous use of deer by Wolves between logged and unlogged areas. The comparison showed, however, high use of fish in Kos pack home range and high use of River Otter in logged areas. The results could be caused by sampling bias, or by biological reasons.

Assuming abundance of fish was homogeneous among pack home ranges because all home ranges contain one or two relatively large streams that support salmonids, the source of spatial difference could be the difference in availability of fish. Human activity at estuaries is high during salmon runs, and extensive road systems on POW allow access to major streams regardless of logging activities along those streams. Accesses to streams on adjacent uninhabited islands including Kosciusko Island are limited to boat or air travel. The frequent presence of humans may limit access of Wolves to fish at estuaries, resulting in lower use of fish by Wolves in such areas.

In contrast to high use of fish in relatively undisturbed areas, use of River Otter occurred exclusively in logged areas without seasonal differences. River Otter has not been reported as recurrent prey of the Wolf in other parts of the United States (Mech 1970; Voigt et al. 1976; Scott and Shackleton 1980; Fritts and Mech 1981; Ballard et al. 1987), except on Coronation Island in southeastern Alaska, where Wolves were introduced in the 1960s and became

locally extinct (Klein *in press*). Observed Wolf predation on River Otter could be attributed to an exceptional behavior of a few individual Wolves, or to a reduction in prey availability.

In summary, diets of Wolves on POW can be characterized by their strong dependence upon deer. Although Beavers are next in importance after deer, occurrence of mustelids and Bear in Wolf diets suggests that the abundance of Beaver be insufficient, probably because of conifer-dominated vegetation. Although Beavers could be important prey locally and temporarily, it is not clear how much the demographic behavior of Beaver affects predator-prey dynamics on POW. Deer abundance seems to determine carrying capacity for Wolves on this island.

Although confounded by small sample size, remains of River Otter occurred exclusively in logged areas. Whether Wolf predation on River Otter occurred routinely when the number of deer decreased in the past, or whether this is a recent event related to logging is unknown. Also, it is not clear if Wolf predation on mustelids is sustainable. Studies on mustelids, especially vulnerability of River Otters to Wolf predation in logged areas and their reproductive success, are to be encouraged.

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Comparison of Emergence Methods to Evaluate Viable Plant Propagules in Forest Soils Following Fire

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A comparison of immediate emergence with stratified emergence to evaluate soil seed banks from forest soils was made for 163 emergents from 12 vascular species. Significantly more plants emerged through the immediate than through the stratified method. *Vaccinium* spp. (blueberry) and *Maianthemum canadense* (Wild Lily-of-the-Valley) were favoured by immediate emergence whereas *Oryzopsis pungens* (a grass) was favoured by the stratified method. Germination of all other species remained unaffected by the emergence method. Depth of seed burial in the soil profile affected seed emergence.

Key Words: Burial depth, emergence, fire, methodology, soil seed bank, vegetative growth.

Fire use for vegetation management within the boreal forest, as well as management emulating the effect of wildfire, requires a knowledge of the relationships between fire and buried reproductive propagules including seed, root buds, and rhizomes. Seeds initiate a large number of less abundant species important for maintaining species diversity in terms of regeneration of understorey vegetation (Parker et al. 1989), while vegetative reproduction is of considerable importance in terms of rapid colonization following fire (Tellier et al. 1995a, 1995b). However, at this point, there is little information about the importance of buried plant propagules in boreal forest ecosystems. Those studies that exist (Ahlgren 1960; Kellman 1970; Ahlgren 1979; Hill and Stevens 1981; Issac 1982; Vermeer 1984; Collins 1985; Morgan and Neuenschwander 1988), include results that seem contradictory, though methods of analysis are often different. Hence, an effective means of evaluating the propagule content in the soil and associated organic layer is needed.

Most investigations on buried propagules have focused solely on the soil seed bank. Methods used to evaluate seed banks include: (1) immediate emergence - soil samples are immediately subjected to standard light, temperature and moisture conditions to promote emergence; (2) stratified emergence - soil samples are held in moist chilled conditions (stratified) prior to emergence; (3) filtering - seeds are filtered through a sieve (often tested for viability using tetrazolium and identified); and (4) floatation - seeds isolated in a salt-water gradient based on their density (Roberts 1981; Gross 1990). Amongst these methods, emergence (either direct or stratified emergence) are considered the most appropriate choices to evaluate

buried propagules, inclusive of vegetative buds. Indeed, these methods provides a measure of propagule viability and take advantage of the fact that identification of grown plants is easier than propagule identification. Given this, the question remains as to whether immediate or stratified emergence results in a better estimation of buried propagules following fire and the time of year of interest.

Soil sampling from a ploughed research field in Michigan by Gross (1990) revealed that stratification may not be necessary for samples taken in early May and June when maximum seed germination naturally occurs. However, sampling near mid-June when far fewer seeds germinate may necessitate stratification because greater number of species revealed using this method. Arguably, Gross' results (1990) from an agricultural ecosystem must be re-evaluated for forest ecosystems. While numerous other studies have examined buried seed in North American forest ecosystems (Ahlgren 1960; Kellman 1970; Ahlgren 1979; Hill and Stevens 1981; Morgan and Neuenschwander 1988), few have included technique rationale. Neither rationale for method chosen or the possible influences of methodology on results was included, for instance, in northern Ontario by Collins (1985) and Vermeer (1984) who stratified soil samples prior to germination, or by Issac (1982) who used immediate germination. These omissions hinder attempts to compare studies (Brown 1992). Determination of how these methods differ in their assessment of buried propagules, both in terms of species richness and abundances is needed. In this investigation we compare the efficacy of immediate and stratified emergence in evaluation of reproductive material within fire treated soils of a Jack Pine (*Pinus banksiana* Lamb.) forest.

Methods

Study Site

The study area is located at Frontier Lake (latitude 46°00'N, longitude 77°33'W) in a Jack Pine stand in eastern Ontario within the middle Ottawa section (L.4c) of the Great Lakes-St. Lawrence Forest region (Rowe 1972). As reported by McAlpine (1995), the site is located near the Petawawa National Forestry Institute, and is relatively flat, with a difference in elevation of approximately 4 m over 1.0 km. The surface deposit is a fine-grained deep sand (10-30 m deep) (Gadd 1962) and the soil is a humo-ferric podzol (Weber 1988). The study site was selected because of its uniformity in tree composition and topography. The site was harvested in 1942 and 1943 leaving behind standing timber with stump diameters of 17.5 cm or less. Dendrochronological analysis of dominant trees and snags with multiple fire scars suggests that the study site sustained several fires, with the most recent in 1943, presumably from broadcast slash burning following harvesting (E. Stechishen, personal communication). Presently, the stand consists of a mix of Jack Pine, Red Pine (*Pinus resinosa*) and White Pine (*Pinus strobus*) with the Red Pine that are presumably residuals of the previous harvest forming an emergent layer (Table 1). Although Jack and White Pine are of similar ages, Jack Pine has higher relative density and is the dominant tree species on the site. Other plant species observed include *Amelanchier* sp. (Shadbush), *Comptonia peregrina* (Sweet Fern), *Gaultheria procumbens* (Wintergreen), *Kalmia angustifolia* (Sheep Laurel), *Lycopodium complanatum* (Flattened Club-moss), *Maianthemum canadense* (Wild Lily-of-the-valley), *Polygonatum pubescens* (Hairy Solomon's Seal), *Pteridium aquilinum* (Bracken Fern), and *Prunus pumila* (Sandcherry).

In the summer of 1990, forty 35 × 70 m plots were established in areas of standing timber. Three years later, sub-plots measuring 3 × 3 m were established and subsequently experimentally burned under various fire weather conditions and fuel loads.

Analysis of Buried Propagules

Soil samples for analysis were taken in twelve controlled-burned 3 × 3 m plots in mid-June. From each of these, a soil monolith measuring 30 × 30 cm in diameter and 8 cm into the mineral soil was removed. Subsequently, monoliths were divided by depth [0-2 (organic layer), 2-4 (upper mineral), and

4-8 cm (lower mineral)], put in plastic bags, and thoroughly mixed. Note: the organic layer ranged in thickness, but was classed as 0-2 cm depth.

Black plastic pots (15 × 15 × 25 cm depth) were filled to three quarters with sphagnum moss and vermiculite (3/1, v/v) and 450 ml of each soil sample was spread on top of two pots: one pot was placed in the greenhouse immediately; and, the other was placed in the dark and at 5°C for two weeks. All pots were incubated in a greenhouse under ambient light conditions. Plant emergence was monitored weekly and identified to species according to Gleason (1968). After six months, pots were discarded except those with specimens of questionable identity which were allowed to grow to maturity.

Statistical Analysis

Statistical analysis was conducted using the Chi-squared test ($P < 0.05$) to distinguish differences in abundance between methods for individual species and pooled results. Methods were similarly assessed for number of emergents by depth class for each species.

Results

The total number of emergents in this study was 163. Significantly more plants emerged through the immediate method than through the stratified method ($P < 0.001$) (Table 2). A greater number of *Vaccinium* spp. ($P < 0.005$) and *Maianthemum canadense* ($P < 0.005$) was observed with immediate emergence than with stratified emergence. However, *Oryzopsis pungens*, was significantly more prominent through the stratified method ($P < 0.01$) than the immediate emergence method.

Significant differences between methods relative to burial depth occurred for *Vaccinium* spp. at 0-2 ($P < 0.01$) and 2-4 cm ($P < 0.001$) (Table 3) but not at deeper levels. The only other difference occurred with *Oryzopsis pungens* at the 2-4 cm ($P < 0.05$) depth. When all species were combined, emergence was greatest in immediately emerged samples at depths of 0-2 ($P < 0.01$) and 2-4 cm ($P < 0.001$) but no difference in emergence levels was evident between methods at the 4-8 cm depth class.

Eleven species emerged using immediate germination whereas eight emerged using the stratified method (Table 2). Four unique species including *Comptonia peregrina*, *Kalmia angustifolia*, *Maianthemum canadense* and *Prunus pumila* emerged from the

TABLE 1. Characteristics of dominant overstory vegetation at the study site, Frontier Lake.

Species	Stems/ha	Age (years)	DBH† (cm)	Volume m ³ /ha
<i>Pinus banksiana</i> Lamb.	505	53	17.1	81
<i>Pinus resinosa</i>	50	105	37.5	45
<i>Pinus strobus</i> L.	100	55	28.7	57

†DBH: Diameter at breast height.

TABLE 2. Number of emergents by species using the immediate and stratified methods.

Species	Immediate	Stratified
<i>Carex houghtonii</i> Torr. (sedge)	16 a [†]	9 a
<i>Comptonia peregrina</i> L. Coulter (Sweetfern)	3 a	0 a
<i>Danthonia spicata</i> (L.) Beauv. (grass)	0 a	1 a
<i>Dennstaedtia punctilobula</i> (Michx.) Moore (Woodfern)	1 a	2 a
<i>Erigeron canadensis</i> L. (Horseweed)	2 a	1 a
<i>Kalmia angustifolia</i> L. (Sheep Laurel)	2 a	0 a
<i>Maianthemum canadense</i> Desf. (Mayflower)	7 a	0 b
<i>Oryzopsis pungens</i> (Torr.) Hitchc. (grass)	4 a	16 b
<i>Panicum lanuginosum</i> Ell. (grass)	4 a	7 a
<i>Panicum xanthophysum</i> A. Gray (grass)	4 a	4 a
<i>Prunus pumila</i> L. (Sandcherry)	1 a	0 a
<i>Vaccinium</i> spp. (blueberry)	59 a	20 b
Total emergents	103 a	60 b
Total species	11 a	8 a

[†]Within lines, values followed by different letters are significantly different at $P < 0.05$ using Chi-squared comparison.

immediate-emergence method whereas *Danthonia spicata* was unique to the stratified method.

Discussion

Although many factors may have contributed to emergence levels, it is clear that in this investigation immediate emergence gave rise to more species and significantly more emergents and than did the stratified method. These findings contradict those of Gross (1990) who showed stratified emergence as more effective for seed bank evaluation in agricultural areas of Michigan at the same time of year as this study. However, many differences exist between these two studies including site type, fire occurrence and inclusion of vegetative growth. Different site types generally feature different floristic composition each with unique dormancy-breaking requirements, hence requiring a careful selection of emergence method. Indeed, fire may stimulate or repress emergence of propagules, which in turn affects the suitability of the emergence method. Therefore our observations emphasize the need to incorporate predominant characteristics of the study area, disturbance regime and study objectives in evaluating buried reproductive potential.

An important aspect determining the suitability of method is time of year of sampling, indicating previous temperature exposure, thus influencing plant mechanisms initiating growth specific to individual species (Baskin and Baskin 1989). Because, for this investigation sampling was conducted in June, observations are in accordance with suitable growth conditions for both seed and vegetative sprouting. For seed, pre-chilling requirements for germination may have remained satisfied from the previous winter (Baskin and Baskin 1989). Thus, unlike the mid-June study of Gross (1990), seed within this study area may be at their natural peak germination period in mid-June making prechilling a hinderance to

emergence. Similarly, for vegetative propagules, spring is favourable for sprouting since considerable reserves are available in plant tissue. Thus, while immediate emergence promoted vegetative growth, it is plausible that stratification in June, negatively influenced sprouting of *Comptonia peregrina*, *Kalmia angustifolia*, *Maianthemum canadense*, and *Prunus pumila*, species that did not emerge in stratified samples. Stratification may also have hindered degree of sprouting of *Vaccinium angustifolium* and *Maianthemum canadense* resulting in higher abundance in the immediate emergence treatment.

Inasmuch as a greater number of unique species arose using immediate emergence, occurrence of *Danthonia spicata* solely by the stratified method suggests a higher efficiency of this method for cer-

TABLE 3. Number of emergents for each species by depth for each emergence method [I= immediate, S=stratified]

Species	Depth(cm)					
	0-2		2-4		4-8	
	I	S	I	S	I	S
<i>Carex houghtonii</i>	7 a [†]	3 a	6 a	4 a	3 a	2 a
<i>Comptonia peregrina</i>	1 a	0 a	2 a	0 a	0 a	0 a
<i>Danthonia spicata</i>	0 a	0 a	0 a	0 a	0 a	1 a
<i>Dennstaedtia punctilobula</i>	0 a	0 a	0 a	2 a	1 a	0 a
<i>Erigeron canadensis</i>	1 a	1 a	1 a	0 a	0 a	0 a
<i>Kalmia angustifolia</i>	0 a	0 a	2 a	0 a	0 a	0 a
<i>Maianthemum canadense</i>	2 a	0 a	4 a	0 a	1 a	0 a
<i>Oryzopsis pungens</i>	2 a	6 a	2 a	9 b	0 a	1 a
<i>Panicum lanuginosum</i>	0 a	0 a	3 a	2 a	1 a	5 a
<i>Panicum xanthophysum</i>	0 a	0 a	2 a	1 a	2 a	3 a
<i>Prunus pumila</i>	0 a	0 a	1 a	0 a	0 a	0 a
<i>Vaccinium</i> spp.	30 a	12 b	25 a	6 b	4 a	2 a
Total emergents	43 a	22 b	47 a	24 b	13 a	14 a

[†]Within depth classes, values followed by different letters are significantly different at $P < 0.05$ using Chi-squared comparison.

tain plant species. However, because only one emergent was observed, other reasons may be more plausible. One such argument is based on the patchy or clustered distribution of both plants and seeds (Roberts 1981) contributing to chance occurrence in the stratified samples, rather than to differences in methods. It is important to note that factors including low levels of sampling and inability to meet all emergence requirements (Gross 1990) may have resulted in absence of other plant species such as *Prunus pensylvanica* for both methods.

Dissimilarity between methods within depths, for *Vaccinium angustifolium*, *Oryzopsis pungens*, and total emergence, suggests that the depth of burial is an important factor determining effectiveness of methodology. Although there is considerable awareness of the importance of burial stratum in terms of post-fire survival (Flinn and Wein 1977; Moore and Wein 1977), seed abundance (Johnson 1975), and environmental conditions (Baker 1989), there has been little reference to the soil profile in terms of influence on emergence. Results of the current study show that investigations incorporating immediate or stratified emergence should take into account the possibility of reduced or altered emergence levels associated with soil stratum. Understanding the rationale for this phenomenon is beyond the scope of this study, but it can be speculated that multiple interactions between pre-sampling microsite conditions, individual species requirements, and method may have yielded the observed differences in germination among soil samples.

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Size and Characteristics of a Wood Turtle, *Clemmys insculpta*, Population in Southern Québec

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A Wood Turtle (*Clemmys insculpta*) population was studied along the Sutton River from May to October 1995. Fifty-two Wood Turtles were captured a total of 97 times at the rate of 0.53 turtles per hour of search time. May appeared to be the best time to survey Wood Turtles. Among North American populations, Wood Turtles along the Sutton River are average in size. Our results, added to those of other studies, support the existence of a negative relationship between Wood Turtle size and the length of the frost-free period. Sex-ratio was not different from 1 : 1. Adults (CL \geq 160 mm) represented 82% of our captures. The remaining were juveniles. Two hypotheses could explain the absence of turtles younger than five years old in our sample. Hatchling recruitment could be non-existent or very low during one or many successive cool summers; our survey method could also be biased. Wood Turtle density in the study area was estimated at 1.2 turtles per 100 m of river (1.0 - 1.4).

Une population de tortue des bois (*Clemmys insculpta*) a fait l'objet d'une étude le long de la rivière Sutton, de mai à octobre 1995. Cinquante-deux tortues des bois ont été capturées à 97 reprises au rythme moyen de 0,53 prises par heure de recherche. Le mois de mai semble la meilleure période pour l'inventaire de la tortue des bois. Les tortues de la rivière Sutton sont de taille moyenne à l'échelle nord-américaine. Nos résultats, additionnés à ceux d'autres études, supportent l'existence d'une relation négative entre la taille des tortues des bois et la longueur de la période sans gel. Le rapport des sexes chez les adultes n'est pas différent de 1 : 1. Les adultes (LC \geq 160 mm) composent 82% de notre échantillon, le reste étant des juvéniles. L'absence de tortue de moins de 5 ans dans notre échantillon peut s'expliquer de deux façons. Le climat pourrait limiter le succès d'éclosion des oeufs à un point tel, que le recrutement pourraient être nul ou très faible durant un ou plusieurs étés frais successifs. La méthode d'inventaire pourrait aussi générer un biais. La densité de la population de tortues des bois de la rivière Sutton est évaluée à 1,2 tortues par 100 m de rivière (1,0 - 1,4).

Key Words: Wood Turtle, *Clemmys insculpta*, size, population density, survey technique, Québec.

The Wood Turtle reaches the northern limit of its distribution in Canada (Ernst et al. 1994; Cook 1984; Conant and Collins 1991). The species is irregularly distributed in Québec up to latitude 47°N (Bider and Matte 1994). Wood Turtle ecology has been studied in New Jersey and Michigan by Harding and Bloomer (1979), in New Jersey by Farrell and Graham (1991), in Wisconsin by Ratner and Anderson (1978*) and Ross et al. (1991), and in Ontario by Brooks et al. (1992). Few of these studies reported population densities (Harding and Bloomer 1979; Farrell and Graham 1991; Brooks et al. 1992). Wood Turtle conservation preoccupies wildlife specialists in many parts of its range (Harding and Bloomer 1979; Obbard 1985*; Brewster and Brewster 1991). In Québec, the Wood Turtle is one of the species that could be designated as threatened or vulnerable (Beaulieu 1992), but its distribution and abundance need to be better documented before such action is taken. A survey program initiated in 1994, and still ongoing, provides some useful information regarding the distribution of the species and in order to give some indication of popu-

lation sizes, the number of turtles found per hour of search time was recorded. The present study was undertaken to create a link between the results of those surveys and real population densities. Daily mark and recapture surveys were used to estimate population sizes and to gain further knowledge of the ecology of the species in Québec.

Methods

Wood Turtles were captured along a 5.7-km section of the Sutton River, Québec (72°38'36"W - 45°03'08"N). Rivers form an important part of Wood Turtles, home ranges. During most of the year, Wood Turtles can be found in or close to a river (Harding and Bloomer 1979; Kaufmann 1992). Searches were concentrated in the river bed and the adjacent first 10 m on each of the shorelines. Limits of the study area were chosen for purely practical reasons; bridges giving access to the river are present at both ends. The Sutton River flows south along the Appalachian Mountains and meets the Missisquoi River in Vermont. Wood Turtles are present in many parts of the Missisquoi River and there is no reason to believe that they do not use the Sutton River, upstream or downstream from the study area.

*Unpublished, listed in Documents Cited section.

Hayfields and pastures intersected by old fields and a few trees or shrub thickets border the river banks in the study area. The most common tree species along the river are willow (*Salix sp.*), Box Elder (*Acer negundo*), Rough Alder (*Alnus rugosa*), and American Elm (*Ulmus americanus*). Herbaceous plant species most frequently found in the study area are Gramineae, Canada Goldenrod (*Solidago canadensis*), Japanese Knotweed (*Polygonum cuspidatum*), Umbellate Aster (*Aster umbellatus*), Common Milkweed (*Asclepias syriaca*), Joe-Pye-weed (*Eupatorium maculatum*), raspberry (*Rubus sp.*), Cape-touch-me-not (*Impatiens capensis*) and ferns. The river bed is gravelly and is about 15 m wide. During summer, water covers only 5 to 10 m of the bottom. Water depth is generally between 15 and 45 cm and pools 1 to 2 m deep intersect the river. Water speed varies from slow to moderate (absence of white water) and the water is relatively clear. The frost-free period averages 120 days (Wilson 1971).

Turtles were captured either by hand or dipnet from May to October 1995. Twenty daily surveys were conducted during this period, with each lasting between 2 and 5 hours and generally consisting of going down the river. Early in spring, three persons surveyed the area. The first 10 m each side of the river were searched by a person walking on each side of the river bank, while a third person walked or canoed in the middle of the river, visually searching both the water and the bank slopes. From the moment vegetation made turtle sighting more difficult (June and later), searches were restricted to the river bed and the bank slopes and only two persons were used to walk in and out of the water along the shore. A single person performed the survey on a few occasions.

Turtles were weighed (± 10 g) and their maximum carapace and plastron lengths (CL, PL) were measured with vernier calipers (forester type, ± 1 mm). Concavity of plastron was used for determination of sex of adults. This character does not appear until sexual maturity of males (Harding and Bloomer 1979); individuals smaller than 160 mm (CL) were designated juveniles. Turtles were roughly aged by counting growth rings on front dorsal scutes (Harding and Bloomer 1979).

Wood Turtles were individually marked by notching marginal scutes with a 6 mm round file (Cagle 1939; Froese and Burghardt 1975; Saumure 1995*). Statistical analyses were performed using the Statistical Software Program (1985). Population size was estimated using the Schumacher and Eschmeyer model, assuming that emigration, immigration, mortality and recruitment were very low, and that marked and unmarked individuals were equally catchable (Caughley 1977).

Results

Fifty-two Wood Turtles were captured 97 times between 1 May and 3 October 1995. Population size (95% confidence interval ranges) was estimated to be 66 turtles (56 - 81). Density was estimated at 1.2 turtles/100 m of river.

Daily surveys conducted with the regular method involving two or three persons produced from 0.32 to 1.07 Wood Turtle per hour ($\bar{x} = 0.53 \pm 0.07$, $N = 12$). Although the sample size was not large enough to test significance, surveys seem to be more productive in May than in other months (Figure 1). During May, 81.7% ($N = 60$) of the Wood Turtles were found on land, usually basking not far from the water ($\bar{x} = 3.0 \text{ m} \pm 0.43$). Later in the summer, turtles were found in the water. In July, they were hidden under cover (peat, trees) whereas in September they were more active, often moving when first seen. At the beginning of October, seven of the eight turtles captured, were found active in the water.

Twenty-seven turtles were captured more than once (2 - 5 times). Greatest distance between recapture points for the same individual (longest axes) averaged $507.0 \text{ m} \pm 123.9$ ($N = 27$, 1 - 2820 m). Nearly half the turtles had longest axes ≤ 200 m. Longest axes were smaller for females than for males ($t = 2.6$, $p < 0.02$). Mean longest axes between capture site was $189.0 \text{ m} \pm 61.1$ ($N = 9$, 1 - 540 m) for females and $707.5 \text{ m} \pm 191.8$ ($N = 16$, 20 - 2820 m) for males. Home ranges overlapped in both sexes.

Males had a longer carapace and were heavier than females, but plastron length was similar. Mean carapace length, plastron length and mass were $195.7 \text{ mm} \pm 1.8$ ($N = 18$, 179 - 211), $176.4 \text{ mm} \pm 1.8$ ($N = 18$, 162 - 193) and $1.05 \text{ kg} \pm 0.03$ ($N = 18$, 0.68 - 1.30) respectively for adult males. For females those values were $181.9 \text{ mm} \pm 2.0$ ($N = 24$, 167 - 209), $170.3 \text{ mm} \pm 1.8$ ($N = 24$, 151 - 190) and $0.88 \text{ kg} \pm 0.02$ ($N = 24$, 0.65 - 1.16). According to the width of growth rings, growth slows down substantially around the fifteenth year. The youngest male to present a concave plastron was estimated to be 10 years old and measured 176 mm (CL).

Adults represented 82.3% of our captures; the remainder were juveniles (Figure 2). No turtles estimated to be younger than five years were captured. Apparent sex-ratio was 1.2:1 in favour of females, but it did not differ statistically from 1:1 ($X^2 = 0.45$, $P > 0.05$).

Discussion

Wood Turtles were uniformly distributed in the study area. Comparisons of densities along the Sutton River with densities found in other study areas are quite hazardous. Other researchers usually express densities as numbers per unit of surface area without giving details on the component of their

TABLE 1. Climate and Wood Turtle size in seven North American studies.

	FFD ^a	Carapace length (mm)						Reference
		Male			Female			
		N	\bar{x}	Range	N	\bar{x}	Range	
New Jersey (41°N)	210	311	178	160-206	464	165	160-188	Harding and Bloomer 1979
New Jersey (41°N)	210	69	177	161-201	49	171	158-200	Farrell and Graham 1991
Virginia (39°N)	190	11	196		14	183		Lovich et al. 1990
Wisconsin (44°N)	140	28	201		48	187		Ross et al. 1991
Michigan (46°N)	140	86	200	169-228	105	182	158-218	Harding and Bloomer 1979
Québec (45°N)	120	19	195	176-211	23	182	167-209	Present study
Ontario (45°N)	90	21	219	199-244	57	202	185-225	Brooks et al. 1991

^a = Frost-free days, U.S. Department of Commerce, Environmental Data Service (1968) and Wilson (1971)

study area. Characteristics of the study areas are often quite different. Some may include the home river and summer habitats while others may include a nesting site and the surroundings. The home river is the heart of Wood Turtles home ranges and it seems appropriate to express densities in unit per length of river. In order to compare densities with other studies, as hazardous as it is, we transformed our results in numbers per units of surface area. The study area along the Sutton River was 35 m wide (river bottom plus 10 m on each side) and 5.7 km long, this representing approximately 20 ha overall. The density of the Wood Turtle population along the Sutton River (3.3 turtles per hectare) was much higher than the value (0.2) found for a more northern population in Ontario (Brooks et al. 1992) but lower than those (10.7, 12.5) reported in New Jersey (Farrell and Graham 1991, Harding and Bloomer 1979). Preliminary results from surveys conducted on other rivers in Québec indicate that a few rivers may host Wood Turtle in densities comparable to the densities found along the Sutton River (Daigle 1996).

Early in the spring, Wood Turtles tend to be close to water (Harding and Bloomer 1979; Kaufmann 1992). Because at this time the vegetation is not fully grown, turtles are easily located and captures are then more numerous (Farrell and Graham 1991). Terrestrial activity increases with increasing air temperature (Kaufmann 1992). Turtles gradually leave the river for more terrestrial habitat, generally staying within 300 m of the river (Kaufmann 1992). Wood Turtles are more difficult to find during their terrestrial stage. Farrell and Graham (1991) made only 9% of their captures between June and September. In this study, 19.6% of our captures were made between June and October, but only one of 27 turtles was found out of the river during this period. These differences could result from the method used for surveys; however, our results indicated that Wood Turtles stopped using river banks for basking during summer months and were more frequently found in the water than in other surveys.

The period before leaf-out appears to be the best time to survey Wood Turtles. Water transparency and depth of the Sutton River allowed us to see the river bottom most of the time during the summer and to maintain relatively high capture rates. In other rivers used by Wood Turtles, greater water depth or lack of transparency do not allow an observer to see the river bottom most of the time.

According to Harding and Bloomer (1979), Wood Turtles are often found basking on logs. Logs and rocks were available in the study area but this behavior was observed only once, on a rock. All other turtles were found on the river banks or in the water.

Wood Turtles have elongated home ranges closely related to the river (Carroll and Ehrenfeld 1978; Strang 1983) and therefore the longest axes between capture sites is an indicator of home range size. Longest axes averaged 507 m in this study, which is slightly higher than those reported for more southern populations. In New York state, Barzilay (1980) reported axes length of 478 m, Strang (1983) and Kaufmann (1995) reported 447 m and 463 m respectively in Pennsylvania. Larger home range could be an adaptation for social interaction between individuals of populations with low densities. Males had much longer axes than females along the Sutton River. In Pennsylvania, males spent more time in creeks than females, possibly because they actively seek mates and dominance-establishing encounters with other males (Kaufmann 1992). The shape of our study area induced a bias in favor of more aquatic individuals and this difference between sexes probably does not mean actual smaller home ranges for females, but home ranges of different shapes with regards to the river.

Wood Turtles along the Sutton River are medium in size on a North American scale (Table 1). Brooks et al. (1992) suggested a correlation between length of the growing season (frost-free days) and adult size of Wood Turtle. With the information now available (male CL), we verified statistically the existence of such a correlation. The correlation analysis (Spearman) reveals a negative

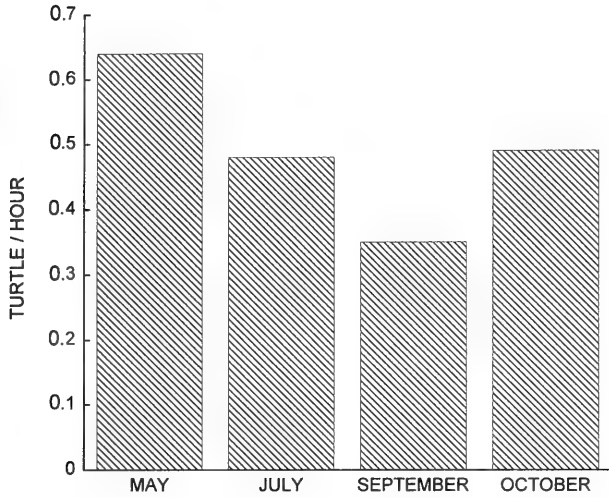


FIGURE 1. Monthly efficiency of daily Wood Turtle surveys along Sutton River, Québec.

Two hypotheses could explain the absence of Wood Turtles under five years old in our study. Lower temperature and a shorter growing season probably reduce the quantity of hatchling turtles produced at northern sites (Bobyne and Brooks 1994). Hatchling success could be very low or non-existent when cool summers do not generate appropriate incubation temperature and successive cool summers could then explain the absence of young in a turtle population. Cold weather did not prevent any emergence from Snapping Turtle (*Chelydra serpentina*) nests in northern sites (Galbraith et al. 1988). The absence of young Wood Turtle in our sample could also be the reflection of skewed sampling. Observation of three Snapping Turtles under 30 mm indicates that the personnel were able to locate small turtles and were not completely biased in their searches. Young turtles are often underrepresented in studies of Wood Turtle populations (Brook et al. 1992; Farrell and Graham 1991; Ross et al. 1991). According to Brewster and Brewster (1991) and Kaufmann (1995) they often hide where the channel has undercut the bank. It is likely that small Wood Turtles were missed during our surveys, which means that our density estimate was biased and should be considered a minimum. For

correlation ($N = 7$, $R = -0.87$, $P = 0.01$) between the length of the growing season and carapace length of adult males. Brooks et al. (1992) suggested many hypotheses to explain this phenomenon, all of which remain to be tested.

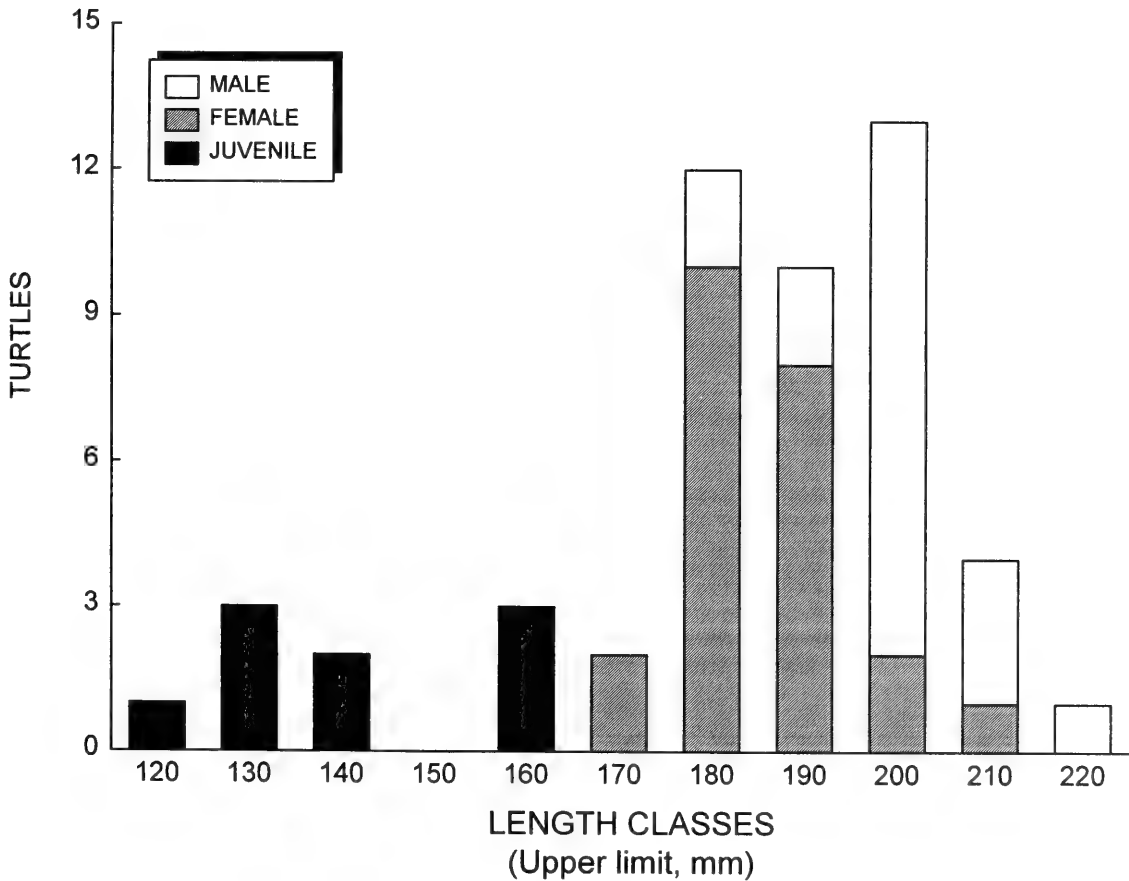


FIGURE 2. Frequency distribution of carapace length for 51 Wood Turtles captured along the Sutton River in southern Québec, between May and October 1995.

the same reasons, the estimated population structure is probably also biased.

In many parts of its distribution, the Wood Turtle is endangered by habitat loss and degradation (Harding and Bloomer 1979; Kaufmann 1992; Obbard 1985*). Terrestrial habitats along the Sutton River seem relatively undisturbed; however, the river itself has been altered by human activities. Chemicals and organics used in agriculture are drained into the river. A local farmer levels the river bed on a regular basis and, on one occasion during this study, discharges from a municipal wastewater treatment station were observed. Sensitization of municipalities and the local population to the presence and needs of Wood Turtles is necessary in order to ensure the conservation of this species in the Sutton River.

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A Preliminary Analysis of the Floral Preferences of the Alfalfa Leafcutting Bee, *Megachile rotundata*

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The comparative attractiveness to female Alfalfa Leafcutting Bees (*Megachile rotundata*) of flowers of 209 species of vascular plants, representing 52 families and 154 genera, was examined by measuring visitation rates to bouquets under standardized conditions. The bees were attracted to only 21 species, representing 14 genera and seven families. Two floral features appeared to be related to bee visitation: a flower length less than 13.5 mm; and a corolla tube up to 5 mm in length and up to 3 mm wide. It is speculated that the critical maximum length of 13.5 mm for the flower, and 5 mm length by 3 mm width for the floral tube, are respectively determined by the insect's length, combined head and extended mouthparts, and head width. No relationship was found between attractiveness of the flowers and visible color of the corolla, radial or bilateral symmetry, density of open flowers, and genus and family of plants. Despite its name, the Alfalfa Leafcutting Bee was attracted to Alfalfa (*Medicago sativa*) half as frequently as it was to White Sweetclover (*Melilotus alba*) and Purple Loosestrife (*Lythrum salicaria*).

Key Words: Alfalfa Leafcutting Bee, *Megachile rotundata*, Alfalfa, *Medicago sativa*, White Sweetclover, *Melilotus alba*, Purple Loosestrife, *Lythrum salicaria*, pollination.

The Alfalfa Leafcutting Bee (*Megachile rotundata*) was inadvertently introduced from eastern Europe or western Asia to North America, as early as 1937 (Gerber and Akre 1969). Over the next several decades, it was realized that it is by far the best pollinator of Alfalfa, and the bee is now managed for the production of Alfalfa seed in western Canada (see, for example, Hobbs 1973), as well as in the western United States, New Zealand, and in some South American and European countries. The bee is currently established at scattered locations across the United States, and extends north to southern Ontario as far as Ottawa (Ivanochko 1979). It is also present in the established fauna of British Columbia (Hurd 1979). While this insect has had some success as a pollinator of several crops in addition to Alfalfa (Fairey and Lefkovitch 1991), it seems to be attracted to the flowers of far fewer plants than the honeybee. It was observed to visit only 21 of 100 plant species in bloom in a general plant nursery at the University of Guelph (Richards 1989). Towards clarifying the capacity of the Alfalfa Leafcutting Bee to employ the vegetation of Canada, we studied its floral preferences using bouquets of flowers harvested from a variety of native and introduced plants from the Ottawa region. We have titled our study "preliminary" because it remains to be determined how closely the trends that we discovered using our experimental conditions are reflected in nature, and because our sample sizes are insufficient to quantitatively characterize the attractiveness of most of the more than 200 species of plants sampled.

Materials and Methods

A leafcutting bee shelter was placed in a field of Alfalfa (*Medicago sativa*) cultivar Comsel in the Central Experimental Farm, Ottawa, Ontario, Canada. The plywood shelter was 2.4 m long, 1.2 m wide, 1.2 m high, and open to the south on the long axis. The commercially produced polystyrene nesting boards now commonly used in Canada (Fairey et al. 1987) were placed on the north wall of the shelter (Figure 1). The nesting material was surface-stained with color patterns to assist bee orientation.

The bees used in these observations came from a population maintained at the Agriculture and Agri-Food Canada Research Station, Beaverlodge, Alberta. The male to female ratio of this population is about 2:1 (Fairey et al. 1987). Batches of dormant prepupae were incubated in Ottawa at 37.6°C until emergence (at 18–23 days). About 6000 prepupae were incubated in batches of about 1000, and released regularly before and during the early part of the experimental period to maintain a constant availability of approximately 1000 bees at the shelter.

Cut inflorescences, referred to as bouquets in this paper, were placed about 3 m from the nesting material as shown in Figure 1. Containers filled with water, in which the bouquets were placed, were permanently positioned in the ground during the study. Alfalfa within 3 m of the bouquets and the shelter was cleared away to encourage the bees to forage on the bouquets. Most bouquets showed little wilting or apparent decrease in attractiveness during the observations, which were generally completed within six

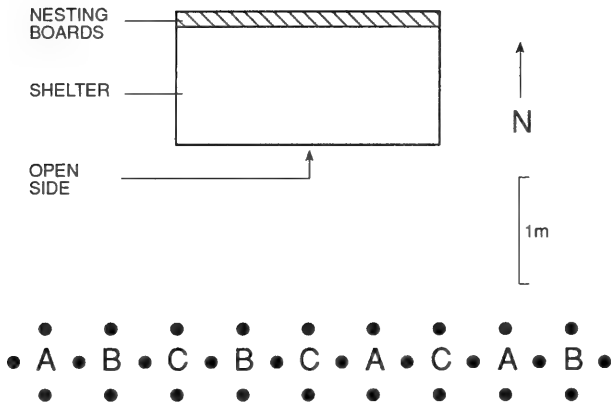


FIGURE 1. Diagram of experimental layout. A, B and C designate positions for bouquets of the three attractive standards, while dots represent positions of bouquets of different plant species.

hours. An attempt was made to equalize the visual area of the flowers in each bouquet to about 200 cm², but because of the very different types of inflorescences, the flowers in some bouquets could only be presented in a compact mass, while others were more diffusely arranged. Flowers were 10 to 50 cm from ground level, depending on the type of inflorescence. Because there may have been a slight tendency for bees visiting an obviously attractive species also to visit others that were adjacent, each plant species tested was placed next to one of three control species, *Medicago sativa*, *Lythrum salicaria*, and *Melilotus alba*, known to be attractive to Alfalfa Leafcutting Bees. The inclusion of the control species on each occasion served two main purposes; first, to provide a monitoring of the bees' activity over the period of the observations, and second, to provide a standard level of competition for the remaining species.

On each of eight days, from 6 August to 25 August, 37 bouquets were tested; the three control species were assigned to positions A, B, and C (see Figure 1). Only one bouquet-trial was conducted for most species, two for 12 species, and 24 for the control species. The sample of plants included 209 species (listed in Table 1 and Appendix 1) representing 52 families (48 dicot and 4 monocot) and 154 genera (146 dicot and 12 monocot). For data analysis, the two available color variants of three of the species were treated as separate species.

Visitation rates were determined from 13:00 to 15:00 hours on sunny, warm days (shade temperature approximately 25°C) with little wind. Bouquets were available to the bees for several hours before visitation rates were assessed; this was important because often some time would elapse before the bees would discover an attractive species, and begin to visit it regularly. An observer (Brookes) and a data recorder (Small) approached no closer than a meter, since nearer observation tended to discourage

visits. A successful visit to a flower was deemed to have occurred only if the bee appeared to have been collecting nectar or pollen (on many occasions the bees merely inspected bouquets, often without alighting). Virtually all of the Alfalfa Leafcutting Bees scored as visiting the flowers were female. The number of successful visits to flowers of each bouquet was counted once every 3 minutes, pausing about 5 seconds to examine in sequence each of the 37 bouquets. This procedure was repeated 20 times, requiring about 2 hours for completion. The total recorded for each bouquet thus represented the number of visits observed during about 100 seconds spread over about 2 hours. Records were also made of bouquets from which the bees cut away leaf or petal segments for domicile construction.

Voucher herbarium specimens were prepared for all of the plant species studied, and were used for morphological comparisons between attractive and unattractive species. The five characters examined were: corolla length (this corresponded to flower length in most of the species examined); length of floral throat less than 3 mm in width (the rationale for this is dealt with later); color of flower (eight different colors distinguishable by humans were encountered); flower symmetry (radial, bilateral, and asymmetrical); and floral density (the number of open flowers on the terminal 10 cm of the main stem of the inflorescence).

Statistical analyses were in the framework of generalized linear models (McCullagh and Nelder 1989) with appropriate error distributions and link functions. The main objectives of the analyses were:

1. To investigate if there had been any date and position effects on the three control species. Since the data consist of counts of the number of bees, a Poisson distribution, with its canonical (logarithmic) link, was used. This analysis was then extended to include the remaining species especially with respect to date (note that for the unreplicated species, date and position are confounded; i.e., one can't interpret the extent to which date alone or position alone may have influenced the observations).

2. To determine the proportion of the total number of bees on the day(s) of observation visiting the species' bouquets. These proportions were obtained by simple tabulation.

3. To classify the plants into attractive and unattractive categories. Since the expected proportion of bees on a bouquet, assuming a uniform random choice (i.e., that the 37 bouquets on each day were neither attractive nor repellent) is $1/37 = 2.7\%$, it was decided to designate species visited by more than 2% of the bees as "attractive" and the remaining "unattractive" (we could have used the figure of 2.7%, but arbitrarily decided to make the criterion slightly less demanding at 2%). The plant species were then assigned to these two categories.

4. To examine the plant characters described above in relation to attractiveness and other categorizations, including taxonomic genus and family.

Dimensions were analysed assuming a constant coefficient of variation (achieved by a gamma error distribution and logarithmic link), which for positive measurements is usually more appropriate than a constant variance. Frequencies for nominal categories were analysed using contingency tables. All numerical procedures were performed using Genstat, Release 5.22 (Lawes Agricultural Trust 1989). Subsequent analyses of the data, and the rationales for carrying these out, are given below.

There is evidence that, for some flowers with a fairly narrow corolla tube, a corolla length of more than 13.5 mm is too long in relation to the body length of the female bees (9.1 mm, range 8-10.5 mm, plus length of mouthparts of ca. 4.5 mm) for the bees to reach the nectaries (Fairey and Lefkovitch 1993). Many of the plant species tested did not have narrow corolla tubes, or lacked corolla tubes, and so the bees could have reached nectaries without difficulty. Nevertheless, during the study it appeared that the bees were avoiding large flowers, and so it was decided to group the plants into two length categories based on the corolla length cited above, namely 13.5 mm or less, and greater than this value.

Many of the plant species examined had at least part of their petals basally joined into a corolla tube. It seemed possible that some unattractive flowers barred access to basal nectaries by having sufficiently long floral tubes narrower than the female bee's head (about 3 mm), and so the length of corolla tubes not exceeding 3 mm in width was measured. Lengths were categorized into classes of <3, 3-5, and >5 mm; the length of 3 mm was arbitrarily chosen while that of 5 mm represents approximately the length of head and extensible mouthparts that might be forced into a narrow corolla tube (as defined above) in order to reach a basal nectary.

A 2 × 3 × 2 cross-classification table based on the three categorizations described above (a flower length of 13.5 mm, length of throat not wider than 3 mm (categorized by values of 3 and 5 mm), and 2% of bees visiting the bouquets on the day of the experiment) was compiled to search for any associations.

A test of independence of plant family and number of visiting bees was carried out to examine if the leafcutting bees differed in their preferences for families of plants. This analysis was restricted to the seven families for which at least one species attracted bees, and on only those species with flowers with a corolla ≤13.5 mm, the only ones attracting bees, as demonstrated by the above analyses. The possibility of conducting a test for the genus category was also examined.

Another factor conjectured to influence attractiveness is the symmetry of the flower; a tabulation con-

ducted on the flowers not exceeding 13.5 mm revealed that only those with radial and bilateral symmetry were visited. All of the 36 plant species with asymmetrical flowers belong to just one family, the Compositae; accordingly, these were excluded from the following analyses, since it is impossible to determine if it is the asymmetry or some other common attribute in the family which deters the bees.

To determine if there is an association between the floral color and the number of visitors, the 102 species that remain after omitting Compositae and species with flowers >13.5 mm in length were formed into a contingency table based on color and whether attractive or not. A likelihood ratio test for marginal independence was conducted.

Based on the sample of 102 species as defined above, an attempt was made to determine if any of the measurements were essentially different in relation to the interaction between the visiting bees and each of color and symmetry, by analyses of deviance.

In addition to the leafcutting bees, wild bees, flies, and other insects visited the bouquets - approximately one wild insect for every 10 introduced Alfalfa Leafcutting Bees. The numbers of these un-introduced visitors were also recorded, but are not reported here as they did not seem to affect leafcutting visitation appreciably (although occasionally the presence of a large wasp or "hyperactive" visitor whirring about the flowers did seem to discourage leafcutting bees from visiting a particular bouquet).

Results

Table 1 lists the 21 plant species attracting more than 2% of the bee visits to the bouquets on the day(s) they were examined. Two of these species included forms with either of two floral colors (both of which attracted >2% bee visits/day). The remaining 188 species (including one with two flower color forms) attracted less than 2% of the bees. [A list of these forms an Appendix which is available, at a nominal charge, from the Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ontario, Canada K1A 0S2.]

The Alfalfa Leafcutting Bees were observed to cut portions of leaves and/or petals for domicile construction from nine of the 209 species examined. Leaves were collected from *Lythrum salicaria*, *Hypericum perforatum*, *Colutea ×media*, *Malva alcea*, and *Thalictrum polygamum*. Petals were collected from *Matthiola incana*, *Pelargonium ×hortulanus*, *Malva alcea*, *Eschscholzia californica*, and *Potentilla fruticosa*.

Table 2(a) shows that there are differences among the control species, further confirmed by the species*date interaction, but no evidence for either a main effect of date or position. The number of visits to *Medicago* appears to be half that compared to each of *Lythrum* and *Melilotus* (Table 2(b)).

TABLE 1. List of plant species considered attractive in this study (defined as having attracted more than 2% of the Alfalfa Leafcutting Bees during one of the eight experimental days), percentage of bees attracted to each plant species, and herbarium voucher codes.

Family & Species	Voucher code ¹	Percent bees ²
Crassulaceae		
<i>Sedum maximum</i> × <i>S. telephium</i> "Vera Jameson"	24.30	8.3
<i>Sedum spectabile</i> "Ruby Glow"	18.18	10.0
<i>Sedum spurium</i>	21.7 & 21.32	17.7
Labiatae		
<i>Mentha</i> × <i>gentilis</i>	21.16	11.9
<i>Ocimum basilicum</i>	21.24	3.5
<i>Ocimum tenuiflorum</i>	7.37	17.9
<i>Origanum vulgare</i>	21.26	2.7
Leguminosae		
<i>Lespedeza bicolor</i>	10.34	4.1
<i>Lotus corniculatus</i>	6.20	3.7
<i>Melilotus alba</i>	6.B	31.3
<i>Melilotus officinalis</i> ³	7.31	5.7
<i>Medicago falcata</i>	7.35	2.9
<i>Medicago sativa</i> (purple-flowered) ³	6.A	16.6
<i>Medicago sativa</i> (white-flowered)	6.18	6.6
<i>Onobrychis viciaefolia</i>	21.30	2.2
<i>Vicia cracca</i>	7.7	2.1
Liliaceae		
<i>Allium pulchellum</i> (purple-flowered)	18.4	3.9
<i>Allium pulchellum</i> (white-flowered)	18.3	2.2
<i>Allium tuberosum</i>	24.34	3.6
Lythraceae		
<i>Lythrum salicaria</i> ³	6.C	32.7
Plumbaginaceae		
<i>Limonium bonduellii</i> "Gold Coast"	17.10	5.8
<i>Limonium latifolium</i>	24.5	2.6
Umbelliferae		
<i>Eryngium amethystinum</i>	24.7	12.0

¹Vouchers at DAO under collections of E. Small and B. Brookes, 1992 series.

²For *Medicago sativa* (purple-flowered), *Melilotus alba* and *Lythrum salicaria*, figures are means of 24 samples. For *Sedum spurium* figure is mean of two samples. For remainder, sample size is 1.

³Control species.

The number of species falling into the three-way cross-classification, based on corolla length, length of throat ≤ 3 mm wide categorized with limits of 3 and 5 mm, and percentage of bee visits, is given in Table 3. For the frequency data restricted to a corolla length less than 13.5 mm, the sub-table has a likelihood ratio chi-square of 13.008, which with 2 degrees of freedom (df) has a probability of 0.0015, indicating that narrow throat length may affect the attractiveness of the flowers. The narrow portion of floral tubes in the attractive species ranged from 0 to 8 mm in length (in fact, only one exceeded 5 mm (Table 3), with nine

having a length of 3.5-4.5 mm). From Table 3, 13 of the 95 non-attractive species and one of the 23 attractive species exceeded 5 mm in throat length; on the assumption that the proportions should be the same, the chi-square is 9.719 which with 1 df has a probability of 0.0024. There is an excess number of plants in the unattractive category with throats longer than 5 mm (and hence a deficiency in the attractive category). This shows that when the width of the throat does not exceed 3 mm, throat lengths less than 5 mm are preferred by the bees.

After excluding Compositae, species having a

TABLE 2. Analysis of deviance of frequency of visits for position and date effects for the three control species.

(a) Analysis of deviance				
Source of variation	Degrees of freedom	Scaled Deviance	Probability	
Species(S)	2	49.615	<0.0001	
Date(D)	7	11.778	0.1081	
Position(P)	8	13.083	0.1090	
S.D	14	30.130	0.0073	
S.P	15	20.564	0.1513	
Residual	25	1.0		
Dispersion factor		1.726		

(b) Mean values (standard errors in parentheses)				
Date	<i>Lythrum</i>	<i>Medicago</i>	<i>Melilotus</i>	Combined
6	19.3(3.3)	8.0(2.2)	11.3(2.5)	12.9(1.6)
7	12.0(2.6)	8.3(2.2)	12.0(2.6)	10.8(1.4)
10	10.7(2.5)	9.7(2.4)	26.3(3.9)	15.6(1.7)
17	26.7(3.9)	9.0(2.3)	16.3(3.1)	17.3(1.8)
18	17.7(3.2)	11.0(2.5)	21.7(3.5)	16.8(1.8)
21	14.0(2.8)	9.0(2.3)	22.3(3.6)	15.1(1.7)
24	20.0(3.4)	9.3(2.3)	16.7(3.1)	15.3(1.7)
25	25.3(3.8)	9.7(2.4)	12.7(2.7)	15.9(1.8)
Combined	18.2(1.1)	9.3(0.8)	17.4(1.1)	—

corolla exceeding 13.5 mm, and families for which not even one species received 2% or more of bees visiting a bouquet during any day, sixty-three species in seven families remained (Table 4a). These species were used to examine whether or not the leafcutting bees differed in their preferences for families of plants. A test of independence of family and visitor category had a likelihood ratio chi-squared of 12.274 which with 6 df has a probability of 0.0574. After pooling the first and last three families (because of small numbers), the chi-square is 5.476 which with 3 df had a probability of 0.1401. Thus there is no evidence of an association with the plant family.

There were eight genera (*Allium*, *Limonium*, *Medicago*, *Melilotus*, *Mentha*, *Ocimum*, *Sedum* and *Vicia*) with at least two species (or color forms) which had been visited (Table 4(b)); unfortunately,

the number of species in each genus was too small for a meaningful test of preferences for some genera over others. Nevertheless, Table 4b does indicate that the attractiveness may not be a property of these genera but of the individual species, although further study will be necessary to investigate this conjecture.

Eight flower colors were recorded, but only six for the 102 species remaining after excluding Compositae and species with a corolla not exceeding 13.5 mm (Table 5). To determine if there is an association between the floral color and the number of visitors, data for the 102 species were formed into a contingency table based on color and whether or not attractive (by the 2% criterion) to bees (Table 5). A likelihood ratio test for marginal independence has a chi-square of 5.371 which with 5 df has a probability of 0.372; even after pooling the blue, pink and red flowers so as

TABLE 3. Number of plant species cross classified by corolla length, length of throat ≤ 3 mm wide, and whether attractive or not to Alfalfa Leafcutting Bees (based on the 2% criterion discussed in the text).

		Number of species	
		unattractive ($\leq 2\%$ bees/day)	attractive ($> 2\%$ bees/day)
Corolla ≤ 13.5 mm	Throat ≤ 3 mm	70	11
	3-5 mm	12	11
	> 5 mm	13	1
> 13.5 mm	≤ 3 mm	55	0
	3-5 mm	9	0
	> 5 mm	30	0

TABLE 4. Comparison of attractiveness to Alfalfa Leafcutting Bees of the plant families and genera examined (where attractive is defined as having been visited by more than 2% of the bee visitors during the day of the trial).

(a). Comparison of numbers of attractive and unattractive species in families in which at least one species was attractive.

	Number of species	
	unattractive ($\leq 2\%$ bees/day)	attractive ($> 2\%$ bees/day)
Crassulaceae	1	3
Labiatae	16	4
Leguminosae	12	9
Liliaceae	7	3
Lythraceae	0	1
Plumbaginaceae	0	2
Umbelliferae	4	1

(b). Comparison of numbers of attractive and unattractive species in genera in which at least one of two or more species examined was attractive.

	Number of species	
	unattractive ($\leq 2\%$ bees/day)	attractive ($> 2\%$ bees/day)
<i>Allium</i>	2	3
<i>Limonium</i>	0	2
<i>Medicago</i>	1	3
<i>Melilotus</i>	0	2
<i>Mentha</i>	1	1
<i>Ocimum</i>	0	2
<i>Sedum</i>	1	3
<i>Vicia</i>	1	1

to eliminate small numbers, the chi-square of 4.666 with 3 df has a probability of 0.198. Accordingly there is no evidence supporting a color preference.

Based on the data for the 102 species, an attempt

TABLE 5. Comparison of numbers of attractive and unattractive species in relation to flower color.

Color	Number of species	
	unattractive ($\leq 2\%$ bees/day)	attractive ($> 2\%$ bees/day)
blue	3	1
pink	8	1
red	1	0
purple	19	11
white	25	5
yellow	23	5

was made to determine if any of the measurements were essentially different in relation to the interaction between the visitors and each of color and symmetry. Table 6, which gives the analyses of deviance, shows that there is no evidence supporting these hypotheses. None of the analyses involving the density of flowers, based on the logarithms of the counts, revealed any association with their attractiveness; therefore, no tables of results are presented.

Discussion

Attractiveness of floral characters

Of the floral characters examined in our attempt to identify those related to attractiveness to female leafcutting bees, the most evident was size of flower. The bees were not attracted to flowers with a corolla length exceeding 13.5 mm. This length approximates the combined body, head, and extensible mouthparts length of the bee. A floral length of 13.5 mm for a number of plant species with narrow corolla tubes was found mechanically to prevent Alfalfa Leafcutting Bees from reaching the basal nectaries (Fairey and Lefkovitch 1993). It should be stressed, however, that almost all of the 94 species with corol-

TABLE 6. Analysis of deviance of three floral measurements.

Source of variation	df	mean deviance		
		flower length	throat length	density open flowers
Symmetry (S)	1	1.717	20.735	16.090
Color (C)	5	0.115	1.022	2.651
S.C.	3	0.344	0.652	0.938
Visitors (V)	1	0.022	0.148	0.237
S.V	1	0.196	0.586	0.393
C.V	4	0.058	1.318	2.099
S.C.V	2	0.209	0.114	0.955
Residual	84	0.288	1.239	1.862

las longer than 13.5 mm presented no obvious mechanical barriers to the bees to collection of pollen and/or nectar. Presumably it was excessive size *per se* that did not conform to the bee's innate sense of acceptability, although it is not clear why the bee's overall length and the maximum length of flower visited are approximately equal. In this instance, perhaps complete insertion of the bee's body into a floral throat would render the bee especially susceptible to floral predators, or simply requires too much time or effort to be worthwhile.

As noted earlier, the head of the female is about 3 mm wide, so that a corolla narrower than this may limit how far the bee could probe into a narrow floral tube, even by extending its tongue. Indeed, we found that if the width of the throat does not exceed 3 mm, throat lengths less than 5 mm are preferred by the bees. This coincidence with the lengths of the mouthparts of the bees (mean 4.56 mm) is hardly surprising, but none the less is interesting. Figure 2 shows a leafcutting bee visiting an alfalfa flower, and diagrammatically summarizes the apparent limiting maximum dimensions of a sympetalous flower, in relation to the female leafcutting bee's dimensions.

Colors distinguishable by humans were not found to differ significantly between attractive and unattractive species. Nevertheless further investigation may well prove that the bees do have at least some color preferences. Goplen (1970) and Goplen

and Brandt (1975) found that the purple-flowered *Medicago sativa* seemed to attract more Alfalfa Leafcutting Bees than the closely related yellow-flowered *Medicago falcata*, although this may be due to floral features other than color. It should also be remembered that "several authors have recently pointed out the hazards of considering colors, whether visible or ultra-violet, independently, rather than as a comprehensive visual stimulus to the pollinator" (Scogin 1983).

Corolla symmetry (whether radial or bilateral) was also found not to be related to floral attractiveness to leafcutting bees. The only species examined with asymmetrical flowers belonged to the Compositae, none of which was attractive, but it remains unclear whether this is due to the asymmetry of the flowers or some other characteristic of the family. It should be noted that another species of *Megachile*, *M. apicalis* Spinola, prefers to collect pollen from the Compositae rather than Alfalfa (Peterson et al. 1992).

Density of open flowers had no bearing on the attractiveness to leafcutting bees. It may be noted, however, that the bouquets used presented higher concentrations of flowers than normal for most species, and that different results might have been obtained with more natural displays of the inflorescences.

Taxonomic specificity

As evident from Table 1, *Megachile rotundata* is

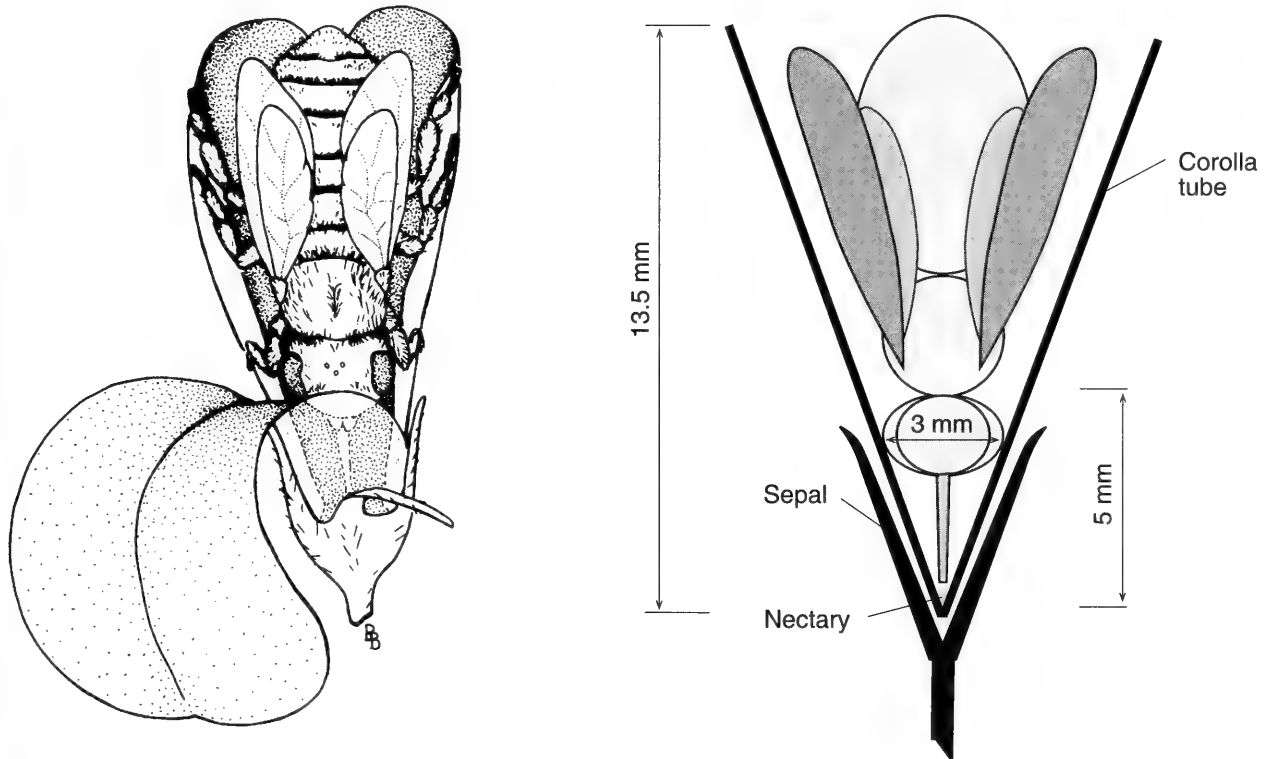


FIGURE 2. Left, female Alfalfa Leafcutting Bee foraging for nectar on an Alfalfa flower (petals displaced for clarity). Right, diagram showing apparent maximum length of a flower (13.5 mm) and dimensions of its corolla tube, for accessibility of the female Alfalfa Leafcutting Bee's head width (3 mm) and combined head and proboscis length (5 mm).

“narrowly polylectic” sensu Michener (1979), i.e. it collects pollen only from a relatively narrow range of plants, most of which are unrelated. Of the 209 species of plants examined, no visits were recorded for 171, and using the criterion of at least 2% of the bees visiting the bouquets under examination during one of the experimental days, only 21 species were defined as attractive (Table 1) with 188, in 40 families, unattractive. It is of interest that, among the control species for which extensive observations were made, purple-flowered Alfalfa (the dominant color variant of this crop) was notably less attractive to leafcutting bees than White Sweetclover and Purple Loosestrife, despite the fact that the bees did forage on the purple-flowered Alfalfa field in which the experiment was conducted. Moreover, it appears that other species also are preferred over Alfalfa (Table 1). This finding is consistent with those of Packer (1970), who compared the Alfalfa Leafcutting Bee’s attraction in Utah to a number of plants (identified as Sweetclover, Tumbling Mustard, Phacelia, Northern Sweet Broom, and Buckwheat), and wrote that “in a truly competitive situation alfalfa was never the favorite pollen source.” Given its name and its utility as a pollinator of Alfalfa, it seems surprising that the Alfalfa Leafcutting Bee prefers species other than Alfalfa. The remarkable explosive tripping mechanism of Alfalfa flowers doubtless evolved in association with particular pollinating bees, quite possibly with Alfalfa Leafcutting Bees in their common Eurasian distribution ranges. However, the preference of Alfalfa Leafcutting Bees for plants other than Alfalfa makes it clear that they did not evolve an obligative dependence on Alfalfa.

Taxonomic preference at higher levels (genus and family) was also investigated, but the small numbers of attractive species (21, representing only 14 genera in seven plant families) limit the conclusions. While no association of attractiveness and plant family was demonstrated, it does seem probable that a preference exists for the Leguminosae, since as noted earlier most crops that have proven to be suitably pollinated by Alfalfa Leafcutting Bees belong to this family. However, several genera of Labiatae were also found to be attractive to Alfalfa Leafcutting Bees. As in the Leguminosae, the Labiatae have a well-differentiated flag-(standard-)blossom and provide pollinators with a foothold on the keel (carina) and (or) wings (alae) for sternotribic pollination. Thus it seems that the Labiatae are also adapted to venter-collecting bees such as the Megachilidae (Van Der Pijl 1972). As many species and genera of Compositae were tested and none was found to be attractive, it appears that this family is unattractive. Ruskowski et al. (1980) recorded a few visits of *M. rotundata* on species of Compositae in Poland, but since this family is often the largest in temperate

regions, their observation is not considered to be indicative of a genuine attractiveness. Inflorescences of the Compositae examined differ from all of the other species studied in having tightly aggregated collections of mostly very small flowers collectively simulating single flowers, and also with respect to having some or all of the flowers possessing asymmetrical corollas.

Limitations of technique of using bouquets to assess pollinating relationships

The present study examined floral preferences of Alfalfa Leafcutting Bees by experimentally presenting them with a choice of bouquets of plant species and examining leafcutting bee visitation rates. Visitation rates are much more commonly (and easily) assessed by observation of wild and field-grown plants, but this limits the range of species observable at the same time and under standard conditions. Comparative studies with plantings in a controlled field plan, such as the examination of the relative attractiveness of 54 plant species to honeybees by Ayers et al. (1987), are uncommon because of the cost and the limitations of resources needed to examine large numbers of plant species; additionally, it is rarely possible to arrange simultaneous flowering of more than a few species. The use of bouquets, as carried out in this study, offers a cost-efficient and convenient means of testing many species simultaneously and rapidly under fairly controlled conditions. At the same time, there are some potential problems with the technique. For example, some species classified as “unattractive” may be attractive in monocultures; examples of this are *Trifolium hybridum* (Faurey and Lefkovitch 1991), *T. pratense* (Faurey et al. 1989), *T. repens* (Richards 1991), and *Coronilla varia* (Richards 1991).

While few bouquets showed evident wilting after cutting, it may be that small if unnoticed changes in turgidity of some plants are sufficient to alter floral attractiveness, for example, in production of odors. Perhaps more critical is the unnaturalness of a bouquet presentation for many plant species, which display their flowers in various diffuse modes. We recommend that before this technique is adapted for other bees, sufficient preliminary experimentation be carried out to ensure that the bees are attracted to the bouquets in a manner similar to their behavior in their natural state.

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Notes

Honey Bee, *Apis mellifera*, Pollen Foraging in Southern Ontario

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Stimec, Jennifer, Cynthia D. Scott-Dupree, and J. H. McAndrews. 1997. Honey Bee, *Apis mellifera*, pollen foraging in southern Ontario. *Canadian Field-Naturalist* 111(3): 454-456.

Honey Bee, *Apis mellifera*, pollen pellets were collected for five days each week for 16 weeks at the University of Guelph. They were sorted by color, the dispersed pollen cleaned by acetolysis and identified under a light microscope. Over 99% of pollen in each pellet was of one pollen type. Twenty-five pollen types were identified. Over 75% of the pellets were pollen from introduced taxa. The pattern of pollen collection by the bees reflected the blooming period of the plants.

Key Words: Honey Bee, *Apis mellifera*, pollen, foraging pattern, Ontario.

Pollen is a necessary dietary source of protein, vitamins, fats and minerals for Honey Bees, *Apis mellifera*. Pollen is collected by foraging worker bees and carried to the hive in pellets packed on their hind legs (Stanley and Linskens 1974). These pellets are stored within the bee hive and eventually consumed by "nurse bees", who metabolize the pollen to produce the protein-rich food "royal jelly" for the bee brood (Hodges 1984). In southern Ontario, during the April-October pollen and nectar foraging season bees visit plant species as they come into bloom, pollinating both domestic and wild plant species, although plant species that provide bees with pollen are not necessarily the same as those that provide nectar. Pollen types in pellets reflect both the sequence of blooming during a foraging season and the local foraging pattern of a bee colony. Pellet colors vary with source species; knowledge of preferred species may assist in choosing optimal sites for apiaries (Kirk 1994) for healthy growth and pollination.

The only published pellet study in southern Ontario is for hives located near Brantford, Ontario. Adams et al. (1978) recorded a 24-week foraging season spanning 18 April - 1 October 1976. Weekly collections of pellets were not sorted by color but mixed together before the pollen was cleaned by acetolysis and the pollen types identified. There were 14 common pollen types (see Table 1 for most equivalent latin names): cf. dandelion, cf. Apple, sumach (*Rhus*), Loosestrife, jewel-weed, maple (*Acer*), willow, Lilac (*Syringia vulgaris*), oak (*Quercus*), buckthorn, White Clover (*Trifolium repens*), Red Clover (*T. pratense*), sweet clover and goldenrod. In addition, there were 32 rare types

including Blue-weed, pink family, thistle, grass family (Gramineae, Poaceae), Horse Chestnut, honeysuckle, crowfoot family, mustard family, Alfalfa-Black Medick, elderberry and burdock.

Our study parallels the report of Adams et al. (1978), but for a shorter period of 15 weeks, 9 May - 10 September 1990, and at a site located 45 km to the north at the University of Guelph (latitude 43° 31.4' N, longitude 80° 12.6' W). We collected pellets from eight hives for five days each week using horizontal grid pollen traps (Scott-Dupree 1987). Instead of mixing weekly pellet collections, we sorted pellets by color. For each pellet color, a pellet was dispersed and the pollen cleaned of surficial oil and internal cytoplasm by acetolysis (Faegri and Iversen 1989); this permitted an unobstructed view of the taxonomic characters of the pollen wall. Pollen identifications followed keys to European pollen types in Faegri and Iversen (1989) and McAndrews et al. (1973) but were checked against pollen from identified species.

During the 1990 season, 13 565 pollen pellets weighing 138 g were sorted and counted (Table 1). Weekly collections ranged from 505 to 122 pellets; three pellets contained fungal spores not pollen. Seven pellet colors were identified, ranging from white to purple, but most pellets were a shade of yellow. Eighteen pollen types were identified where the pollen pellet color and shade was distinctive. The remaining seven types were less color-distinctive, with several colors and shades representing a single plant taxon (cf. Kirk 1994).

Over 99% of pollen grains in any one pellet were from a single plant species, demonstrating the high

TABLE 1. Honey Bee, *Apis mellifera*, pollen pellets collected from hives at the University of Guelph during 1990. An asterisk indicates an introduced plant. Collection weeks are numbered from 1 beginning 9 May; bold face indicates most abundant pellet type for week. Some pellets from week 1 (9 May) collection were sweet clover although the season was too early for it to flower; among all the samples only this one appears mislabelled. Nomenclature follows Gleason and Cronquist (1991).

Common Name	Latin Name	Pellet Color	Collection week	Pellets	Pellets (g)	Comments
*Apple	<i>Pyrus malus</i>	yellow/green	1 2 4 7	1322	26.17	Local ornamental and crop tree.
*Black Medick	<i>Medicago lupulina</i>	green/grey	8 9 10 12 13 15	1446	17.74	Local weedy herb.
*sweet clover	<i>Melilotus</i>	yellow	1 7 9 13	1919	15.55	Local weedy herb.
*buckthorn	<i>Rhamnus</i>	yellow/green	3	507	12.83	<i>R. frangula</i> naturalized shrub locally common on wet soil.
*spurge	<i>Euphorbia</i>	yellow/green	7 8 9 10	1620	12.43	<i>E. corrolata</i> reported to be local.
rose family	Rosaceae	orange/brown	11	844	9.71	Trees, shrubs and herbs.
Nannyberry	<i>Viburnum lentago</i>	orange/brown	5 6	1361	8.86	Shrub of forest edges and openings not recorded and local.
aster-goldenrod	<i>Aster-Solidago</i>	yellow/orange	14 15	719	7.76	Local weedy herbs.
*bellflower	<i>Campanula</i>	dark yellow	12	459	5.74	<i>C. rapunculoides</i> weedy ornamental herb not recorded as local.
*mustard family	Brassicaceae	yellow/green	2 6 8 9 15	423	4.18	Weedy herbs.
*Bird's-foot Trefoil	<i>Lotus corniculatus</i>	beige/brown	10 11	720	4.10	Local weedy herb.
touch-me-not	<i>Impatiens</i>	cream yellow	14 15	305	3.93	Local weedy herb.
*dandelion-type	<i>Taraxacum-Hieracium</i>	orange	1 2 3 4 5 15	1038	2.86	Local weedy herbs.
*Loosestrife	<i>Lythrum salicaria</i>	green/purple	12	287	1.81	Local weed naturalized in wetland forest.
*crowfoot family	Ranunculaceae	red/purple	5	156	1.53	<i>Ranunculus</i> has local weedy herbaceous species.
*willow p.p.	<i>Salix</i>	yellow/orange	1	121	0.86	Local ornamental trees.
*burdock	<i>Arctium</i>	yellow/orange	12	107	0.72	<i>A. minus</i> is a local weedy herb.
ragweed	<i>Ambrosia</i>	yellow	15	40	0.45	<i>A. artemisiifolia</i> is a local weedy herb.
*honeysuckle p.p.	<i>Lonicera</i>	yellow/orange	3 4	32	0.29	<i>L. tartarica</i> local ornamental shrub, sometimes escaped.
*Blue-weed	<i>Echium vulgare</i>	purple	7 8	37	0.24	Local weedy herb.
*Horse-chestnut	<i>Aesculus hippocastanum</i>	white/yellow	10	26	0.20	Local ornamental tree.
elderberry	<i>Sambucus</i>	orange	11 12	20	0.13	<i>S. canadensis</i> local weedy shrub.
*pink family	Caryophyllaceae	dark green	7	26	0.13	<i>Silene</i> and <i>Saponaria</i> common herbaceous weed species.
aster subfamily	Tubuliflorae	red/purple	8 15	13	0.07	Herbs, often weedy.
*thistle	<i>Cirsium</i>	white/yellow	11	4	—	<i>C. arvense</i> common local weedy herb.
unidentified				13	—	
Total				13 565	138.27	

fidelity an individual honey bee has for a plant species. The minor pollen in a pellet is best attributed to surface contamination from other bee loads; all of the minor pollen was of a type present in the weekly collection.

Our foraging pattern results generally compare with those of Adams et al. (1978). They identified 46 taxa while we found only 25 taxa. However, their collection period began in April and extended into October. Due to our shorter trapping season, we missed, for example, the early maple and Skunk Cabbage (*Symplocarpus foetidus*) of March and April and the late Witch Hazel (*Hamamelis virginiana*) of October. There were notable differences in pollen percentages between studies; for instance, we found abundant Alfalfa-Black Medick and Nannyberry, but these were minor in Adams et al. (1978). On the other hand, they found willow and aster subfamily to be abundant whereas we found them to be uncommon; our dearth of willow is probably due to a later collection start. Another difference between the two studies is that there are some pollen types that were present in our study, yet were absent in theirs, such as spurge, bellflower and ragweed. Because bellflower is a garden plant, perhaps it is localized in Guelph but was not grown in the foraging area near Brantford. Also, there were numerous pollen types reported by Adams et al. (1978) which were absent in our collections, e.g. sumach, a weedy shrub, was only found near Brantford and not in the Guelph foraging area. The results of our study and the subsequent comparison of data collected by Adams et al. (1978) indicate the strong regional differences in the forage available to Honey Bees even though the locations of the two studies are close in proximity.

The results of this study also indicate that of the 25 plant taxa identified, Honey Bees tend to forage most heavily on introduced taxa even when native plant species that require insect pollination are available as forage. Of 13 565 pellets identified, 82% came from introduced taxa while the remaining 18% came from native species. Similarly, 85% by weight were gathered from introduced taxa and 15% from native species. It is possible that Honey Bees, a

species introduced to North America in the 1600s, preferentially forage on introduced plant species many of which evolved in Europe along with the Honey Bee.

Honey Bees generally forage on plants adapted to insect pollination but during this study forager bees collected 40 pollen pellets containing pollen grains from ragweed which is wind-pollinated.

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The Pairing Success of Male Black-and-white Warblers, *Mniotilta varia*, in Forest Fragments and a Continuous Forest

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We compared the pairing success of male Black-and-white Warblers (*Mniotilta varia*) in forest fragments (2.0–140 ha) dominated by mature Trembling Aspens (*Populus tremuloides*) and in a similar continuous forest (>1000 ha) in central Alberta, Canada. Of 18 males in forest fragments, 10 were paired. Four out of five males were paired in continuous forest. We failed to detect a significant difference in the pairing success of males in forest fragments versus those in continuous forest ($P = 0.36$). However, the power of our statistical test was low (0.37). Due to small sample sizes, our results failed to statistically determine whether the pairing success of male Black-and-white Warblers is severely affected by forest fragmentation in the study area.

Key Words: Black-and-white Warblers, *Mniotilta varia*, forest fragments, pairing success, Alberta.

As part of a study of Black-and-white Warblers (*Mniotilta varia*) in central Alberta, we attempted to compare the pairing success of males in forest fragments versus in a continuous forest. The Black-and-white Warbler nests on or close to the ground and it is the only warbler species (Emberizidae, Parulinae) that mainly gleans arthropods from the bark of trees (Peck and James 1983; Ehrlich et al. 1988; Morse 1989; Kricher 1995). Several studies of the Ovenbird (*Seiurus auricapillus*), another ground-nesting wood warbler, have shown that the pairing success of males is lower in forest fragments than those in continuous forest (Wander 1985; Gibbs and Faaborg 1990; Porneluzi et al. 1993; Villard et al. 1993; Wenny et al. 1993).

We conducted research around Meanook Biological Research Station (54°37'N, 113°20'W) near Athabasca, Alberta. In this landscape, approximately 30% of the area is wooded, the rest is pasture or crop land. We selected eight forest fragments that were dominated by mature (>80 yr old) Trembling Aspens (*Populus tremuloides*) and that ranged from 2 to 140 ha in area (areas were calculated from 1:30000 aerial photographs using a Placon® digital planimeter). We defined a forest fragment as a wooded area separated from other wooded areas by ≥ 30 m on all sides (cf. Villard et al. 1995). However, one of the fragments was connected to another wooded area by a fencerow < 10 m wide. Besides these fragments, a 30-ha plot was established in a continuous forest at Narrow Lake, about 13 km from the nearest fragment. This plot was in a larger forest (>1000 ha) that was dominated by mature Trembling Aspens and was known to contain Black-and-white Warblers.

All sites (fragments and continuous forest) were flagged into 100 x 100 m grids. To locate male Black-and-white Warblers, fragments were sur-

veyed three times between the end of May and end of June 1993 using the spot-mapping method (International Bird Census Committee 1970). Two similar surveys were made between mid-May and mid-June 1994 in forest fragments and continuous forest. In addition, in both years, the territory of each male was visited almost weekly (eight weeks/year) for periods of 30 (when the male not detected on territory) to 90 min (when the male detected on territory). During territorial visits, if the male was located, we followed him closely to determine his pairing status. Early in the breeding season (mid to late May), females visited but did not settle on some territories (two of nine territories in 1993). A male was only considered paired if we verified the presence of a female (the female in this species can be easily distinguished in the field from the adult male in having a white throat; Kricher 1995) during later visits (early June onwards). Paired males sing softly when close to the female and unpaired males sing actively throughout the breeding cycle (Kricher 1995).

Nine males were located in both 1993 and 1994 in the same four forest fragments (2, 50, 107, and 140 ha). The four unoccupied fragments were 4, 6, 9, and 32 ha in area. Five males were located in continuous forest in 1994. Pairing success of male warblers in forest fragments remained the same between years (56%). Ten (56%) of 18 males were paired in forest fragments. In continuous forest, pairing success was 80%; four of five males were paired. The pairing success of male warblers did not differ significantly between forest fragments and continuous forest ($G = 0.88$, $df = 1$, $P = 0.36$; for this test, only 1994 data were used).

The 24% difference in the pairing success of male Black-and-white Warblers occupying forest fragments versus those in continuous forest was not sta-

tistically significant. However, it is important to determine the power of a statistical test when it fails to reject the null hypothesis, because nonsignificant results may be due to a lack of statistical power rather than absence of the effect being tested (Toft and Shea 1983, Peterman 1990). With our sample sizes, we obtained a low value for the power of our statistical test - 0.37 (Cohen 1988). Thus, 63% of the time our test would indicate that the pairing success of male Black-and-white Warblers did not differ significantly between the habitat types when in reality males in fragments had a lower pairing success than those in continuous forest. In order to only have 20% and 10% chance of making such an error, we would have required sample sizes from both sites of 68 and 95, respectively. Based on 1993 Breeding Bird Census data (Journal of Field Ornithology, 1994 supplement), Black-and-white Warblers occur at rather low densities in most forest types (0.03-0.61 males/ha). Therefore, it would have been beyond the scope of our study to obtain sample sizes required for high statistical power. For example, based on 1992 bird surveys of other comparable forest fragments (mature Trembling Aspen-dominated) in the study area, there were only two other fragments that were known to contain one or two male Black-and-white Warblers each (Sodhi, unpublished data).

If Black-and-white Warblers are highly sensitive to forest fragmentation, they should have shown pronounced negative effects of such a phenomenon (e.g., low pairing success of males) in our study area. First, the study area lies in the northwestern edge of this species' range. A species may be more vulnerable to habitat perturbations in the periphery of its range (Møller 1995). Second, based on the analysis of the Breeding Bird Survey data, Black-and-white Warblers are showing significant long-term population decline (1966-1994) in central Alberta (Sauer et al. 1996). Intuitively, a species should be more vulnerable to environmental perturbations when it is declining in abundance. We therefore hypothesize that the pairing success of male Black-and-white Warblers in the study area may not be severely impacted by forest fragmentation. The study area is in the boreal mixed-wood forest. Boreal mixed-wood forest has a history of natural fragmentation through forest fires and insect outbreaks. Therefore, it is possible that some boreal forest bird species such as the Black-and-white Warbler are adapted to cope with some level of habitat perturbations. However, our study shows that for some species that are rare in a landscape, it may not be possible to obtain enough sample size to statistically test the data.

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Range Extension and Unusual Occurrences of the Heather Vole, *Phenacomys intermedius*, in Minnesota

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Jannett, Frederick J., Jr., and Richard J. Oehlenschlager. 1997. Range extension and unusual occurrences of the Heather Vole, *Phenacomys intermedius*, in Minnesota. *Canadian Field-Naturalist* 111(3): 459–461.

Three specimens of the Heather Vole, *Phenacomys intermedius*, were secured in northeastern Minnesota at two proximate sites on two consecutive days in 1995. Only two specimens of this species had previously been secured in Minnesota. The captures represent an extension of 48.4 km S of the known range of the species. The specimens were secured in sample lines which had been undertaken in each of the previous 11 and 10 years, respectively, in a study of small mammal community dynamics. A fourth specimen was secured at one of the two sites in 1996.

Key Words: Heather Vole, *Phenacomys intermedius*, rare, rarity, Superior National Forest, Minnesota.

The Heather Vole (*Phenacomys intermedius*; Rodentia: Muridae) has one of the largest geographic distributions of any North American small mammal. The range extends from Labrador to British Columbia, and from the Northwest Territories south through the Rocky Mountains to New Mexico (Figure 1) (McAllister and Hoffmann 1988). A review of its biology (McAllister and Hoffmann 1988) categorized it as essentially a rare species in that it is not commonly secured in trapping.

We secured one, and, at a proximate site, another two specimens, of Heather Voles on 8 and 9 September 1995 in Superior National Forest, Cook County, northeastern Minnesota (Figure 1). These sites are approximately 48.4 km south of the previous known locality, and are the southern-most localities for the species in the eastern United States. Identification was verified using dental characters (McAllister and Hoffmann 1988). The specimens are one female and two male subadults.

The specimens were taken in standard sample lines of 50 Museum Special (MS) snap-traps baited with peanut butter, oats, and apple chips, set by the same individual (FJJ) annually. The first specimen was secured on an esker where the same standard MS trap-line was set each September since 1984. Live-traps had also been set for small mammals on a contiguous boulder field in September 1983. The other specimens were secured 0.7 km eastward in a boulder field in a forest clearcut in about 1976. The sample line there had been set with MS snap traps each September since 1983, except in 1984 when live-traps were deployed at the site. Part of the area traversed by the line was also trapped in August 1983 with MS, Sherman live-traps, and pit-traps. Each standard line during those years was left out for two to four days. On the esker there have been 1550 MS trap-nights through 1995 (where one trap for one 24-hour period=one trap-night); on the clearcut there have been 1800 MS trap-nights. These two sites are among as many as 33 sites where samples have been

made annually in a long-term study of population and community dynamics of small mammals (Jannett 1990). No Heather Vole had previously been secured. Other small mammals obtained have been Arctic Shrew (*Sorex arcticus*), Masked Shrew (*S. cinereus*), Smokey Shrew (*S. fumeus*), Pygmy Shrew (*S. hoyi*), Water Shrew (*S. palustris*), Northern Short-tailed Shrew (*Blarina brevicauda*), Star-nosed Mole (*Condylura cristata*), Least Chipmunk (*Tamias minimus*), Eastern Chipmunk (*T. striatus*), Northern Flying Squirrel (*Glaucomys sabrinus*), Deer Mouse (*Peromyscus maniculatus*), Boreal Red-backed Vole (*Clethrionomys gapperi*), Rock Vole (*Microtus chrotorrhinus*), Meadow Vole (*M. pennsylvanicus*), Southern Bog Lemming (*Synaptomys cooperi*), Meadow Jumping Mouse (*Zapus hudsonius*), and Woodland Jumping Mouse (*Napaeozapus insignis*).

The first *Phenacomys intermedius* specimen was taken on the second of four days in a trap beneath a rotting log at the edge of an exposed 5x6 m patch of boulders, midway up a steep west-facing slope. It was 11 m from the bottom of the slope, itself 14 m from a creek. The broken overstory was dominated by Black Spruce (*Picea mariana*) and had Balsam Fir (*Abies balsamea*), White Pine (*Pinus strobus*), White Birch (*Betula papyrifera*), Pincherry (*Prunus pensylvanica*), Mountain Ash (*Sorbus americana*), and willow (*Salix* sp.). Ground cover included abundant crustose and foliose lichens, liverwort, *Cladonia* spp., *Sphagnum* and other mosses, fern (*Polypodium virginianum*), Twinflower (*Linnaea borealis*), and Wild Sarsaparilla (*Aralia nudicaulis*).

The other specimens were taken on the third of four days in an exposed boulder field about 91x37 m; boulders were about 2x2.5 m, each with abundant crustose lichens. At the trap stations, grass was sparse and included Reed-grass (*Calamagrostis canadensis*); other plants included Hairy Goldenrod (*Solidago hispida*), Bracken Fern (*Pteridium aquilinum*), Lady Fern (*Athyrium angustum*), *Aster* sp.,

Canada Mayflower (*Maianthemum canadense*), Woodland Horsetail (*Equisetum sylvaticum*), Knotweed (*Polygonum cilinode*), Green Alder (*Alnus viridis*), and Fireweed (*Epilobium angustifolium*). Shrubs were also sparse; for example, there was none within 3 m of one of the stations where a Heather Vole was captured. Shrubs at the boulder field and elsewhere on the clearcut were dominated by Lowbush Blueberry (*Vaccinium angustifolium*) and Labrador Tea (*Ledum groenlandicum*), and included serviceberry (*Amelanchier* sp.), willow, and Mountain Ash (*Sorbus americana* and *S. decora*). Trees were sparse and included Black Spruce, Jack Pine (*Pinus banksiana*), Tamarack (*Larix laricina*), Trembling Aspen (*Populus tremuloides*), Balsam Fir, and White Birch. Adjacent mature forest was Trembling Aspen, White Birch, Black Spruce, Red Pine (*Pinus resinosa*), and Jack Pine. Mosses and *Cladonia* spp. were abundant in boulder crevices. There was probably water within 1 m of the accessible recesses of the boulders; water had been seen in the recesses in previous years. Most of the clearcut had dense *Vaccinium* spp. and Labrador Tea. Boulders and rocks at both sites were predominantly coarse grained granophyric granite.

In 1996, one additional subadult male Heather Vole was secured at the site where two were taken in 1995. The specimen was trapped on the second of six nights of trapping. No other Heather Voles were taken at eight other sites, including the site where a specimen was secured in 1995, despite an extended six-day trapping session at each locality. Nor was any Heather Vole taken in 10 other traplines, each set for two days, or in more intense trapping efforts at two sites where small mammal censuses were attempted.

Some (e.g., Negus 1950; Millar et al. 1985) have reported the habitat distribution of Heather Voles as relatively broad. The western habitats reported for Heather Voles were reviewed by Edwards (1955) who summarized that 72% of the records were of obviously dry sites, proximity to surface water, or both, and 64% had successional vegetation. McAllister and Hoffmann (1988) cited several reports of habitat which include *Vaccinium* spp. and rocks. The sites where we took specimens were similar to those profiles.

The reasons for the rarity of Heather Voles in field collecting are not clear. Innes and Millar (1982) noted low trappability, and Edwards (1952) reported them more trappable in pit-traps than in snap-traps. They are perhaps more common than trapping efforts would indicate. Douglass and McDonald (1976) took only one in 70 000 trap-nights but found them in 5% of Marten (*Martes americana*) feces in the same area.

The first specimen of *Phenacomys intermedius* in Minnesota was secured by Aldous in 1940 from the

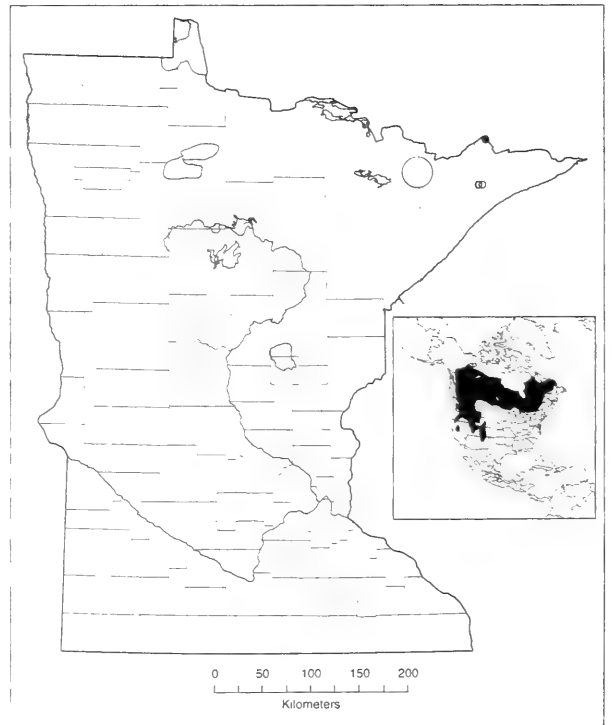


FIGURE 1. Range of *Phenacomys intermedius* [after Hall (1981)], approximate location where first Minnesota specimen was taken [open circle, after Hazard (1982)], location of second specimen [filled circle, after Etnier (1989)], and two new localities (overlapping open circles).

vicinity of Ely (Handley 1954; Hazard 1982). The only other previous specimen was reported by Etnier (1989) from 20 years of trapping along the Canadian border (Figure 1). The Minnesota Department of Natural Resources Natural Heritage Information System lists no other from the state (M. Miller, personal communication).

Why we secured Heather Voles in 1995 and 1996 but not between 1983 and 1994 is problematic. It is not because of a change in trapping design or technique, inasmuch as those have not changed since 1983. The Heather Vole may be expanding its range in Minnesota. The Smokey Shrew (*Sorex fumeus*) is apparently expanding its range in the same area (Jannett and Oehlenschläger 1994, and unpublished). There are rare instances of unusual abundances of *Phenacomys intermedius* (reviewed by McAllister and Hoffmann 1988), and our findings could have been part of a similar occurrence. Continued monitoring of the small mammal community will hopefully distinguish between these possibilities.

The Boreal Red-backed Vole (*Clethrionomys gapperi*) was unusually uncommon in 1995 and 1996, in the latter year probably at a nadir of its cyclic abundance (unpublished observations). The relative scarcity of *C. gapperi* may have allowed for increased trappability of *Phenacomys intermedius*, but Heather Voles have not been secured in other

years of low *C. gapperi* population numbers since 1983.

The averages for standard measurements (total, tail, hindfoot, in mm; weight, in g) of the four specimens are, respectively, 124, 27, 18.0, and 19.0 and the specimens are in the Science Museum of Minnesota collection, accessions Z95:14 and Z96:7.

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Unusual Movement by Bison, *Bison bison*, in Response to Wolf, *Canis lupus*, Predation

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Carbyn, L. N. 1997. Unusual movement by Bison, *Bison bison*, in response to Wolf, *Canis lupus*, predation. *Canadian Field-Naturalist* 111(3): 461–462.

Pursuit of Bison by Wolves was studied in conjunction with predator-prey studies in Wood Buffalo National Park. The average distance of chases was 4.9 km. This paper describes an unusual chase that was observed when a herd fled for 4.3 km before a calf was killed, then continued to run another 81.5 km within a 24-h period.

Key Words: Bison, *Bison bison*, Wolf, *Canis lupus*, Wood Buffalo National Park, movement, predation.

Information published on the pursuit of prey by Wolves (*Canis lupus*) prior to killing indicates that prey generally flees less than 8.0 km (Chrisler 1956; Kolensky 1972; Mech and Korb 1978; Carbyn et al. 1993). Mech and Korb (1978) stated that White-tailed Deer (*Odocoileus virginianus*) stopped running soon after Wolves abandoned pursuit "so that deer rarely travelled more than 6.0 km". Studies of Wolf predation on Elk (*Cervus elaphus*) and Moose (*Alces alces*) in Riding Mountain National Park, Manitoba, indicated that recorded chase lengths of

these species averaged 129 metres and 883 metres, with maximum lengths of 1 km and 2.4 km respectively (L. N. Carbyn and P. Paquet, unpublished data). Successful chase lengths by Wolves killing Bison (*Bison bison*) in Wood Buffalo National Park averaged 4.9 km, with the maximum chase recorded being 16.2 km (Oosenbrug and Carbyn 1985). For most species, prey generally stop running soon after Wolves abandon pursuit (Mech and Korb 1978). This does not appear to be the case for Bison. In 15 of 37 attacks recorded, Bison continued running an

average distance of 17.5 km (Carbyn et al. 1993). When instances in which there was no flight after a kill were included, the average distance run was 7.1 km. One observation of particular interest was made on 9 March 1981 when a herd of Bison moved 81.5 km after a kill.

A mixed herd of 90 Bison was first encountered in association with a radio-collared Wolf pack on 8 February 1981. On that day, eight Wolves were seen chasing the herd at 1510 hrs. After several attempts, the Wolves discontinued their attacks by 1525 hrs. Tracks in the snow indicated that during the next 18 hours the pack repeatedly tested the herd but did not make a kill. When the same pack was contacted on 14 February, evidence again indicated several attempts (at least three) to press the Bison herd. By 16 February, the pack had killed a cow and the herd had moved 20 km to another site. It was not until 6 March that the same pack (minus one pack member) again pressed the attack. When the herd was first spotted at 1725 hours, the Bison had been in a tight formation and the pack had just left the herd. During the night or following morning, the Wolves had again unsuccessfully pressed their attack and the Bison had fled more than 7.2 km. On 8 March, at 1000 hours, the pack had moved closer to the herd and were keeping the Bison under surveillance. On 9 March, the pack was again observed, this time resting near a freshly-killed Bison calf. Snow conditions were such that evidence of the chase could be clearly traced from the air. The Wolves had chased the herd through open meadows for 4.3 km from the site at which they had last been observed. The calf was killed when the herd ran through forest cover. It is conceivable that obstruction from trees and undergrowth might hinder calves more than adult Bison when herds are pressed into vegetation cover. During summer, Wolves tend to seek out herds with calves (Carbyn and Trottier 1987; Carbyn et al. 1993). Once a kill is made, Wolves generally do not continue to chase the prey. On this occasion, the Wolves remained with the kill and the herd continued to flee. Tracks indicated that the movements

initially were in a tight herd formation and that the herd had not stopped to feed. Later, this pattern was less compact and the tracks were more "braided", but there was still no evidence of feeding. After a 20-km route through brush, the Bison reached a snow-ploughed road and rested (as evidenced from beds and dung piles). The bison continued their travel for another 61.5 km before they were seen around 1200 hours (March 9).

I question the adaptive advantage of Bison moving away from a pack that has just made a kill and of running into an area where they risked moving into a territory of another pack. Furthermore, the Bison herd had moved out of an area of prime sedge (*Carex*) ranges to an area that appeared to be poor range. On the other hand, this strategy would work well to avoid multiple kills by the same pack. Multiple kills have been observed in this area (Carbyn et al. 1993).

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Identifying Coast Moles, *Scapanus orarius*, and Townsend's Moles, *Scapanus townsendii*, from Tunnel and Mound Size

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Sheehan, S. Tim, and Carlos Galindo-Leal. 1997. Identifying Coast Moles, *Scapanus orarius*, and Townsend's Moles, *Scapanus townsendii*, from tunnel and mound size. *Canadian Field-Naturalist* 111(3): 463–465.

We compared the mounds and tunnels of Townsend's (*Scapanus townsendii*) and Coast (*Scapanus orarius*) Moles in southwestern British Columbia. Species association was accomplished by live-trapping and from carcasses provided by professional mole trappers. We measured mound width, mound height and tunnel diameter at 25 Townsend's Mole and 35 Coast Mole encampments. Tunnel volume and vertical shaft depth measures were taken from 16 and 23 Townsend's Mole and 11 and 35 Coast Mole encampments, respectively. All five measurements were significantly ($P < 0.01$) larger for Townsend's Mole. Mound and tunnel measurements provide a simple, indirect technique to assist in the delineation of the restricted distribution of the threatened Townsend's Mole in British Columbia.

Key Words: Coast Mole, *Scapanus orarius*, Townsend's Mole, *Scapanus townsendii*, encampments, mounds, tunnels, British Columbia.

In Canada, the Coast Mole (*Scapanus orarius*) and Townsend's Mole (*Scapanus townsendii*) are sympatric and found exclusively in British Columbia (Nagorsen 1996). The range of the abundant Coast Mole encompasses the lower Fraser River drainage basin from Vancouver east to Hope (van Zyll de Jong 1983; Nagorsen 1996). In contrast, the larger Townsend's Mole is a threatened species (Sheehan and Galindo-Leal 1996) restricted to a 13 to 15 km² area near the international border around Huntingdon (Glendenning 1959; Nagorsen 1996).

The Coast and Townsend's Mole are solitary, fossorial mammals that construct extensive tunnel systems, referred to as "encampments" (Glendenning 1959), for hunting and movement purposes. The encampments of both mole species are generally comprised of three types of tunnels: surface, shallow and deep (Glendenning 1959; Pedersen 1963). Surface tunnels occur just below the ground surface and are characterized by a ridge of soil and the absence of mounds. These tunnels are used only temporarily for feeding or finding a mate. Coast Mole tunnels are circular and roughly 5 cm in diameter (Glendenning 1959); similar information for Townsend's Mole is not available. Permanent shallow tunnels are the most common type and both mole species conduct the majority of their daily hunting and encampment reconfigurations within them. The regular hunting tunnels of Townsend's Mole are relatively shallow (5 to 20 cm, Pedersen 1963; Carraway et al. 1993) compared to those of the Coast Mole (7 to 90 cm; Glendenning 1959). When the surface soil becomes frozen or excessively dry both mole species will retreat into deep tunnels which can exceed 2 m in depth.

The loose soil produced by tunnelling is either compacted against the tunnel walls or pushed to the surface to form a mole mound which is conical and cloddy in appearance. Although Kuhn et al. (1966) provide the dimensions of Townsend's Mole "fortress" nest mounds, those they referred to as "normal-sized" were not quantified. Coast Mole mounds average 30 cm in width and 15 cm in height (Glendenning 1959) and are smaller than those made by Townsend's Mole (Hartman and Yates 1985).

Townsend's Mole is larger than the Coast Mole in almost every body size measurement (Carraway et al. 1993; Nagorsen 1996). Size differences suggest that the physical characteristics of their mounds and tunnels may also differ. The characterization of mounds and tunnels has not been possible because the necessary information has been lacking. Verification of interspecies mound and tunnel differences would expedite research on the range of the threatened Townsend's Mole in British Columbia. Although previous attempts to live-trap either the Coast or Townsend's Mole in British Columbia have been unsuccessful (Schaefer 1978; Kremsater, L., and L. Andrusiak. 1991. Status Report for the Townsend's Mole (*Scapanus townsendii*). British Columbia Ministry of Environment, Lands and Parks, Wildlife Branch, Victoria, B.C. 44 pages), removal trapping was not undertaken due to the status of Townsend's Mole in Canada.

The objective of this study was to live-trap Coast and Townsend's Moles to determine if there were measurable, discriminating differences between their mounds and tunnels.

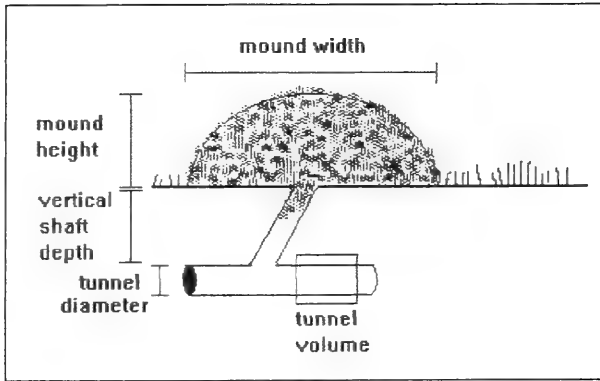


FIGURE 1. Measured characteristics of a mole burrow system: mound width, mound height, tunnel diameter, tunnel volume and vertical shaft depth.

Study Area and Methods

The study area was located in the agricultural region around Huntingdon (49° 01' N, 122° 16' W), within the municipality of Abbotsford in the central Fraser Valley, British Columbia. A review of historical records indicated that Farmer Road, Huntingdon produced the majority of the Townsend's Mole voucher specimens stored in Canadian museums.

Moles were live-trapped (Moore 1940) and directly captured (Glendenning 1959) from November 1994 to February 1995 and November 1995 to March 1996. Two professional mole trappers from the area were also contacted and asked to save any Townsend's Moles they kill-trapped. The following criteria was used to differentiate Townsend's Mole from the Coast Mole in the field: total length ≥ 175 mm (Nagorsen 1996), hind foot ≥ 24 mm (Carraway et al. 1993), weight ≥ 90 g (Pedersen 1963).

At most sites where a mole was captured we measured five parameters: mound width and mound height aboveground, and tunnel diameter, vertical shaft depth and tunnel volume belowground (Figure 1). The width and height of three mounds unaffected by wind or rain were measured at these sites. Mound width was defined as the greatest diameter at the base of the molehill.

Mound height was defined as the distance from the ground to the apex of the mound.

Belowground variables were obtained from casts created by injecting "Monofoam" (Tremco Ltd., Toronto, Ontario M4H 1G7) into the vertical shaft below the molehill. This expanding substance flowed into the tunnel and after three hours was completely dry. Careful excavation of these casts provided replicas of the mole tunnels dimensions. We used callipers to measure the greatest vertical diameter of the ovoid-shaped tunnels. All tunnel diameters were taken approximately 10 cm from either side of the fork where the vertical shaft originates. Vertical shaft depth was the distance measured from the shallow point of the fork up to the ground surface. Tunnel volume provided a validity check for tunnel diameter because of the similarity in the two parameters. One 10-cm section of the shallow tunnel was cut from the cast on each side of the fork and included the site from where the tunnel diameter was taken. Each tunnel "plug" was then submerged in a graduated cylinder and the amount of water displaced was recorded. Mean values for the five variables were compared between the two mole species using one way t-tests (Zar 1984).

Results

Forty-six Coast Moles (38 live-trapped, 8 directly captured with shovel) and 25 Townsend's Moles (18 live-trapped, 7 directly captured) were collected during nine months of fieldwork.

Townsend's Mole mounds and tunnels were larger than those of the Coast Mole (Table 1). The average height of Townsend's Mole mounds (\bar{x} = 17.4 cm, SD = 2.52, n = 25) was greater (t = 13.4, P < 0.01) than those of Coast Moles (\bar{x} = 10.7 cm, SD = 1.32, n = 35). The average width of Townsend's Mole mounds (\bar{x} = 44.0 cm, SD = 5.88, n = 25) was greater (t = 12.2, P < 0.01) than those of Coast Moles (\bar{x} = 29.7 cm, SD = 3.12, n = 35); however, this variable demonstrated slight overlap. The average Townsend's Mole shallow tunnel diameter (\bar{x} = 5.15 cm, SD = .404, n = 25) was greater (t = 16.1, P < 0.01) than the Coast Moles (\bar{x} = 3.56 cm, SD = .357, n = 35). The aver-

TABLE 1. Dimensions and discriminating statistics of Townsend's Mole (TM) and Coast Mole (CM) burrow systems.

	Mound width		Mound height		Tunnel diameter		Tunnel volume		Vertical s. depth	
	TM	CM	TM	CM	TM	CM	TM	CM	TM	CM
\bar{x}	44.0	29.7	17.4	10.7	5.15	3.56	249.	121.	14.3	11.5
(SD)	(5.88)	(3.12)	(2.52)	(1.32)	(.404)	(.357)	(60.9)	(17.1)	(4.07)	(2.11)
Degrees of Freedom	58		58		58		25		56	
t-value	12.2		13.4		16.1		6.78		3.41	
Significance	p < 0.0001		p < 0.0001		p < 0.0001		p < 0.0001		p < 0.0089	

age Townsend's Mole tunnel volume (\bar{x} = 249.4 cc, SD = 60.7, n = 16) was greater (t = 6.78, P < 0.01) than the Coast Moles (\bar{x} = 121. cc, SD = 17.1, n = 11). The average Townsend's Mole vertical shaft depth (\bar{x} = 14.3 cm, SD = 4.07, n = 23) was greater (t = 3.41, P < 0.01) than the Coast Moles (11.5 cm, SD = 2.11, n = 35); however, some overlap existed.

Discussion

The results of our study indicate that the burrows of Townsend's Mole and the Coast Mole can be differentiated based upon mound height and width, tunnel diameter and volume, and vertical shaft depth. Although vertical shaft depth differed between species, there is too much overlap in this variable to be useful in the field. Also, the calculation of tunnel volume is too impractical for widespread measure in the field. We recommend the use of three variables. Specifically, encampments containing mounds which exceed 15 cm in height and 40 cm in width with shallow tunnel diameters greater than 4.5 cm strongly indicate the presence of Townsend's Mole.

We encourage researchers to verify our findings and use mound width, height and tunnel diameter to investigate the distribution of the threatened Townsend's Mole in Canada. Our results provide an inexpensive and rapid methodology for this purpose. Also, the use of these criteria prior to live-trapping would allow for a more focused, species-specific trapping schedule. In addition, the extent of Townsend's Mole habitat fragmentation and the effects of agriculture and urbanization could be studied along with this species association with soil type, habitat, and the Coast Mole.

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Unsuccessful Colonization of a Naturally Depopulated Area by the Deer Mouse, *Peromyscus maniculatus*

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A decline in abundance of the Deer Mouse, *Peromyscus maniculatus*, in the Kananaskis Valley, Alberta in 1992–1993 was followed by a slow recovery of some local populations. We attempted to recolonize one depopulated area by releasing laboratory raised mice and monitoring persistence by livetrapping. Only 14 (15%) of 92 mice released were subsequently recorded at the release site, with only one mouse persisting until the end of the summer. However, 8 (9%) of the introduced mice were recovered on another depopulated area 1 km away, where they remained until the end of the summer. We suggest that factors other than the colonization ability of the introduced mice may have played a role in the unsuccessful colonization.

Key Words: Deer Mouse, *Peromyscus maniculatus*, extinction, colonization, local population, Alberta.

Populations of *Peromyscus* are noted for their stability relative to populations of other small mammals (Terman 1968; Ostfeld 1988). Nevertheless, long term studies indicate that population numbers occasionally deviate considerably from the norm. For example, Gilbert and Krebs (1991) compiled data on abundance (minimum number alive) of the Deer Mouse, *P. maniculatus*, at Kluane, Yukon during 1976–1989. Abundance in May averaged 3.8 per ha over 14 years, but only 0.3 per ha (8% of the average) during 1989. Other long term studies of *Peromyscus* have also documented periodically low populations (Grant 1976; Fuller 1985; Kaufman et al. 1995).

During a long term study of the Deer Mouse, *P. maniculatus*, in the Kananaskis Valley, southwestern Alberta (1987–1994), we recorded low numbers of mice in 1993, followed by a slow recovery. This slow recovery may have been the result of several, potentially interacting factors, such as poor colonizing ability, excessive predation pressure, or lowered resources throughout the study area. We investigated whether the release of a large number of *P. maniculatus* onto a depopulated area would result in successful colonization.

The study area consisted of four grids (A–D), located in rocky, ephemeral stream beds, which constitutes suitable habitat for Deer Mice (Millar et al. 1985). Grids A and B were located approximately 3 km north of grids C and D. All grids were monitored by mark recapture livetrapping over eight breeding seasons (1987–1994). Trap stations were established at 20 m intervals over each study area, resulting in 24–41 trapping stations per grid. A single Longworth trap, baited with oats and sunflower seeds was set at each trapping station during the evening, and checked the following morning. Standard mark-recapture techniques (Millar et al. 1985) were used to monitor the population and deter-

mine reproductive events. All grids were trapped twice each week from May - August inclusive. Other small mammals commonly recorded on these grids included Yellow Pine Chipmunks (*Eutamias amoenus*), Red-backed Voles (*Clethrionomys gapperi*), Long-tailed Voles (*Microtus longicaudus*) and Western Jumping Mice (*Zapus princeps*). Population abundance was recorded as the number of overwintered females exhibiting lactation in the spring (Table 1). The number of overwintered females was used as a measure of population size because it describes the degree to which the population on the grid is viable, i.e., has the opportunity to breed. Spring populations were relatively stable between 1987 and 1992, with a total of 20–32 breeding females across all grids. In 1993 however, spring populations exhibited evidence of a decline, with grids A and B becoming effectively extinct and grids C and D exhibiting their lowest abundance in seven years. In 1994, recovery over the entire study area was approximately 50% of normal population levels, with no recovery on grid A, partial recovery on grids B and D, and full recovery on grid C (Table 1).

In 1992, an additional grid (E) was established near an ephemeral stream 1 km north of grids A and B. A total of 132 trap stations were set at 15-m intervals over the 3.8 ha grid, which was trapped at the same rate as grids A - D. Animals captured on this grid were not tagged, and abundance was recorded as the number of captures per 100 trap nights (Seiler 1994). In the spring of 1994, grid E was again monitored, with all animals being tagged. Abundance on grid E had fallen from 13.1 mice per 100 trap nights during 1992 to 0.6 mice per 100 trap nights during 1994 (Table 2). Comparisons between the long-term study area (grids A–D) and grid E indicate that capture rates in 1994 had fallen drastically on grids A, B and E (Table 2), while grids C and D showed little effect. The correlation between the number of lactat-

TABLE 1. Number of overwintered lactating female *Peromyscus maniculatus* on four grid sites in the Kananaskis Valley, Alberta, from 1987 to 1994. (Data from 1994 does not include *P. maniculatus* from the introductions.)

YEAR	GRID A (1.7 ha)	GRID B (1.7 ha)	GRID C (1.3 ha)	GRID D (2.2 ha)	TOTAL
1987	8	3	10	10	31
1988	3	4	6	7	20
1989	10	6	6	4	26
1990	6	5	4	5	20
1991	5	6	4	5	20
1992	7	7	10	8	32
1993	0	0	3	2	5
1994	0	2	9	3	14

ing females and the capture rate per 100 traps on each grid (pooling data from 1992 and 1994) was significant ($r = 0.814$, $p = 0.014$), indicating that the number of animals caught per 100 trap nights provides a reliable indicator of the population size. This suggests that grid E was subjected to the same pressures that drastically reduced the population on all other grids between 1992 and 1993, and similarly to grids A and B, had not recovered to normal population levels by 1994.

In June 1994, we commenced the introduction of mice onto grid E. The introduced mice were wild conceived mice whose mothers had been captured in the Kananaskis valley, at a distance of at least 20 km from the study area. Females were brought into the lab just prior to parturition, and juveniles were reared with their dams until 21 days of age, then separated from their mothers and maintained in the laboratory (one litter per cage) until six weeks of age. All introduced mice were eartagged prior to release. In total, 92 young-of-the-year (47 males, 45 females) were released onto grid E. Mice were introduced by placing nest boxes containing a single litter, food and water in the center of the grid, and then opening the box, allowing the mice to leave and return if desired. Only 14 (15%) of the introduced mice were subsequently trapped on grid E during 1994, with one introduced male persisting on the grid until August. The average residency of the other trapped mice ($n = 13$) was 16.1 ± 2.4 SE days (range 9–36). This subsequent recapture rate is similar to a comparable study, where 15% of lab born and reared mice introduced to a depopulated area were recaptured (Jimenez et al. 1994). However, average persistence

was much lower on grid E than found by Jimenez et al. (1994). Introductions onto islands using adult mice and voles that were born and reared in the wild have generally been successful (Sheppe 1965; Crowell 1973; Mehlhop and Lynch 1978). In addition, studies that released juveniles born in captivity into established populations have also reported successful colonization (Healey 1967; Boonstra 1978). Overall, the introduction of 92 mice onto the grid was unsuccessful, because only one mouse became established on grid E.

Of the 78 introduced mice that were never captured on grid E, eight (9% of all introduced mice) were recorded on grids A and B during 1994 located at a distance of 1 km away from grid E. These individuals took an average of 9.1 ± 1.3 SE days (range: 4–14) to reach grids A and B after release from grid E. All eight of these mice (5 females, 3 males) remained on grids A and B until the end of the trapping season in 1994. Presumably, these grids provided suitable resources/conditions that facilitated establishment of these eight mice. These movements involved traveling 1 km through unfamiliar and relatively unsuitable terrain. While previous studies (Teferi and Millar 1993) have indicated that *P. maniculatus* are capable of returning home over long distances (>1 km), the findings of this study suggest that neither prior experience nor familiarity is necessary for successful long-distance movements. As trapping was restricted to the five grids, we were unable to determine whether any other mice established into populations that were not monitored by our investigation.

The finding that these eight introduced *P. maniculatus* established themselves in a relatively depopu-

TABLE 2. Capture of *Peromyscus maniculatus* per 100 trap nights (May-August inclusive) on grids A - E during 1992 and 1994. Introduced *P. maniculatus* are not included in the 1994 data.

YEAR	GRID A	GRID B	GRID C	GRID D	GRID E
1992	23.9	25.3	58.3	35.5	13.1
1994	1.1	8.1	87.4	20.8	0.6

lated site (grids A and B), but did not establish at the release site (grid E) provides insights into the population dynamics of this species. The unsuccessful colonization of the depopulated area was likely affected by a variety of factors, but the results of this study suggest that at least some of the introduced mice were capable of establishing themselves in appropriate habitat, as demonstrated by the eight mice that moved to grids A and B. In addition, the abundance of other small mammals on grid E does appear to rule out any possible effect of high predation pressure. Comparisons between abundance of other small mammal species between 1992 and 1994 on grid E indicated that while the numbers of *E. amoenus* and *M. longicaudus* were relatively stable, there appeared to be a negative relationship between the abundance of *P. maniculatus* (1992: 13.1/100 trap nights, 1994: 0.6/100 trap nights) and *C. gapperi* (1992: 5.9/100 trap nights, 1994: 17.7/100 trap nights). It is possible that conditions on grid E (e.g., lowered resources and potential competition from other small mammal species) relative to grids A and B made it unsuitable for widespread colonization by *P. maniculatus*. Future studies of this nature should focus on the relative abundance of resources, in order to better understand the population dynamics of small mammals following drastic declines in numbers.

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Northern Extension to the Known Breeding Range of the Black Tern, *Chlidonias niger*, in the Northwest Territories

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Barrett, G. M., and D. G. Kay. 1997. Northern extension to the known breeding range of the Black Tern, *Chlidonias niger*, in the Northwest Territories. *Canadian Field-Naturalist* 111(3): 469–471.

A breeding colony of Black Terns, *Chlidonias niger*, was observed 300 km north of the previously recognized range for this species. A general lack of qualified observers in this and similarly remote areas may account for the lack of records for intervening areas.

Key Words: Black Tern, *Chlidonias niger*, boreal forest, range extension, Northwest Territories.

The Black Tern (*Chlidonias niger surinamensis*) breeds locally across the northern United States and central Canada, concentrated in areas with productive wetland habitats (Godfrey 1986; Dunn and Agro 1995). North of 60° N latitude, breeding has been reported in south-central Mackenzie District (Godfrey 1986) and also in the Great Slave Lake region of the Northwest Territories (Sirois and Fournier 1993). Black Terns are considered accidental in the Yukon and Hudson and James bays (Anonymous 1992; Sirois and Fournier 1993; Dunn and Agro 1995). A single confirmed breeding record exists for Alaska (Gabrielson and Lincoln 1959) where they are considered accidental as well (Armstrong 1990).

Previous observations of Black Terns breeding in the Northwest Territories are scattered. Sirois and McRae (1994) considered them common mainland breeders, based on observations in the Great Slave Lake and Slave Delta regions (Sirois and Fournier 1993). Neily and Scotter (Scotter et al. 1985) reported a colony of approximately 20 adults in Nahanni National Park, in the southwest Mackenzie District. A single nest was reported from the Fox Islands of Hudson Bay (Taverner and Sutton 1934). Nests have also been found at Wood Buffalo National Park in the southern Northwest Territories (Sirois and Fournier 1993). Small flocks of adults and fledglings are seen annually in the wetlands surrounding the north arm of Great Slave Lake (D. G. Kay, personal observation). Here, we report a new observation representing the northernmost documented breeding record in Canada for this species.

Study Area

The Brackett Lake wetland complex lies at the terminus of the most northerly extension of boreal forest habitat in Canada. It occurs at the boundary of high boreal and low sub-arctic ecoclimatic regions (Ecoregions Working Group 1989) and as such, contains micro-habitats ranging from closed boreal forest to open sub-arctic tundra.

The study area consists of a 700 km² wetland complex in a valley of the Franklin Mountains (65°06'N, 125°19'W) (Figure 1). A remnant post-glacial lake bed, the area is underlain by deep, ice-rich lacustrine deposits. Numerous thermokarst lakes occur there, with wetlands and open water comprising more than fifty percent of the area. Bog-fen sequences are the dominant wetland type (Wakelyn 1990).

The local climate consists of long, cold winters and brief, cool summers. Its proximity to the Mackenzie Valley, however, moderates it to some degree, particularly during summer. In the months corresponding to use by breeding migratory birds (May through August), mean daily maximum temperatures, number of degree days above 18°C and average monthly rainfall are significantly higher than at Yellowknife, 600 km to the southeast (Atmospheric Environment Service 1993). Consequently, break-up is accelerated, resulting in spring chronology slightly earlier than that of Yellowknife. The ice-free period on smaller water bodies is approximately early May to late September (P. Latour, personal communication).



FIGURE 1. Brackett Lake, Northwest Territories, study area described in text.

In wetlands, the most common emergent vegetation consists of sedges (*Carex* spp.), horsetail (*Equisetum* spp.), maretail (*Hippuris* spp.) and Bur-reed (*Sparganium hyperboreum*). Bulrush (*Scirpus* spp.) and Narrow Leaf Cattail (*Typha latifolia*) occur infrequently, but can be locally abundant. Submergent flora is dominated by Yellow Pond Lily (*Nuphar variegatum*), pondweeds (*Potamogeton* spp.), Bladderwort (*Utricularia vulgaris*) and water milfoil (*Myriophyllum* spp.).

Results and Discussion

Black Terns were observed 31 May 1994 during aerial surveys conducted as part of a study of breeding waterfowl at Brackett Lake, Northwest Territories. A breeding colony was discovered upon subsequent ground surveys of the study area. Thirty adult terns were observed entering and leaving the apparent nesting site at this time, carrying food and exhibiting aggressive attack displays at our presence. Although active nests were not seen, the parental behaviour observed constitutes unambiguous evidence of breeding (Roe 1975; Federation of Alberta Naturalists 1992).

The breeding colony was located on a wetland remnant of a larger lake, whose basin occupied an area of approximately 3.75 km² at an elevation of 370 metres. Low water levels resulted in an extensive (> 300 m) sedge periphery, with only 50% of the original basin remaining as open water. Drainage occurred recently, as willows (*Salix* spp.) had not yet invaded the sedge meadow border. The terns were nesting in a dense bed of Hardstem Bulrush (*S. acutus*), 15 metres from shore. Water depth was approximately 1 metre.

The area was accessed the following year, on 2 July 1995, and 20 adults were observed. We were reluctant to search the nesting cover thoroughly because of the agitated state of the terns, and for fear of either destroying nests or injuring young. It is likely that hatching had already taken place, as many birds were carrying prey items (tadpoles and bait-fish), and entering and leaving the nesting site, presumably to feed nestlings. This timing concurs with the hatching chronology of Black Terns on the Yellowknife Study Area (M. Fournier, personal communication).

This observation represents a 300 km extension to the previously known northern limit of the breeding range of the Black Tern, as recognized by Sirois and Fournier (1993). They considered their observations to be evidence of a northerly shift in breeding range, and cited several causative factors, including climate warming trends, and northward expansion of boreal ecosystems.

We contend that the current distribution of species is more an artifact of the presence of qualified observers and does not necessarily reflect the

true breeding range. This is particularly true of remote areas, where wetlands are often difficult and expensive to access. With the suitable climate and habitat conditions provided by the numerous wetlands in the Taiga Plains of the Northwest Territories, it is likely that other northern areas contain breeding populations of Black Terns. Without good baseline data from similarly remote sites, it is impossible to conclude anything more significant from these observations.

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Early Coral-root, *Corallorhiza trifida* Chatelain: A New Addition to the Vascular Flora of the Canadian Arctic Archipelago

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Gould, Joyce. 1997. Early Coral-root, *Corallorhiza trifida* Chatelain: a new addition to the vascular flora of the Canadian Arctic Archipelago. *Canadian Field-Naturalist* 111(3): 471–472.

Two populations of Early Coral-root (*Corallorhiza trifida*) were discovered on Baffin Island, Northwest Territories in 1995. These populations appear to represent the first records for the Canadian Arctic Archipelago.

Key Words: Early Coral-root, *Corallorhiza trifida*, Baffin Island, Auyuittuq National Park Reserve, Northwest Territories.

Two populations of Early, or Pale, Coral-root (*Corallorhiza trifida* Chatelain) were found in Auyuittuq National Park Reserve, Baffin Island, in July 1995. These populations appear to represent the first documented occurrences of this species in the District of Franklin, Northwest Territories.

Early Coral-root is not included in *The Flora of the Canadian Arctic Archipelago* (Porsild 1964). Distribution maps in *Vascular Plants of the Continental Northwest Territories, Canada* (Porsild and Cody 1980, page 220) and *Flora of Alaska and Neighboring Territories* (Hulten 1968, page 329) do not show any records for the Canadian Arctic Archipelago. A search of the herbarium at the National Museum (CAN) and at Agriculture Canada (DAO) by W. J. Cody (August 1995) failed to show any collections for this area.

One population in Auyuittuq National Park Reserve was located on the east side of the Weasel River at the base of an end moraine and of a fluvial terrace just south of a small tributary. The position determined using a Magellan global positioning system was 66° 25' 30" N and 65° 27' 04" W. Fifty-six plants were counted in an area of approximately 36 × 17 m on 2 July 1995. All plants counted were in flower although several old fruiting stalks were also observed. Most of the plants seen appeared as individuals although there were approximately four clumps with 4–5 flowering stalks.

The vegetation at this location was dominated by Arctic Willow (*Salix arctica*) and the moss (*Pohlia drummondii*). Vascular plant species including Arctagrostis (*Arctagrostis latifolia*), Large-flowered Wintergreen (*Pyrola grandiflora*), Poa (*Poa arctica*), Bistort (*Polygonum viviparum*), Lousewort (*Pedicularis flammea*) and sedges

(*Carex* spp.) were common in the community. Associated mosses included *Aulacomnium palustre*. Total plant cover exceeded 100% of the ground surface. The soils at this location were sandy and were described as regosolic static cryosols (C. Tarnocai, 1995, personal communication). The moisture regime was mesic.

A second population was located north of the previously described population at 66° 31' 02" N, 65° 29' 51" W. Three plants, individual flowering stalks, were seen on 3 July. All plants were found in a small ephemeral drainage channel at the base of a colluvial slope. The vegetation was dominated by Arctic Willow (*Salix arctica*) with the lichen *Stereocaulon* sp. and the moss *Aulacomnium turgidum*. Plant cover was approximately 80%. Soils were sandy and were classified as regosolic static cryosols (C. Tarnocai, 1995, personal communication). The moisture regime was dry mesic.

Case (1987, page 226) describes several forms of *Corallorhiza trifida*. The northern and European form is brownish in colour with a spotted lip. The population on Baffin Island fits this description. A specimen of Early Coral-root was collected from the first population in Auyuittuq National Park Reserve and deposited at the herbarium, Agriculture Canada, Ottawa (DAO). Identification was confirmed by W. J. Cody.

Early Coral-root is a circumboreal species (see Hulten 1968, page 329). Porsild (1943, page 26) indicated that it was "fairly common in the Mackenzie District, north to the limit of trees or a short distance beyond" and in Ungava it is known from 61° 49' 30"N, 72° 48' 00"W (Cayouette 1984, page 267). It is known from western Greenland (Hulten 1968, page 329; Scoggan 1978) north to ca.

69° 30' N (Scoggan 1978, page 528) so its discovery on eastern Baffin Island is not altogether unexpected.

The habitat of Early Coral-root has been described as "turfy, open places" (Porsild and Cody 1980, page 213), "bogs, thickets and woods" (Scoggan 1978, page 528) and "wet places, woods, bogs" (Hulten 1968, page 329). Case (1987, page 227) describes this species as having a wide range of habitats from wet swamps to drier upland habitats, especially the northern populations. The two populations on Baffin Island were in different plant communities with different moisture regimes—the presence of Arctic Willow appeared to be the only common factor.

All species of *Corallorhiza* are saprophytic — growing in symbiotic association with soil fungi or deriving nourishment from soil organic matter (Case 1987, page 216). Porsild and Cody (1980, page 213) note that *Corallorhiza trifida* is "often growing in the centre of well-established *Dryas integrifolia* mats". *Dryas integrifolia* was absent from where it was found on Baffin Island, however, *Salix arctica* was the only vascular plant noted that was found near both populations.

One other vascular plant, the sedge *Carex microglochin*, was noted within the Park Reserve that appears to be a northern extension to its known range (see Porsild and Cody 1980, page 181). It is also found in western Greenland north to ca. 71° N (Scoggan 1978, page 405) but unlike *Corallorhiza trifida* it is known from southern Baffin Island.

Additional surveys of previously unexplored areas of Auyuittuq National Park Reserve and other parts of southern Baffin Island may reveal more populations of this orchid and other plants with notable range extensions.

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Brood-Defense Behavior of a Ruffed Grouse, *Bonasa umbellus*

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McIsaac, Hugh P. 1997. Brood-defense behavior of a Ruffed Grouse, *Bonasa umbellus*. *Canadian Field-Naturalist* 111(3): 473-475.

Observations are reported concerning the reactions of a Ruffed Grouse (*Bonasa umbellus*) and its offspring to an intruder. At my approach the adult bird appeared to scatter its offspring from a common hiding-place into separate hiding-places. Later the young birds were apparently gathered together by the adult and they vanished into the woods. The grouse's behavior may have reduced the risk that a predator could capture the entire brood.

Key Words: Ruffed Grouse, *Bonasa umbellus*, brood defense.

Ruffed Grouse (*Bonasa umbellus*), like many bird species (see Gochfeld 1984; Hudson and Newborn 1990), defend their offspring with distraction displays. Feigning injury, grouse attempt to lead intruders away from their offspring (Bent 1932; Sawyer 1923). Additionally, a female may noisily rush an intruder, thereby distracting the intruder while her offspring scatter and hide. Apparently both distraction displays are relatively common and on occasion have been used as indices of aggression (see Davies and Bergerud 1988; Hudson and Newborn 1990). Despite this, a detailed description of the "rush" distraction display has not been published for any species of the Tetraoninae; although, Bent (1932) and Bump et al. (1947) each briefly mentioned the display. I report here detailed observations of a "rush" distraction display, and present a possible interpretation of this behavior.

I came upon a mature red-phased Ruffed Grouse in northeastern Connecticut (Tolland County, near the village of Storrs) while walking along a woodland trail. It was approximately 17:00 EDT on 13 June 1993, and the times listed below are rough estimates. Some 60 - 80 m into the woods off a well-traveled road I first saw the grouse. The day was sunny and warm ($\approx 28^{\circ}\text{C}$ in the woods) and a light breeze quietly animated the green leaves. A fairly even-aged stand of open second-growth oak (*Quercus* sp.), maple (*Acer* sp.), and Black Cherry (*Prunus serotina*) dominated the overstory. A few shrubs (e.g., Pink Azalea, *Rhododendron nudiflorum*) and saplings composed the understory. The ground cover was moderately thick although I could see the forest floor to a distance of 2 - 3 m when standing. Ferns covered much of the ground with some grasses and wildflowers interspersed (e.g., Jack-in-the-pulpit, *Arisaema atrorubens*; Wild Geranium, *Geranium maculatum*; and Wood Strawberry, *Fragaria vesca*). The ground cover rose as high as 30 - 50 cm but taller plants were widely separated, allowing me a reasonable view of the grouse.

I first sighted the grouse when it was 8 - 10 m

away and 2 - 3 m off the trail. It was slinking away from me with its head down, its tail held straight back and folded tight, and its wings held tight to its body. Suddenly, and quite unexpectedly, it turned and ran straight toward me. It held its head up with crest erect, its wings were spread slightly with tips dropped and shoulder ruffs expanded, and its tail was held straight up and fanned. It called, but I do not recall the notes. At 2 - 3 m from me, yet still off the trail, the bird suddenly stopped and simultaneously 6 - 8 sparrow-sized birds exploded out from the ferns immediately around the mature grouse. I had failed to notice the small birds before that moment. The small birds flew off in all directions except toward me and landed as far away as 10 m, disappearing quickly among the ground cover.

Immediately following the departure of small birds the mature bird ran 8 - 10 m away from me and started calling loudly. It made no noticeable attempt to conceal itself. The call, a three syllable (occasionally four) "whoi-wohi-whoooo", was hoarse and nasal, and sounded somewhat like the alarm call of the Eastern Gray Squirrel (*Sciurus carolinensis*). The call was repeated perhaps 6 - 10 times per minute with each call lasting several seconds. The last note of the call lasted approximately as long as the first two combined. The first several minutes of calling were conducted from the ground with the bird hopping onto fallen branches and logs from time to time. It appeared quite agitated because of its frequent and loud calling and its nearly constant movement.

After perhaps 5 - 8 minutes on the ground the grouse flew 7 - 8 m up into a tree and perched on a branch. In the tree calling continued for a couple of minutes. The grouse then flew back to the ground where it continued its agitated calling and motion. While in the tree the grouse was more easily visible to me, and vice versa (I presume). It returned to the trees three more times; each time to about the same height. On the second flight into a tree, the return to the ground was only a minute or two after ascent. Upon descent the landing placed the mature grouse in the hiding spot of one of the small birds, causing the

small bird to fly to a new hiding spot several meters away. The mature bird spent several minutes in a tree after its third ascent. Finally, on its fourth and ultimate ascent the bird spent 15 - 20 minutes in a tree. Its calling rate and amplitude gradually decreased; however, the calls never stopped completely.

After approximately 5 - 10 minutes into the fourth tree ascent, I walked further into the woods along the trail in an attempt to put the bird at its ease. I walked away from the road until I was 50 - 60 m from the mature bird. I stood quietly at this distance, concealed behind a large cherry tree.

Eventually, the grouse dropped to a dead branch about 1 m above the ground and called. These calls were not as loud as those given earlier in our encounter; instead they were similar in amplitude to the last calls uttered in the tree. It now rapidly called "whi-whi-whi", sounding somewhat like the "yank" call of the White-breasted Nuthatch (*Sitta carolinensis*). Again this call was hoarse and nasal. After a minute or two of calling the grouse jumped to the ground and thereafter was completely silent.

I lost sight of it almost as soon as it jumped to the ground and never caught sight of the small birds. Two or three minutes later I walked over to the spot where I had last seen the grouse and searched the area. I found neither the mature grouse nor any of the small birds.

I suggest the following interpretation of the mature grouse's behavior; other interpretations are possible for some aspects. This interpretation assumes the grouse's behavior to have been adaptive. Furthermore, I expect the intensity and type of behavior to vary from one context to another. For example, the bird's behavior might vary with different types of intruders, in different habitat types, with younger or older offspring, and with the number of offspring (Gochfeld 1984; Montgomerie and Weatherhead 1988).

I presumed the small birds to be offspring of the mature grouse. I also presumed the mature grouse to be female, as male Ruffed Grouse do not participate in brooding or rearing of offspring (Bump et al. 1947; Johnsgard 1973). The grouse apparently detected me before I noticed it and hid its brood among the ground cover. The initial slinking behavior of the mature bird may have been an attempt to slip away without drawing attention to its brood or itself. Alternatively, this behavior may have reduced risk to the brood by drawing the intruder away from its hidden brood. As the intruder approached the offspring too closely, the parent ran in among the brood, scattering the small birds from their common hiding place into separate hiding places. Dispersing the brood might reduce the risk of capture of the entire brood (Andersson et al. 1980; Lazarus and Inglis 1986; Sandercock 1994). After scattering its offspring, the squirrel-like calls of the parent appar-

ently kept the offspring in hiding as long as the intruder remained nearby, and may have provided the offspring with information concerning the location and mood of the parent. The calls also may have relayed information concerning the intruder, such as the risk posed by the intruder. The bold behavior of the mature grouse, including its calls, flights into trees, and lack of effort to conceal itself on the ground, may have reduced risk to the brood by distracting the intruder away from its offspring. Such behavior also may have improved the grouse's efficacy in monitoring the position and behavior of the intruder. The mature grouse's second descent from the trees, which flushed one of the youngsters, may have forced the chick out of a poor hiding spot; alternatively, the landing of the grouse in the chick's hiding spot may have been simply coincidence. Finally, the nuthatch-like calls of the parent after its final descent from the trees may have pulled the offspring out of hiding and back to the parent when it was safe to re-aggregate and leave the area.

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Horn Growth of a Castrated Bighorn Sheep, *Ovis canadensis*

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Henderson, Robert E., and John E. Firebaugh. 1997. Horn growth of a castrated Bighorn Sheep, *Ovis canadensis*. *Canadian Field-Naturalist* 111(3): 475–477.

In 1987 a 21 month-old Rocky Mountain Bighorn Sheep (*Ovis canadensis canadensis*) was captured, castrated, and released into a free-ranging population. In September 1995, the ram was recovered and examined. When compared to normal mature rams from the same population, measurements indicated that following castration both basal and linear horn growth were greatly diminished.

Key Words: Bighorn Sheep, *Ovis canadensis*, horn growth, castration, hormonal control.

Rocky Mountain Bighorn Sheep, *Ovis canadensis canadensis*, Populations provide prized opportunities for hunting, viewing, and photography in the western United States and Canada. Horn and body size are sexually dimorphic characters of individuals greater than one year of age. Adult males typically are larger and produce longer and heavier horns than adult females (Cowan 1940). Social dominance and reproductive advantage have been attributed to males with more massive horns (Geist 1971). Factors believed to affect rates of horn growth are individual, genetic, environmental, date of birth, health and nutritional variability (Cowan 1940; Taylor 1962; Geist 1971).

Castration of Bighorn Sheep has not been reported. The role of sex hormones in horn growth in Bighorn Sheep has received little attention. A review of the literature resulted in only one, speculative citation. Jensen and Seabloom (1989) observed a Bighorn ewe with larger than normal horns and masculine behaviors, and suggested that either a genetic defect or unusually high levels of testosterone might have been responsible.

We report on the horn growth of a 10-year-old Rocky Mountain Bighorn ram, which had been castrated at approximately 21 months of age, and compare those measurements with those of normal mature rams from the same population.

Methods

In March 1987 five Bighorn sheep near Thompson Falls, Sanders County (approximately latitude 47°N and longitude 115°15'W) were captured and relocated to Lower Rock Creek, Granite County (approximately latitude 46°40'N and longitude 113°35'W),

near Missoula, Montana. Before release, the sheep were sexed, aged, and eartagged with sequentially numbered metal tags, using standard methods.

In an unusual action, a heavy rubber band was wrapped around the scrotum and above the testicles of one yearling male (approximately 21 months-old). In September 1995, a licensed hunter with an adult-ewe permit mistakenly shot the bighorn which had been castrated in 1987. The animal was field dressed, caped, quartered, removed from the field, and turned over to state wildlife personnel in Missoula. The hunter reported that this sheep had a penis, but that no scrotum nor testicles were evident. No attempt was made to verify the hunter's observations by trying to locate sex organs in the field.

Age was determined by counting annual growth rings (annuli) on the horns (Cowan 1940; Taylor 1962). For comparison, 2 incisors (I_1) also were extracted and sent to Matson's Laboratory, Milltown, Montana, for examination of cementum layers.

Horns were measured to both the nearest 1/8 inch (in) and millimeter (mm) with a steel tape measure and calipers. Measurements were of the circumferences at the bases and each annulus, and of linear distances between the base, tip and annuli on the outside curve of the horns.

Comparison to Normal Mature Rams

Comparative horn measurements were compiled from 11 normal mature rams, 6 to 9 years-old, harvested in the same area during 1991 and 1995. Horn dimensions were recorded to the nearest one-eighth inch, and later were converted to millimeters for this analysis. Measurements included tip-to-tip distance, total length on outside curve, tip-to-ring 1, tip-to-

ring 2, tip-to-ring 3, tip-to-ring 4, and circumferences of base, ring 1, ring 2, ring 3, and ring 4. Ring 1 was defined as the annulus formed during the animal's second winter, ring 2 during the third winter, ring 3 during the fourth winter, and ring 4 during the fifth winter.

Results

Horn Growth Comparisons

Total lengths of each horn of the castrated ram were just 543 and 544 mm, and basal circumferences were 247 and 248 mm. Those values were well below the range of values for the 11 normal mature rams (Table 1). Values for the normal mature rams were within the ranges for mature bighorn rams elsewhere (Cowan 1940; Taylor 1962; Geist 1971).

Compared to the normal rams, horn growth was normal during the ram's first 1.5 years prior to castration (Table 1). Linear growth during the first 6 months was 150 and 152 mm for each horn, respectively. During the next 12 months, 270 and 272 mm were added. However, following castration, linear horn growth of the castrated ram declined dramatically compared to normal mature rams. Only 120 and 122 mm were added during the 9 years following castration, far less than the 413–775 mm added to the horns of normal rams after their second winter of life (Table 1).

Basal horn growth was normal during the castrated ram's first 1.5 years of life. Circumferences at ring 1 were 237 and 241 mm for each horn, respectively, well within the range of values for normal mature rams. However, following castration, basal horn growth declined. While horn bases of normal rams progressively enlarged with age, attaining final basal circumferences between 356 and 425 mm, there was no basal increase following castration. Circumferences remained essentially unchanged (about 240 mm) between ring 1 and the base (Table 1).



FIGURE 1. Photograph of castrated 10-year-old Bighorn Sheep showing condition of horns and annuli. Note location of ring 1 (arrow) formed at 1.5 years of age.

Discussion

The result of castration in this Bighorn Sheep was a dramatic and abrupt decline of horn growth. Compared to normal mature rams both linear and basal growth were greatly diminished following castration. No other effects such as change in shape were observed in this specimen. Interestingly, total lengths and basal circumferences were very similar to those (500 mm and 250 mm, respectively) reported by Jensen and Seabloom (1989) for a 5-year-old bighorn ewe with unusually large horns and masculine behaviors.

One would expect secondary sex characters, such as horn size, to be affected by sex hormones. Castration typically results in smaller than normal horns in domestic sheep (*Ovis aries*), but is not reported in the literature (Rodney Kott, Montana State University, Bozeman, personal communication). In other bovids Dobie (1941) maintained that castrated Longhorn Cattle (*Bos taurus*) produced

TABLE 1. Comparative horn measurements for castrated ram and normal mature rams harvested near Lower Rock Creek, Montana, during 1991-1995.

	Castrated Ram (mm)		Normal Rams (mm) ¹	
	Right Horn	Left Horn	Right Horn	Left Horn
Total Length	542	543	743–1010 ²	787–1018 ²
Tip-lamb Ring	150	152	NA	NA
Tip-ring 1	420	423	215–508 ²	222–540 ²
Ring 1-Ring 2	22	21	127–247	121–235
Ring 2-Ring 3	20	18	95–183	92–203
Ring 3-Ring 4	19	20	67–139	67–155
Ring 1 Circumference	237	241	222–342	215–349
Ring 2 Circumference	232	234	305–377	305–387
Base Circumference	247	248	358–418	356–425

¹Rams (6-9 years-old, n=11); original measurements in inches and converted to millimeters.

²Includes measurements of broomed and broken horns for some mature rams.

longer horns than either bulls or cows, while Groves (1992) observed that Muskox (*Ovibos moschatus*) castrates had smaller horns than bulls. Castrated Pronghorn Antelope (*Antilocapra americana*) may not cast their horns and displayed abnormal growth (Pocock 1905; O'Gara et al. 1971). Among cervids the effects of castration on antler development include delay of antler casting, initiation of antler growth and abnormal antler development, but the exact effects vary with species, age and season of castration (Goss 1983).

This study provides evidence that castration and, by extension, reduction of sex hormone production negatively influence the growth of horns in Bighorn Sheep. If castration is being considered as a management tool, one can expect that diminished horn growth will be one result.

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Immediate Post-fire Nesting by Black-backed Woodpeckers, *Picoides arcticus*, in Northern Alberta

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Villard, Marc-André, and Jim Schieck. 1997. Immediate post-fire nesting by Black-backed Woodpeckers, *Picoides arcticus*, in northern Alberta. *Canadian Field-Naturalist* 111(3): 478–479.

An active Black-backed Woodpecker nest was found in a forested area that had been severely burned the same summer. By backdating, nest excavation was estimated to have started within a few days after the passage of the fire. This observation indicates that the Black-backed Woodpecker is not only closely associated with recently-burned forests, but that it can nest successfully immediately after the occurrence of a forest fire.

Key Words: Black-backed Woodpecker, *Picoides arcticus*, forest fires, colonization of burned sites, source-sink dynamics, Alberta.

Several authors have reported the close association of Black-backed Woodpecker (*Picoides arcticus*) with recently-burned forests (Bock and Bock 1974; Apfelbaum and Haney 1981; Raphael et al. 1987; Villard and Beninger 1993; Hutto 1995). Hutto (1995) suggested that recent (0–6 years old) fire sites may represent source habitats (Pulliam 1988) for Black-backed Woodpeckers, in the sense that local reproduction exceeds mortality, whereas adjacent unburned forest patches may represent habitat sinks whose populations are maintained by individuals emigrating from burned sites when post-fire conditions become less favourable. Although presence and nesting activities of Black-backed Woodpeckers in recently-burned forests have been reported elsewhere, the minimum time elapsed between a forest fire and the (re)settlement of nesting pairs has not been documented.

Here, we report on a Black-backed Woodpecker pair that initiated a nest within the first two weeks after a severe fire in the boreal mixedwood forest of Alberta and successfully raised young. We do not have information on the location of the members of this pair prior to the fire, but the timing of their nesting suggests that Black-backed Woodpeckers may be able to colonize, or resume their nesting activities in burned areas immediately after the passage of a forest fire.

On 20 July 1995, we were surveying stands within a large (>110 000 ha) burn approximately 50 km south of Fort McMurray, Alberta (56° 17' N; 111° 45' W) when we heard the begging calls of young woodpeckers. We found the nest cavity in a Trembling Aspen (*Populus tremuloides*), approximately 4 m above the ground. A pair of Black-backed Woodpeckers was present in the vicinity. The male flew to the nest cavity and fed the young through the cavity entrance without having to enter the cavity. It appears that this pair successfully raised at least one young, as a group of three Black-backed Woodpeckers was

seen foraging within 100 m of the nest tree on 8 November 1995 (Dave McKinnon, personal communication).

We backdated the onset of the nesting activities of the pair based on our observations and on data available in the literature. We estimated that the young were >1 week old on 20 July, because they were able to reach the nest entrance to take food from their parents. This estimate is conservative, as Short (1982) reported that nestlings' eyes open only at 8–10 days in the closely-related Three-toed Woodpecker (*Picoides tridactylus*). The duration of the incubation period is 14 days and the mean clutch size is four (Bent 1939). We estimate that the first egg was laid at least 24 days before we discovered the nest, assuming that incubation began with the fourth egg. The earliest date that the fire could have burned through the area (11 June 1995 - see below) was 40 days prior to our observations and thus, at most 16 days prior to the pair producing eggs.

We do not know whether the cavity was excavated prior to or after the fire, but Three-toed Woodpeckers are known to create a new nesting cavity every year (Short 1982). We could not find estimates of the time that this species, or the Three-toed Woodpecker, require to excavate a nesting cavity, but the Hairy Woodpecker (*Picoides villosus*) takes between one and three weeks to excavate a cavity (Bent 1939). Two types of evidence suggest that nest excavation may be similar in Black-backed and Hairy Woodpeckers: both species (1) are of similar size (Godfrey 1986), and (2) they usually excavate cavities through sound sapwood and into decayed heartwood (Miller et al. 1979). Therefore, if the cavity was excavated after the fire, the pair of Black-backed Woodpeckers we observed would have started excavation within a few days after the burn. The duration of pair formation activities and their location relative to the future nest have not been described in either the Black-backed or Three-toed Woodpeckers (Short 1982).

Prior to the fire, the area where the nest was found was dominated by Trembling Aspen, along with White Spruce (*Picea glauca*), and there were a few small pockets (ca. 1 ha) of Black Spruce (*Picea mariana*). The understory was dominated by Trembling Aspen and White Spruce seedlings. According to detailed fire progression maps produced by the Alberta Forest Service, we estimate that the area where the nest tree was located burned between 11 and 13 June 1995. The intensity of the fire appeared to have been high in that area, as the nest tree and all adjacent trees were dead on 20 July. The nest tree had no leaves, it was scarred at its base, on the trunk around the cavity, and on the upper branches. Adjacent trees were similarly scarred. The nest tree was located only 100 m away from a large patch that burned only lightly or not at all during the fire. It is possible that the woodpecker pair took refuge in that patch during the fire.

This is, to our knowledge, the first direct evidence that this species has the ability to start nesting within days after the passage of a severe fire. Early colonization of burned sites may be advantageous to Black-backed Woodpeckers, as they feed extensively on wood-boring larval beetles (Short 1982). Wood-boring insects rapidly colonize burned areas to oviposit on freshly killed trees (Evans 1966). Their eggs may hatch within a few weeks (e.g., 2 weeks in *Agrilus liragus*, Coleoptera: Buprestidae; Barter 1965). Trembling Aspens represent a suitable host for both Buprestid and Cerambycid beetle larvae (Barter 1965; Drouin and Wong 1975). However, beetle larvae populations may not reach high densities until two years after colonization (e.g., Zhong and Schowalter 1989 for long-horned beetles, Coleoptera: Cerambycidae).

We did not measure the abundance of beetle larvae at the site upon the discovery of the nest. Perhaps the pair we observed was foraging in the nearby patch of unburned forest. Nonetheless, the apparent success of the nesting attempt we document suggests that it is advantageous for Black-backed Woodpeckers to promptly colonize recent fires or to maintain territories after the passage of intense fires. Observations made by one of us (JS) in the summer of 1996 reinforce our impression that the 1995 nesting pair had been successful. A Black-backed Woodpecker pair was observed in the vicinity of the 1995 nest, and another pair was detected approximately 500 m to the west. The latter pair was also found in the burned area, at least 700 m from the edge of the fire, and 400 m from a 5 ha unburned patch of forest.

Our observations and the literature on Black-backed Woodpeckers suggest that this species may be sensitive to forest management practices altering the frequency or extent of natural disturbance events such as fires, windfalls, or spruce budworm

outbreaks that leave sizeable patches of standing dead or dying trees. Landscape or regional-scale demographic studies would be useful to determine whether recent burns actually represent source habitats for this and other species.

Acknowledgments

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An Arboreal Encounter between a Long-Tailed Weasel, *Mustela frenata*, and Three Red Squirrels, *Tamiasciurus hudsonicus*

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Bowman, Jeffrey C. 1997. An arboreal encounter between a Long-tailed Weasel, *Mustela frenata*, and three Red Squirrels, *Tamiasciurus hudsonicus*. *Canadian Field-Naturalist* 111(3): 480–481.

A Long-Tailed Weasel, *Mustela frenata*, chased three Red Squirrels, *Tamiasciurus hudsonicus* through the canopy of a mature Sugar Maple, *Acer saccharum*.

Key Words: Long-Tailed Weasel, *Mustela frenata*, Red Squirrel, *Tamiasciurus hudsonicus*, arboreal, prey switching.

Long-Tailed Weasels, *Mustela frenata*, are aggressive carnivores that specialize on voles and mice, although other animals (e.g., sciurids, lagomorphs) are taken when available (Fagerstone 1987). Weasels are adapted to foraging in vole tunnels and runways, and as such, are primarily ground-dwellers. Reports of arboreal tendencies in this species are rare (Fagerstone 1987, but see Nams and Beare 1982), although there are arboreal members of the closely-related genus *Martes* (Buskirk 1994).

On 2 August 1996, I observed a Long-Tailed Weasel chasing three Red Squirrels, *Tamiasciurus hudsonicus*, through the canopy of a mature Sugar Maple, *Acer saccharum*. The observation took place on the private industrial forest of Fraser Papers (47° 22' N, 67° 25' W), in the Appalachian Highlands of north-central New Brunswick. The mature canopy of the partially-cut tolerant hardwood stand was a mixture of Beech, *Fagus grandifolia*, and Sugar Maple, and the understory was dominated by raspberries, *Rubus* spp. The events described took place between 1445 hrs and 1515 hrs.

During a vegetation sampling session in the area, I heard an unusually frenetic series of Red Squirrel chirping calls, and attempted to locate the source of the noise; this took about 1 minute during which time the calls continued. The calls were coming from a tall (height, ca. 20 m) Sugar Maple, positioned <20 m from where I observed the following encounter. Three Red Squirrels were stuck out on a narrow branch (a "tree-exposed" position, Stuart-Smith and Boutin 1995); farther up the branch (closer to the tree) was a Long-Tailed Weasel. The weasel's weight prevented it from getting out far enough to catch the squirrels, although it repeatedly attempted this, with no success. On two occasions, the weasel lunged after the squirrels, only to have a squirrel drop from the branch and hit the ground 15 m below. I was unable to determine if the two squirrels that dropped did so intentionally, but I did observe them running (presumably) to safety after hitting the ground. The weasel, clinging with its hind legs, hung below the branch in an

effort to reach the third squirrel, which hung from the branch's tip. The weasel could not reach low enough, and began pacing back-and-forth, along the branch, finally settling down on the trunk. At this point, the Red Squirrel ran up the branch, past the weasel, and down the trunk. The weasel chased the squirrel down the tree and out of my sight. I continued to hear chirping calls for a few minutes from the direction of the chase, however, I was unable to relocate the individuals, or to determine how this encounter ended.

The present observation raises a question about the extent to which Long-Tailed Weasels do, or do not, forage in trees. Small mammal surveys in the same partially-cut stand, and adjacent stands, indicated that forest floor-dwelling small mammal densities were low (J. C. Bowman, unpublished data), which may have required weasels to broaden their foraging strategies, possibly including a shift toward more arboreal prey (e.g., sciurids, bird nests) (prey switching, *sensu* Hanski et al. 1991). If small mammals were abundant, foraging in trees would be an energetically expensive choice for weasels. It is likely that the squirrels included young-of-the-year siblings. Red Squirrels breed in late March and April (often denning in tree holes) while juveniles become active around the den in late July and early August (Dilworth 1984). This coincides with the timing of the present observation, although I was unable to determine the age of the squirrels, or to locate a den. A weasel foraging in an arboreal squirrel den is consistent with the idea that this carnivore was prey switching in response to low small mammal numbers; the idea is further supported by the awkward foraging strategy used by the weasel, as though it was not experienced at hunting in trees.

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Inc., the organizations responsible for my being in the field at the time of this observation. Two anonymous reviewers contributed to the text.

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Early Den Digging by Wolves, *Canis lupus*, in Wisconsin

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Thiel, Richard P., Wayne H. Hall, and Ronald N. Schultz. 1997. Early den digging by Wolves, *Canis lupus*, in Wisconsin. *Canadian Field-Naturalist* 111(3): 481–482.

We report five observations of Wolves initiating den digging between late October and mid February in Wisconsin. Two packs that initiated den digging in November produced pups at these sites the following denning season.

Key Words: Gray Wolf, *Canis lupus*, dens, digging, denning behaviour, early denning.

Various aspects of Gray Wolf (*Canis lupus*) denning behaviour have been studied over the past several decades (Ballard and Dau 1983; Mech and Packard 1990; Ballard et al. 1991; Ciucci and Mech 1992; Boyd et al. 1993). Wolves dig their dens or enlarge the burrows of other animals (Mech 1970; Fuller 1989). Caves and hollow logs are also utilized by Wolves as dens (Mech 1970; Ballard and Dau 1983; Fuller 1989). Wolves may use dens from periods of several years to perhaps centuries (Ballard and Dau 1983; Fuller 1989; Mech and Packard 1990). Fuller (1989) suggested that repeated use of dens from year to year was related to success in raising litters, or the lack of other suitable dens.

Little information is available on the initiation of den construction. Ryon (1977) observed a captive Wolf pack initiate den digging one month before the birth of the litter which occurred on 19 April. Packs with radio-collared members are known to occupy den-sites beginning in mid March, 1 to 17 days before whelping (Fritts and Mech 1981; Fuller 1989). Den construction and digging may occur at that time. Mech et al. (1996) reported den digging by Wolves in April, May and July. We

report on several instances of den digging by two Wisconsin wolf packs initiated prior to the breeding season (mid February).

The Bootjack pack lives in Oneida and Price counties in Northcentral Wisconsin. Wolves have been studied in this pack since 1982. On 11 February 1989 fresh diggings were observed on snow at the entrances of two dens located 75 m apart at Latitude 45°51' N. Beds of six Wolves were nearby, and at least two pups were born at this site in 1989. This den-site had been used periodically by the Bootjack pack since 1982.

A freshly dug den was found 24 November 1994 and was investigated by R. Schultz on 27 November. Two wolves appeared to have dug a hole measuring 0.7 × 0.6 × 1.0 m into the side of a sandy hill. This site was approximately 4 km East of the aforementioned den, but the Bootjack pack Wolves denned 1.7 km to the Southwest of this site in 1995.

Den digging by the Bootjack pack Wolves was observed at Latitude 45°50' N on 13 January 1996. The hole extended back 1.5 m. Sand was observed in the tracks and beds of five Wolves 10 m from the hole. The Wolves did not den there in 1996, possi-

bly because of disturbance created by a logging operation. A logging skidder collapsed the den, which had been completely excavated.

On 19 October 1996, R. Schultz discovered recent evidence of den digging by Bootjack pack Wolves at Latitude 45°50' N. A hole measuring 0.5 m tall, 0.4 m wide extended back 1.2 m. No digging was present at this site on 23 September 1996.

On 30 November 1994 a citizen reported the location of two dens used in spring 1994 by Wildcat pack Wolves in Jackson county, Wisconsin. According to the citizen, the entrance to one den had been closed by a bulldozer the previous spring. Thiel inspected the site on 1 December 1994. Tracks of two Wolves in 4.5 cm of fresh snow led to two den holes 150 m from each other, precisely as reported. The Wolves had initiated construction of a new den at the bull-dozed site. The tunnel extended approximately 1.75 m, and fresh dirt lay on top of the snow. The Wolves had also enlarged the tunnel at the second den hole.

Three to five Wolves in the Wildcat pack were tracked in the snow during winter 1994-1995. Several times the pack was trailed to the vicinity of the dens, but were not followed in that area to minimize disturbance of the site. When inspected on 25 March 1995, fresh Wolf tracks and digging were found at each den, and the first den had been completed. We were unable to determine which of the dens was used for whelping, but the pack produced pups there in April 1995.

Mech et al (1996) hypothesized that den digging activities may be related to circannual rhythms in the production of prolactin, which peaks in Wolves shortly after parturition (Kreeger et al. 1991). This does not explain our observation of den digging activity which occurred at the nadir of circannual prolactin production in Wolves (Kreeger et al. 1991).

The October and late November den digging we observed occurred 2-3 months before the breeding season and 4-5 months prior to parturition. Harrington and Mech (1982) believed summer homesites may serve as refuges where pack mates retreat if disturbed or separated from others during fall and winter. Wolf pack visits to dens throughout the non-denning season may provide opportunities to "tidy" up den holes. We suggest the fidelity to dens during successive seasons as observed by Fuller (1989), Mech and Packard (1990) and others may be reinforced by periodic visits to such sites by Wolf packs throughout the year. This observation and those of Mech et al. (1996) greatly extend the

length of time that dens are known to be used by Wolves during the year and may have implications for managing Wolves.

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News and Comment

Ottawa Field-Naturalists' Club Awards for 1996

The Ottawa Field-Naturalists' Club Annual Awards Ceremony was held during the club's traditional spring Soiree wine and cheese party at the Unitarian Church Hall, 30 Cleary Street, Ottawa, on Friday 25 April 1997. The election of two new honorary members were announced, bringing the total back to 25. As well the years winners of the

regular annual awards were announced and presentations made to the recipients. No President's Prize was given this year. An account of the evening will appear in *Trail & Landscape* 31(3), July-August 1997. The following citations by the Awards Committee were read at the presentations.

Honorary Member: William O. Pruitt, Jr.

Dr. William O. Pruitt, Jr. has been an associate editor of *The Canadian Field-Naturalist* for two periods which total 20 years and contributed greatly to its high standards, and thus to the prestige of the Ottawa Field-Naturalists' Club as its publisher.

After receiving his Ph.D. from the University of Michigan in 1952, Bill became the staff mammalogist at the Rocky Mountain Biological Laboratory in Colorado, then a research biologist for the Arctic Aeromedical Laboratory in Fairbanks, Alaska. He has since held posts in both the United States and Canada, including the Canadian Wildlife Service, the University of Alaska, the University of Colorado, the University of Oklahoma, Memorial University, St. John's, Newfoundland, and the University of Manitoba. Although he "retired" last June after 26 years in the latter post, he continues in active research and in supervision of graduate students. Bill founded the Taiga Biological Station in eastern Manitoba in 1973, and is actively soliciting donations to establish an endowed chair of

Natural History of the Boreal Forest at the university to continue the station.

Not content to thrive within the world of academia, Bill shares his knowledge through many lectures, field trips, and demonstrations of winter ecology to schools, groups, clubs and outdoor centres in Manitoba, Saskatchewan, Ontario, and across the ocean in Finland. He is a respected member of the Canadian Society of Zoologists and the American Society of Mammalogists, and was elected a Fellow of the Arctic Institute of North America and of The Explorers Club.

Bill Pruitt uses his life-time dedication to ecology and the scientific method to ensure that *The Canadian Field-Naturalist* remains of the highest quality and answers to the most rigorous scientific standards. For this and for his outstanding career contribution to research and public education the Ottawa Field-Naturalists' Club formally recognizes his invaluable service to the Club and Canadian natural history studies.

Honorary Member: Bruce Di Labio

Bruce Di Labio is an exemplary and untiring representative of the Ottawa Field-Naturalists' Club, both within the province and elsewhere. He is well-known for his quick and accurate bird identifications. Although he is completely self-taught, many both local journalists and naturalists value him as a primary contact for information and expert opinion.

He is best known for leading some of the Club's most popular field trips over the years. such as Derby Hill, Point Pelee, Presqu'ile and Cornwall, as well as his waterfowl, owl and shorebird outings - usually 7 to 8 per year - since 1975. He has actively participated in Christmas birds counts in Ottawa and elsewhere for over 20 years. He is a long-time member of the Bird Records Sub-committee and is co-founder of the Ottawa Field-Naturalists' Club Seedathon.

He has already received the Anne Hanes Natural History Award for his diligent record keeping, and his observations have led to new understandings of bird populations, migration and life histories.

Bruce's open personality and his enthusiastic willingness to pass on his love for birds is one reason why his field trips have become so popular over the years. The sharing of his knowledge has also led to the recruitment of many members to the Ottawa Field-Naturalists' Club. His efforts have long been appreciated by Ottawa Field-Naturalists' Club members and other students of natural history. The Club now recognizes him for his 20-year outstanding contribution to the successful operation of the Club and for his superb contribution to birding.

1996 Conservation Award to a Member: Sandra Garland and Christine Hanrahan

When the dream of the Fletcher Wildlife Garden became a reality there was still considerable scepticism as to what role it would play. Would it die a-borning? Would it be wise to take on the responsibility of the decrepit and abandoned building to serve as its centre?

The doubting Thomases did not take into consideration the enthusiasm, exuberance, drive, and ability of Sandra Garland and Christine Hanrahan. From the very beginning they have given unstintingly of their time and energy to enhance the flora

and fauna of the Wildlife Garden, and to make the building an Interpretive Centre which serves as an attractive focus of numerous, year-long, and worthwhile activities.

Many people have contributed to the present success of the venture, but Sandra and Christine stand out in their lively, sustained interest. To a large extent, it is they who have made the Fletcher Wildlife Garden a welcoming place, with many interesting events to attract and interest visitors of all ages.

1996 Conservation Award for Non-member: J. Gordon Nelson

Dr. J. Gordon Nelson has made an outstanding contribution to the cause of conservation during his thirty-five years in the geographical field as a teacher, researcher and consultant. He has provided effective leadership in areas of his special interest; parks, protected areas and coastal regions.

He has over two hundred publications to his credit. These include *Man's Impact on the Western Canadian Landscape* (1976), and *Tourism and Sustainable Development, Monitoring, Planning and Managing* (1993), which indicate that he confronts these most difficult and controversial problems head-on.

During his distinguished career, he has served in

a variety of administrative posts. He has been a professor at Calgary and Western universities, and Dean of the Faculty of Environmental Studies at University of Waterloo, where he continues as Chairman of the Heritage Resources Centre.

Dr. Nelson is presently following dedicated interests at Long Point, Ontario, where he is studying new techniques to measure the effectiveness of current conservation practices. He has received many awards during his professional life, including the Natural Heritage Award, the Distinguished Scholarship Award, the Massey Medal presented by the Royal Canadian Geographical Society.

1996 Anne Hanes Natural History Award: Jack Gillett

The Anne Hanes Natural History Award is given in recognition of an outstanding contribution to our knowledge, understanding and appreciation of the natural history of the Ottawa Valley. We can think of no more deserving recipient of this award than Dr. Jack Gillett. Since he joined the Ottawa Field-Naturalists' Club in 1946, Jack has made an impressive contribution, both to the operation of the Club and to our knowledge of the local flora.

His *Checklist of Vascular Plants of the Ottawa-Hull Region*, written in conjunction with Dave White, has, by itself, earned the gratitude of all naturalists who have ever led a field trip in this area. When we add his botanical keys to the Liliaceae, Smilacaceae and Thoroughworts of the district, we have indeed received a unique and val-

ued contribution to the knowledge and understanding of the natural history of the Ottawa Valley.

He has always been available to help out in other ways with the fieldwork aspects of the Club as well as with the Council. He served with the Publicity Committee in 1969; the Education and Publicity Committee from 1984 to 1986; conducted field walks in 1968, 1970, 1972, 1980, and 1984; presented a series of flower recognition slide workshops in 1970; and participated in the Gatineau Park nature walk in Canada's Centennial Year.

In addition to the above activities, Jack has always been approachable at his office by both amateur and would-be professional botanists alike. In this respect, some of the older ex-Macoun Club members here hold fond memories of the help that Jack has given them along the way.

1996 George McGee Service Award: Monty Brigham

The Ottawa Field-Naturalists' George McGee Service Award is presented in recognition of a member who has contributed significantly to the smooth running of the Club over several years. For 1996 the Ottawa Field-Naturalists Club is pleased to present this award to F. Montgomery "Monty" Brigham. Monty has been a member of the Ottawa Field-Naturalists' Club since 1966, and served as auditor between 1978 and 1990. Over the years, he has led a number of Club outings, given many talks, and presented workshops on recording the sounds of nature. In recent years, Monty has led an early-morning June outing to experience the "dawn chorus" in the Richmond fen. Along with Tony Beck, he has staged

a "bird sight and sound" identification evening in the late winter that has served to whet the appetite of area naturalists looking forward to spring. Monty's many nature recordings from the Ottawa area and across Canada have been a great source of joy for seasoned naturalists and have served as an impressive introduction to the natural world for many non-naturalists. He is always ready to share his knowledge, enthusiasm and expertise with the Ottawa Field-Naturalists', the Macoun Field Club, and others in the Ottawa area.

BILL ARTHURS, Chair, and the
Members of the OFNC AWARDS COMMITTEE

Notice of the 119th Annual Business Meeting of The Ottawa Field-Naturalists' Club

The 119th Annual Business Meeting of the Ottawa Field-Naturalists' Club will be held in the auditorium of the Victoria Memorial Museum Building, McLeod and Metcalfe streets, Ottawa, on

Tuesday 13 January 1998 at 19:30 h.

DAVE SMYTHE
Recording Secretary

Call for Nominations: The Ottawa Field-Naturalists' Club 1998 Council

Candidates for Council may be nominated by any member of The Ottawa Field-Naturalists' Club. Nominations require the signature of the nominator and a statement of willingness to serve in the position for which nominated by the nominee. Some rel-

evant background information on the nominee should also be provided. Deadline for nominations is 15 November 1997.

FRANK POPE
Chair, Nominating Committee

Call for Nominations: The Ottawa Field-Naturalists' Club 1997 Awards

Nominations are requested from members of The Ottawa Field-Naturalists' Club for the following: Honorary Membership, Member of the Year, George McGee Service Award Citation, Conservation, and the Anne Hanes Natural History Award. Descriptions of these awards appeared in *The Canadian Field-Naturalist* 96(3): 367 (1982). The Service Award was renamed the George McGee Service Award for 1993

presentations [see *The Canadian Field-Naturalist* 108(2): 243-244 (1994)]. With the exception of nominations for Honorary Member, all nominees must be Club members in good standing. Deadline for nominations is 1 December 1997.

STEPHEN DARBYSHIRE
Chair, Awards Committee

***The Canadian Field-Naturalist* Book-review Editor's Report (1996)**

At the end of each year it is nice to look back and see what has been accomplished. The year 1996 was extremely difficult for keeping up with the reviews and *The Canadian Field-Naturalist* due to work pressures, extensive periods of travel and medical reasons. Things do not look like they will be improving quickly. For this reason, I once more have to thank my faithful reviewers and beg their indulgence to continue helping me somehow get this all together. Please let me know if there are books that you feel need to be reviewed and for which you are willing to write reviews. I just do not have the time to be always keeping up with all of my correspondence. Also feel free to remind me if you think I have forgotten something. The use of internet is also a great time and money saver. I can receive attached messages and translate almost any word processing files (except the most recent Mac files). It is the preferred way to communicate with me whenever possible.

Due to some of the above pressures and some commendable catching up by the Editor, not all of the issues had new titles nor reviews published last

year. The volume was, however similar to the previous years. Eighty-five books were sent out to reviewers and most have come back. This has created a significant backlog at present and the statistics are thus a bit misleading. I only managed to edit and send 49 of these to the journal for publication so far and only 33 were published last year. At the same time, I have received 92 books from publishers and many of these are still on hand awaiting interested reviewers.

As a repetitive plea, I am always looking for new reviewers and to re-establish contact with those who have provided reviews in the past. Without these people, my job would be impossible. If any available new titles (marked † in the New Titles) are of interest, please let me know. Even if they have been assigned, I will try to find something similar for you.

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***Canadian Association of Herpetologists Bulletin* Fall 1996**

Volume 10, Number 2, features a lead article on "Legislation pertaining to the collection, study and keeping of amphibians and reptiles in Canada" by Anthony Russell which includes responses from all provincial and territorial governments except Federal, Nova Scotia and Ontario which did not reply to the request for this information. A "News from Here and There" section contains the account "An honorary Canadian Far Afield - Herpetology at La Sierra University [Riverside, California]" by Hinrich Kaiser. A "Meetings" section features "Herpetologists in the Deep South: The 76th Annual Meeting of the ASIH [American Society of Ichthyologists and Herpetologists] in New Orleans" by Heather Gray; "A report on the Combined 1st Annual WGARCC [Working Group on Amphibian and Reptile Conservation in Canada] and 6th Annual DAPCAN [Declining Amphibian Populations in Canada: IUCN/SSC Task Force] Conference (University of Calgary Oct. 5-7, 1996)" by Sheri Watson, Larry Powell, and Janice James); "Declining Amphibians and the World Conservation Congress" [IUCN = World Conservation Union; Montreal 11-23 October] by David Green; and "World Congress of Herpetology [to be held in Prague in 1997]. A "Miscellany" section contains

"What are rubber boas and why?" by Robert St. Clair; "COSEWIC Update [including a new checklist of amphibians and reptiles of Canada with many recent nomenclatureal changes, although the new genus suggested for the Smooth Green Snake, *Liochlorophis* Oldham and Smith 1991 (Bulletin of the Maryland Herpetological Society 27(4): 201-215) is not included] by David M. Green; and "Request for observations and/or other records of anuran behaviour" by Jim Duncan. The issue concludes with "Thesis Abstracts in Canadian Herpetology": Robert St. Clair. 1996. How developmental environment affects life history in box turtles. Ph.D. thesis, University of Oklahoma; and Patrick Galois. 1996. Turtle nest sensory perception by raccoon (*Procyon lotor*) and striped skunk (*Mephitis mephitis*): an approach through discrimination learning of potential nest clues. Ph.D. McGill University. Membership in the Canadian Association of Herpetologists is \$10.00 per year (students \$5.00) and is available from Dr. Patrick T. Gregory, Treasurer CAH/ACH, Department of Biology, University of Victoria, British Columbia V8W 2Y2.

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Biodiversity Priorities from the Perspective of Canadian Agriculture: Ten Commandments¹

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Biodiversity priorities for Canadian agriculture are to: (1) preserve vanishing genetic diversity of domesticated species and their wild relatives using *ex situ* techniques; (2) conserve wild crop relatives in nature; (3) protect wild habitats, which supply natural pools of pollinators, beneficial soil organisms and control agents of crop pests, and which may harbour as yet unidentified economically valuable species; (4) expand environmentally-friendly agriculture, including low-input and organic agriculture, integrated pest management and soil conservation; (5) minimize the impacts of agricultural practices that degrade planetary life-support systems; (6) employ the biodiversity enhancing properties of crop diversification; (7) minimize risks from release of genetically engineered organisms; (8) develop sustainability as a concept of benefit to both biodiversity and agriculture; (9) promote harmony between agriculture and environmentalism by making biodiversity and the protection of wildlife sustainably profitable; and (10) invest in biodiversity research.

Key Words: Biodiversity, Canada, conservation, environmentalism, genetic engineering, germplasm, sustainable agriculture.

Agriculture and the food industry constitute an economic cornerstone of Canada, accounting for sales of over \$60 billion annually, 8% of the Gross National Product, a third of Canada's trade surplus, and employment of 15% of the labour force (including 280 000 farmers and over a million in the food processing sector) (Science Council 1991; Reid 1995). Unfortunately, until recently the environmental costs for these benefits have not been well known. Of all human activities, agriculture is thought by some to have the greatest detrimental effect on biodiversity (Schultz et al. 1994). This is the result of clearing forests and draining wetlands, displacing natural vegetation with crops, introducing weeds, and destabilizing ecosystems with fertilizers, insecticides, fungicides, and herbicides. Of course, without the food produced by these activities, the cost in human suffering would be enormous. Nevertheless, there are substantial costs associated with agriculture in Canada. The agri-food sector is responsible for about 11% of total energy consumption (of which 38% is dedicated to application of agrochemicals) and a very large proportion of water use (almost 90% on the Prairies) (Science Council 1991). Estimates of the annual cost of soil erosion from farming activities in Canada range from \$125 million to over a billion dollars (Science Council 1991). About 85% of Canada's wetlands have been drained and converted to agricul-

tural use, a substantial cost since these resources are valued in the billions of dollars (Environment Canada 1991). There are, however, at present no rigorous methods for conducting benefit-cost analysis associated with endangering and eliminating species, habitats and ecosystems. The continuing erosion of biodiversity threatens the economic foundations of agriculture and the future welfare of Canada. The biodiversity of all organisms - animals and microbes as well as plants, is critical to agriculture, although this presentation is concerned mainly with the importance of higher plants.

Canada is the second largest country in the world, and not surprisingly harbours large proportions of the planet's wilderness: 24% of the wetlands, 20% of the freshwater, and 10% of the forests (Biodiversity Working Group 1995). However, 90% of Canada's land cannot support any kind of agriculture, 5% is severely limited in crop production potential, less than 2.5% of the total area of Canada is prime agricultural land, and much of this has succumbed to urban development (Science Council 1991). Agriculture currently covers 7% of the total land base of Canada (Reid 1995), and Acton (1995) suggested that Canada may already be approaching its upper limit of farmland development. It might seem that if such a small proportion of Canada is used for agriculture, the biodiversity problem associated with

¹This paper was originally presented as part of a symposium, "Biodiversity and Conservation in Canada," held at the annual meeting of the Canadian Botanical Association/ L'Association botanique du Canada, in Charlottetown, Prince Edward Island, on 24 June 1996. The ten commandments theme has been employed to provoke reflection on fundamental human values concerning the natural world, and certainly no spiritual disrespect is intended.

TABLE 1. Ten commandments of agricultural biodiversity¹.



1. Thou shalt save endangered crop germplasm in genebanks.
2. Thou shalt save germplasm of wild crop relatives, in nature.
3. Thou shalt protect wild habitats, which furnish agriculturally valuable organisms.
4. Thou shalt conduct agriculture in ways friendly to the environment.
5. Thou shalt not harm the planet, nor the ecological systems that maintain its viability.
6. Thou shalt cultivate many different crops, in recognition that diversification promotes biodiversity.
7. Thou shalt not create forms of life harmful to biodiversity.
8. Thou shalt maintain biodiversity through sustainable agriculture.
9. Thou shalt promote harmony between agriculture and environmentalism.
10. Thou shalt support biodiversity research.

¹As noted in the text, this review is from the viewpoint of botany. Commandments mentioning “crops” generally apply also to livestock. Table 2.

agriculture is limited. Unfortunately 1) it is precisely where agriculture is localized that there are major threats to biodiversity; 2) as prime agricultural land is urbanized there is pressure to use marginal lands; and 3) the detrimental effects of agriculture spill over to non-agricultural lands.

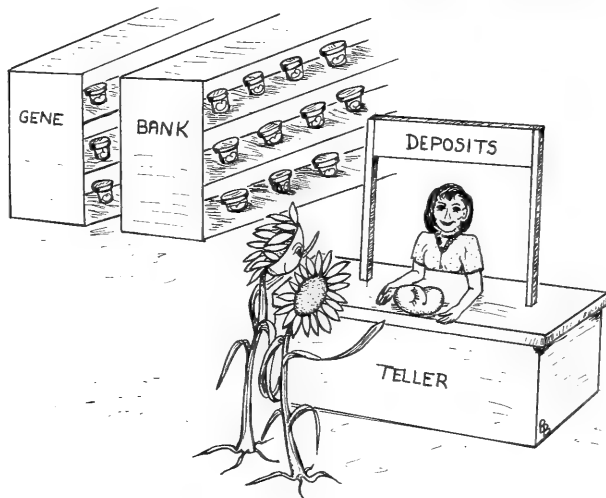
An additional misconception needs to be addressed: the fact that Canada has far fewer endangered species than tropical lands, so that it would appear that our attention should be focussed on the tropics. However, from the point of view of agriculture in Canada, 1) the foreign species of interest that most deserve protection

are in temperate Eurasia, not in the tropics; 2) Canada has many wild species that should be protected because of their potential for economic benefit for Canadians; and 3) as explained below, the threat to species numbers, while important, is but one of several aspects of biodiversity degradation which deserve immediate attention in Canada.

In the following presentation, 10 major issues that concern the relationship of biodiversity and agriculture are examined. As an abbreviated action plan for dealing with these issues, 10 “commandments” addressing these issues are presented (Table 1).

Issue 1: *Ex Situ* Preservation of Endangered Genetic Resources of Crops and Their Relatives

Thou shalt save endangered crop germplasm in genebanks.



The genetic heritage provided by both wild and domesticated organisms is essential for agricultural purposes. Most crops require periodic rejuvenation by plant breeding, to thrive under changing consumer and industrial preferences, altered cultural practices, environmental changes, and evolving pests and diseases. Germplasm in related wild species, many of which are unfortunately in danger of extinction, is the ultimate source of genetic renewal. "Preserving biodiversity of relevant plant species is in effect an inexpensive insurance policy to safeguard future low-cost supplies of food" (Abelson 1991). There is no crop for which a sufficient range of germplasm has been preserved for potential needs (Frankel and Bennett 1970). It has been estimated that perhaps 20 000 higher plant species are edible, and of these 3 000 are regularly consumed (Vietmeyer 1990). However, very few of these 3 000 are adequately represented by germplasm collections (Hawksworth 1995). Unfortunately an unprecedented elimination of wild species is occurring, comparable to the mass extinctions that marked Earth's geological epochs (Myers 1979; Wilson 1985), and these disappearing wild species include crop relatives representing critically important germplasm. It is estimated that there are 74 extinctions of species every day, or 27 000 annually (Wilson 1992), a frequency considered 1 000 to 10 000 times faster than the natural rate (Biodiversity Working Group 1995).

From the point of view of breeding Canadian crops, the most important wild biodiversity is represented by wild crop relatives of our major crops. These occur predominantly in warm-temperate areas of the world, mostly in Eurasia, where population pressures are decimating natural biodiversity. Wild relatives of the relatively few important native American crops (notably corn, potato, peppers, tomato and sunflower) are also being subjected to habitat reduction. While preserving habitats that sustain wild crop relatives is almost always the best way of ensuring the survival of genetic resources, it is clear that unless rescued, most wild germplasm critical to modern crops will disappear. Considerable important germplasm seems destined to survive only in gene banks. Canada's national germplasm centre, Plant Gene Resources of Canada located in Ottawa (to be moved to Saskatoon), has over 100 000 accessions, many collected from outside Canada, that are critical for our major crops (Small 1995; Baillargeon et al. 1996). There is also a clonal collection of more than 2 500 accessions (for vegetatively reproduced fruit crops such as apples and strawberries) currently being moved from the Smithfield Experimental Farm near Trenton, Ontario, to the Greenhouse and Processing Crops Research Centre at Harrow, Ontario (Warner 1996). There are also specialized research collections at various research stations across Canada. Witt (1985) credited the U.S.

Department of Agriculture's germplasm collection of about 400 000 samples with increased crop productivity worth \$1 billion annually. Prescott-Allen and Prescott-Allen (1986) assigned a higher value to wild germplasm with respect to U.S. crop improvement: \$6.036 billion annually. It is clear, therefore, that preservation of crop germplasm is not merely an ethical imperative - it is also a wise business investment. Gene "banks" are aptly named, because some of the seeds they contain have genes capable of improving the value of crop plants by millions, even billions, of dollars. The finding of a wild maize, *Zea diploperennis*, and the invaluable genes it carries for corn improvement, has been estimated to have increased the value of corn by 4.4 billion dollars annually worldwide (Small and Cayouette 1992). The discovery of a dwarfing gene in a wheat variety is credited with literally saving over 100 million people from starvation (Witt 1985). For additional examples of the value of wild germplasm, see Shands and Wiesner (1991, 1992).

Historical occurrences of crop failures due to inadequate crop resistance also show that germplasm resources are invaluable. The classic illustration of the danger of crop vulnerability due to genetic depauperization is the potato failure stemming from potato blight in the mid-1800s. The Irish great potato famine (1845-1848) led to widespread starvation (1.5 million died) and social upheaval (2.5 million emigrated). Following the potato famine, a tiny American louse, called grape phylloxera (*Daktulosphaira vitifoliae*), attacked the root systems of European grapes, again resulting in crop devastation (Rhoades 1994). In 1969-1970 and again in 1980, southern corn leaf blight (*Helminthosporium maydis*) on cytoplasmic male sterile hybrid corn caused over a billion dollar loss to the U.S. corn crop (Williams and Levings 1992). In 1979 the blue mold infestation of tobacco, that nearly decimated Central American and Cuban crops and badly damaged U.S. crops, also reduced Canadian production by hundreds of millions of dollars.

Just as wild species are endangered, so are old-fashioned varieties and land races of domesticated species. For example, of the 7000 cultivars of apples that were grown at the beginning of this century, nearly 5000 are now extinct (Sollenberger 1992). So-called "obsolete" cultivars frequently vanish without a trace. This loss can be far-reaching, because modern breeders often sacrifice taste and novelty for such considerations as resistance to damage during long-distance transportation. Old-time varieties of vegetables and fruits are commonly too tender to withstand mechanical harvesting and ripen irregularly, providing a long-term harvest. Such qualities, although desirable in the home garden, are not valued by large-scale producers, who have concentrated on high-yielding, disease-resistant hybrids.

Fortunately, organizations have developed to save the older, heirloom varieties of plants. These organizations provide citizens with the opportunity to participate in the maintenance of particular varieties. The best known in Canada is Seeds of Diversity Canada (commonly called by its previous name, the Heritage Seed Program), which has over 2000 volunteer members. Those wishing to assist in this work may write to: P.O. Box 36, Station Q, Toronto, Ontario M4T 2C7. Compared to old cultivars, preservation of old livestock breeds is on a much smaller scale. One organization dealing with preservation of domesticated breeds of animals that aren't suited to today's agricultural practices is: Rare Breeds Canada, General Delivery, Campbellford, Ontario K0L 1L0.

Do crop cultivars and domesticated animals

deserve equal consideration to wild organisms with respect to the issue of conservation? Domesticated creatures by definition are the result of "artificial" selection and, apart from their economic importance, the absence of "naturalness" might seem to warrant less concern. However, domestication is a type of enslavement symbiosis, which in principle is perfectly comparable to natural examples of this phenomenon, such as between some ant species and their cultivated fungi (Higgs and Jarman 1969). If the enslaved species in natural symbioses deserve to be sustained, it would seem that man's domesticates also merit consideration. Those who own pet animals will readily sympathize with the concept of a "social contract" requiring man to exercise care for his domesticates. Domesticated plants and animals are an integral part of the issue of biodiversity conservation.

Issue 2: *In situ* Germplasm Conservation of Wild Crop Relatives

Thou shalt save
germplasm of wild
crop relatives,
in nature.



An outstanding example of *in situ* germplasm conservation is provided by a 139 000 ha nature area, the Sierra de Manantlán Biosphere Reserve in southern Mexico, created in 1987 with the specific intent of conserving the natural habitat of the wild corn *Zea diploperennis* (Guzmán and Iltis 1991). This is one of only a few preserves in the world established specifically to maintain wild germplasm related to crops. The conservation of this single wild species has proven enormously beneficial not just for corn but also for a wide range of other forms of life in the park. Within the area of the Mexican preserve there are over 1800 other species of flowering plants, as well as jaguars, ocelots, parrots, and thousands of other animal species. By preserving a small proportion (ca. 0.07%) of the area of Mexico for a single species, a sizable proportion (ca. 9%) of the huge flora of Mexico has also been at least partially protected (Small and Cayouette 1992).

The conservation of wild Canadian germplasm has been a concern to Canadian agriculture for many

years. Canada's Expert Committee on Plant and Microbial Genetic Resources has identified use, erosion and conservation of Canadian native genetic resources as an important priority (Reid 1995). In 1992, the Canadian Agricultural Services Coordinating Committee endorsed a strategy to conserve native wild Canadian plants of economic significance (Reid 1995).

In Canada, there is excellent potential for employing parks as *in situ* genebanks. It has been estimated that there are 400 indigenous species of potential economic value in Canada's national parks (Prescott-Allen and Prescott-Allen 1984). For wild plants, native preserves are usually greatly preferable over seed and garden preservation, because of the difficulty and expense of maintaining much diversity under artificial circumstances. It should not be thought, however, that existing parks in Canada and elsewhere suffice, even if they were to acquire the status of genebanks, since wild relatives of crops are known to occur in many areas outside designated

parks. Indeed, only about 1% of the world's biodiversity occurs within designated park areas (Roberts 1988), although perhaps three quarters of Canada's known economically important species occur in parks (Catling 1996). As outlined by Catling (1996), however, parks provide inadequate preservation for some genetic resources because of the impact of recreational uses and lack of monitoring.

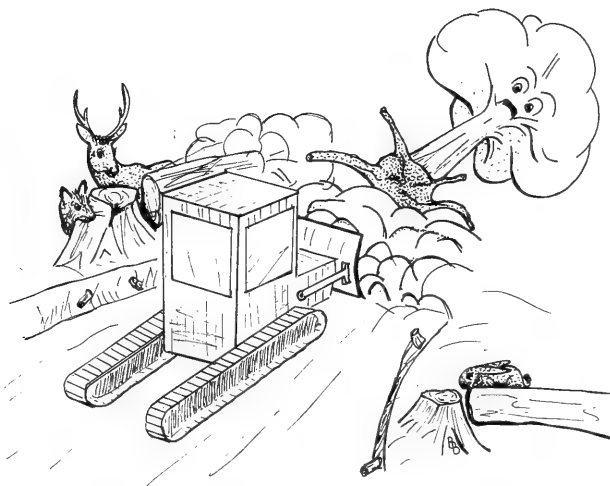
It needs to be stressed that conservation in nature (*in situ*) and outside of the natural habitat (*ex situ*) are complementary approaches (Damania 1996). As explained above, gene banking is the only alternative for many important wild plants on the verge of extinction, and for many crops it is unrealistic to expect that an adequate representation of wild relatives can be preserved in nature (Hoyt 1988). As noted below, however, there are many agriculturally significant wild plant species in Canada, and on the whole *in situ* conservation of their genetic resources is most appropriate.

There are important crop relatives indigenous to Canada, and indeed Canada has been designated as a heritage centre for several crops (Davidson 1995; Small and Catling 1996). A few native Canadian plants have been major contributors to the

germplasm of some minor or moderately valuable crops that are both cultivated and harvested from natural stands, notably blueberries and cranberries (*Vaccinium*), saskatoon (*Amelanchier*), and wild-rice (*Zizania*). Several fruit-producing genera indigenous to Canada represent valuable northern germplasm of cultivated crop plants, notably for strawberries (*Fragaria*), raspberries and blackberries (*Rubus*), gooseberries (*Ribes*), grapes (*Vitis*), cherries and plums (*Prunus*), and ground-cherries (*Physalis*). More likely than not, anyone drinking beer is indebted to wild Manitoba hop (*Humulus lupulus*), whose germplasm is incorporated in many of the world's hop cultivars (Small 1997). Other wild Canadian plants offer potential for development. Ginseng (*Panax quinquefolius*) has become an important cultivated crop. Several genera of trees indigenous to Canada provide well known commercial harvests, such as maple syrup (*Acer*), and walnuts and butternuts (*Juglans*). Fern fiddleheads (*Matteuccia*) are also harvested from the wild and sold commercially, especially in Nova Scotia and New Brunswick. Turner (1981) provided a list of 100 wild species meriting commercial development for use as food.

Issue 3: Habitat Conservation

Thou shalt
protect wild
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which furnish
agriculturally
valuable
organisms.



Lawton (1991) evaluated the principal arguments for preservation of habitats, and concluded that the most important economic justification is that "humankind needs to set aside sufficiently large areas of the planet to make sure that we carry as many as possible of the yet-to-be identified minority of useful species forward into the next century and beyond." In the previous section the importance of wild preserves specifically for germplasm of obvious usefulness for crops was emphasized. Of course, one can't protect potential new crops that we don't know about today, and so agriculture has a vested interest in protecting all wild habitats that may harbour new

crops. Wild habitats also supply natural pools of pollinators, beneficial soil organisms and control agents of crop pests that are of great value to agriculture. As emphasized in a later section, wild habitats also provide invaluable services at the ecosystem level.

More than half the habitable surface of Earth has been significantly altered by human activity (Hannah and Bowles 1995), and indeed no part of the world can be considered as truly undisturbed (Heywood et al. 1995). Agriculture is by no means the only force that has brought about the changes: forestry, road building, industrial development, urbanization and pollution have also been potent forces. At least in the

developing world, agricultural expansion has been alleged to be the main habitat-displacing activity (Pearce and Moran 1994).

The Canadian Committee on Ecological Areas developed a registry of significant sites that provides a framework for conserving habitats essential for the preservation of biodiversity. Of the 177 ecoregions recognized, 148 (83%) have 1% of their areas protected (Gauthier 1992). Canada already has about 3500 publicly owned protected areas, covering about 788 000 km², with an additional 10 000 km² held by non-government groups (Reid 1995). Nevertheless, considerable work is still required to develop a comprehensive, nation-wide system of ecological reserves in Canada (Catling 1996). In Canada, more than 90% of Canadian agriculture is located within five ecological zones: Pacific Maritime, Boreal Plain, Prairie, Mixed-Wood Plain and Atlantic Maritime (Reid 1995). These areas obviously deserve particular attention.

Paradoxically, agriculture as formerly practised often significantly benefitted surrounding biodiversity (Hampicke 1978). By planting small cultivated plots amidst various landscapes, transitional habitats were created that tended not only to preserve but also to promote diversity. Only in the last few decades has this tendency been dramatically reversed. It is ironic that most of the world's current destruction of habitat is to advance agriculture, forestry, and industry, all of which are in danger of destroying bio-resources that are critical for their own future progress.

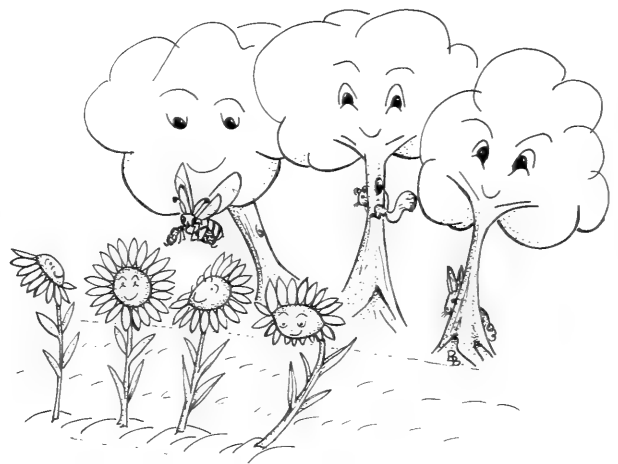
Much of the landscape of our planet has been fragmented into mosaics of human-dominated vegetation interspersed with small patches of more or less natural vegetation. One minimal measure for protection of biodiversity that needs to be undertaken is very simple: protect representative areas of land-

scape, along with their unique habitats and native species, in preserves. Even fragments of landscape can be critical, and in this regard, the agricultural woodlot assumes some significance. Woodlots are not necessarily representative of natural habitats, but they can often serve as a partial substitute. Natural woodlots are excellent for preservation of some biota, and can be maintained profitably by farmers.

Monocultural woodlots are of much less benefit to maintaining a variety of wildlife than are natural mixed woodlands. However, there are some environmental benefits to all types of woodlots, as noted below, and harvest of cultivated trees may result in sparing wild trees. Fast-growing planted trees, especially willows and poplars, can be sources of biomass and wood products, including pulp for paper, secondary wood products, and even feed preparations for livestock and food for humans (Small 1995). Canadian-bred hybrid willows have yielded up to 3.7 t/ha/year of biomass, and it has been estimated "that if the willows were grown on just 10 percent of Canada's marginal farmland, farmers could produce the raw material for enough fuel to replace 10 nuclear generating plants and much of the gasoline used in Canada" (Gogerty 1991), results that could be of indirect benefit to the environment. Canada has large tracts of marginal, unproductive farmland that could be used for growing selected trees. Curiously, "more than half of farmers in western Canada think their woodlots are nearly worthless" (Dietz and Henkes 1992). It is important to note that this is an avenue of crop diversification open to the farmer, not just to agroforestry, and as noted by Loughton et al. (1991) "may have enormous relevance to the future of farming." Moreover, farmers could grow the trees as shelterbelts, getting the benefits of crop protection, erosion prevention, and moisture retention, as well as a crop of trees.

Issue 4: Environmentally-friendly Agriculture

Thou shalt conduct agriculture in ways friendly to the environment.



Many of the environmental problems caused by agriculture today are due to a half century of the

agricultural sciences ignoring "all but the most superficial ecological relationships in most cropping

TABLE 2. Examples of environmentally-friendly solutions to agriculturally-related problems

Problems	Causes	Solutions
SOIL: wind and water erosion, salinization, declining soil organic matter levels, soil acidification, deterioration in soil structure, reduction in fertility and productivity	Cultivating up and down steep slopes, failure to maintain adequate soil cover, excessive tillage, failure to control surface water runoff, unnecessary summerfallowing combined with tillage for weed control, irrigation of unsuitable soils, excessive irrigation, over-reliance on shallow-rooted crops	Reduce cultivated summerfallow, reduce tillage, initiate sustainable use of marginal and fragile lands, crop rotation, retain crop residues, use cover crops, shelter-belts, conservation tillage practices, develop crop varieties appropriate to environments
WATER: toxic contamination, eutrophication	Improper management: accumulation of pesticide residues and metabolites, misuse of agricultural nutrients, effluents from livestock manures and food/crop processing plants	Strengthen guidelines for pesticide residues, chemical fertilizers and manures; improve crop varieties minimizing need for fertilizers; integrated pest management; improve environmental monitoring; improve soil testing; education targeted to farmers
WILDLIFE AND HABITAT REDUCTION	Lack of appreciation of beneficial roles of non-cultivated lands; lack of policies promoting wildlife management	Promote shelterbelts, farm woodlots, uncultivated margins around sloughs and marshes; farmer education; programs to compensate farmers for maintaining wetlands and other habitats and for damage from wildlife
AIR AND CLIMATE: changes in air chemistry leading to climate change	Intensive energy consumption leads to release of greenhouse gases (CO ₂ , NO ₂ , CH ₄ , trophospheric ozone) & chlorofluorocarbons which trap heat and lead to global warming and ozone depletion; poor soil management leading to declining organic matter, increasing atmospheric gases; ruminants and animal manures release methane gas; agrochemicals contributing potentially damaging chemicals to atmosphere	Maintain soil organic matter levels as a sink for atmospheric carbon (e.g. longer crop rotations, reduce summerfallowing, reduce tillage, reduce crop residue burning); develop techniques to reduce methane production; reduce energy consumption; improve management of agricultural chemicals

systems" (Paul and Robertson 1989). Attempts to remedy this problem have led to supposedly new approaches, denoted by such adjectives as "alternative," "holistic," "ecological," "low-input" and "organic" agriculture (Vandermeer 1995). A principal approach, sustainable agriculture, is dealt with below as a separate issue, because of its key importance. Environmentally-friendly approaches are largely based on pest, soil, water and farm management practices which protect health and environmental quality and promote natural biological processes, with the result that the negative effects of agriculture on the environment and biodiversity are reduced or even eliminated. Table 2 analyses some common problems that agriculture poses to biodiversity and lists some environmentally-friendly measures (e.g., as recommended by Leblond 1990 and Government of Canada 1991).

The intensity of agricultural practices in a given area determines whether or not biodiversity is negatively impacted, and the extent to which there are

harmful effects. (However, high productivity achieved through intensive agriculture may reduce the pressure to encroach upon non-agricultural lands.) Rangelands are more compatible with many forms of natural biodiversity than are intensive cropping systems such as commonly employed for the cereals. In rangelands, native vegetation is allowed to grow, although frequently weedy species and deliberately introduced foreign range species displace much of the native vegetation. With more intensively managed lands, competing higher plants are generally not allowed to survive. Particularly where agricultural lands are used intensively, one needs to examine possibilities of minimizing damage to adjacent areas of wild vegetation.

Biodiversity is normally reduced when natural habitats are converted to permanent cultivation. Several standard agricultural practices are especially destructive to natural biodiversity. Of course, simply clearing land, by definition, eliminates above-ground wild plants. In the soil, mechanical

cultivation destroys most invertebrate groups. Agrochemicals further reduces the taxonomic and genetic diversity of soil organisms. By contrast, zero or minimum tillage practices at least allow very substantial co-existence of crops with many soil species. Maintaining a constant ground cover prevents soil erosion, although fallowing land periodically, as once commonly practiced, may be detrimental. While low-input agriculture is of benefit to invertebrates and other species that live in the soil, on the whole it has restricted effects on higher plant biodiversity, since appreciable presence of either weeds or native species of plants is not economical. Minimum or no-till practices tend to conserve the world's shrinking supply of fossil fuels, while lessening the damaging effects of burning fuels on the atmosphere.

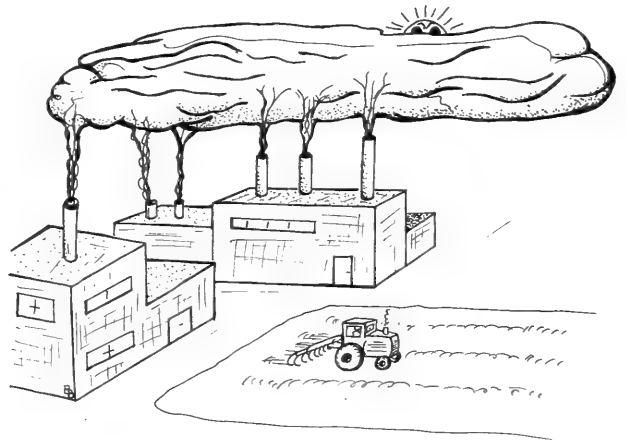
Organic agriculture, meaning agriculture practiced without the use of pesticides and herbicides (sometimes also without inorganic fertilizers), is probably often advantageous to biodiversity. Since the diminished use of agrochemicals results in less transfer of these chemicals to surrounding wildlands, biodiversity benefits. However, mankind has not yet learned how to achieve the high productivity of most crops that is needed to avoid world starvation through just the use of organic agricultural techniques. The decreased productivity often associated with organic techniques could result in increased use of marginal lands and consequent harm to biodiversity. The growing attraction of organic agriculture largely reflects the current public perception that foods

grown "naturally" are healthier and safer. So-called "organic" and "green" products have captured a small but growing consumer market. "Integrated pest management" represents a compromise between organic and traditional agriculture. Biological control agents and management practices are used to the extent that seems practical, but pesticide use is permitted as an ancillary control measure.

Just as crops can be bred to meet the needs of mankind, it is possible to breed crops that are relatively environmentally friendly. It is desirable to have crops that can withstand insect pests with a minimum of insecticide application, can compete well with weeds to reduce herbicide application, can tolerate minimum-till or zero-till cultivation, and indeed will remain productive with little or no application of fertilizer (Henkes 1992). An example of the complexities that deserve consideration is illustrated with respect to sulphur fertilization. Carbonylsulphide is oxidized in the stratosphere to produce sulphate aerosols which influence the Earth's radiation budget by scattering sunlight back into space and interfering with stratospheric ozone (Hofman 1990). Crops that require considerable sulphur, such as rape, may be linked to increased biogenic emissions (Hofman 1990), and have been characterized as constituting a biodiversity risk (Rennenberg 1995). It is possible, however, to choose varieties of crops that are relatively benign. For example, there are dramatic differences among alfalfa cultivars with respect to their need for sulphur fertilization (Small and Lefkovitch 1982).

Issue 5: Threatened Ecosystem Services

Thou shalt not harm the planet, nor the ecological systems that maintain its viability.



Natural ecosystems supply society in general and agriculture in particular with a variety of so-called "free services." These include maintenance of the gaseous quality of the atmosphere, climate regulation, generation and conservation of fertile soils, dispersal and breakdown of wastes, and cycling of nutrients. The consequences of disturbing ecosystem

functions are, of course, potentially catastrophic. The results include increased emissions of greenhouse gases, increased UV radiation, soil degradation by wind, water and pollution, loss of sediments and nutrients from land to water, accumulation of toxins, and loss of biodiversity. With the possible exceptions of increased accumulation of CO_2 , which

increases photosynthesis, and the possible benefits in some regions of warming of climate, these changes are generally extremely deleterious to agriculture. One of the pressing unanswered questions concerning ecosystems is the extent to which cultivated plants can replace natural vegetation without damaging the essential ecosystem services that are supplied (Mooney et al. 1995). Agricultural ecosystems are very much simpler than natural ecosystems, and almost certainly are more susceptible to fluctuation and instability, for example from pathogens. Nevertheless, the concept that there are many more species in nature than are essential for ecosystem maintenance - the so-called "redundant species hypothesis" (Walker 1992; Lawton and Brown 1993), does suggest that at least some level of loss of the world's natural biodiversity is tolerable. It is not possible at present to predict what level of biodiversity and landscape destruction or modification can be tolerated, that is, what level will not lead to irrepara-

ble catastrophic consequences. Ehrlich and Ehrlich (1981) formulated the "rivet hypothesis" to address this uncertainty. According to this, it is foolish to remove species just as it would be foolish to remove rivets from an airplane's wing. Although there are more rivets in an airplane's wing than are necessary for the wing to function, continually removing rivets is certain to lead to disaster. About 11% of the world's terrestrial surface is now covered with crops (Mooney et al. 1995), and this figure is certain to increase to meet the demands of population growth. A further 26% of the world's land area is used as permanent pasture (World Resources Institute 1994), so that agriculture already occupies more than a third of all land. Global agreements to which Canada is a signatory (e.g., Convention on Biological Diversity, Framework Convention on Climate Change, Montreal Protocol on Substances that Deplete the Ozone Layer) are encouraging signs that mankind recognizes the gravity of the issue.

Issue 6: Promoting Biodiversity Through Crop Diversification

Thou shalt cultivate
many different crops,
in recognition that
diversification
promotes
biodiversity.



In many countries, including Canada, just a few crops, particularly cereals, oilseeds, fibre crops and forage crops, tend to be grown in very large monocultures. Monocultures increase the efficiency of management, facilitate harvesting, and simplify marketing. However, the homogenization of large regions dramatically decreases biodiversity. Much of the negative influence of modern agriculture is related to the practice of cultivating huge monocultures. The highest known yields in terrestrial systems occur in species monocultures, but these require substantial amounts of energy, fertilizer and pesticide (Heywood 1995). Acton (1995) identified the move from small, low-mechanized mixed farms to larger, highly mechanized farms growing monocultures as the main cause of the degradation of Canada's agricultural soils. Canada will likely be called on to supply increasing amounts of cereals and oilseeds to

meet the world's growing demands in future years, and it is unrealistic to expect that the areas devoted to monocultures will decrease. What is important, however, is to develop additional crops. This is desirable from the point of view of biodiversity because the more heterogeneous the landscape the better are the chances for promoting a diversity of organisms and microecosystems. Surpluses and depressed markets have brought home the danger of overdependence on a restricted number of agricultural commodities in the modern world, so that diversification is also a good policy for agriculture.

Estimates of the number of plant species used in agriculture in the world vary. Ehrlich and Wilson (1991) quoted a figure of about 7000 plant species employed for food, and noted that at least several times that number have edible parts. Pimentel (1991) concluded that 25 000 species are cultivated for vari-

ous purposes, including food. That is, about one of every 10 species of higher plant is presently actually cultivated for some purpose. Most estimates of the number of species that are primarily responsible for feeding the world vary from about 7 to 30, although Prescott-Allen and Prescott-Allen (1990) suggest the number is actually around 100. In any event, it is evident that both the world and its constituent countries have become overdependent on a limited number of crops. It is abundantly clear that there are huge risks in relying on a narrow range of crops. A mixture of crops is an excellent strategy for maintaining productivity across good and bad years for the individual crops (e.g. Vandermeer 1988). Indeed, subsistence farmers, whose survival often depends on the success of their crops, have traditionally minimized risk by planting several species and varieties. Agricultural diversification is good for both agriculture and biodiversity, and therefore is a strategy that needs to be vigorously encouraged.

Thousands of plant species have been identified as potentially important commercial crops, and there are tens of thousand of unevaluated species with potential for new drugs, food, feed, industrial feedstock, fuel, and fiber (Jolliff and Snapp 1988). Thirty thousand species have been used in traditional medicine, providing enormous scope for cultivating

new pharmacological crops (Heywood et al. 1995). There is a widespread belief that the industrial use of crops offers North American agriculture the most promising avenue for expansion, although erratic price incentives and lack of processors are important obstacles (Gogerty 1991). There is growing interest in using plant products as biofuels and industrial chemicals (U.S. Department Agriculture 1993). Many plants contain essential oils useful for perfumery, flavoring, medicinals, and as industrial raw material for conversion to other chemicals. Oils and waxes are important plant extractives. Vegetable oils are in competition with petroleum-based synthetics, and find uses such as coatings, plasticizers, surface active agents, and lubricants. There is potential for replacement of some petrochemicals with "botanochemicals" (Wang and Huffman 1981).

Canada's native vegetation offers interesting agricultural possibilities that haven't been sufficiently considered. For example, native halophytes (especially certain Chenopodiaceae such as *Atriplex* species) could be domesticated for growth in saline environments that preclude any other type of vegetation. Halophytic forage could be used to exploit the widespread salinized soils in the prairie provinces, which represent a badly degraded habitat of limited use to either agriculture or wildlife.

Issue 7: Risks and Benefits of Genetic Engineering

Thou shalt not create forms of life harmful to biodiversity.



It is often pointed out that by selecting plants, animals and microorganisms for thousands of years, mankind has practised genetic engineering since the dawn of agriculture. However, this has been limited to choosing gene recombinations from sexual reproduction, as well as gene mutations in vegetatively propagated species. In the 1970s recombinant DNA techniques made it possible to transfer genes between highly unrelated species. Techniques were

also developed to alter specific nucleotides within a gene and to insert artificially synthesised DNA sequences into species. Modern genetic engineering allows novelties to be created that were not achievable through conventional plant breeding. There are now potatoes that have acquired genes from viruses, bacteria, quite unrelated higher plants, and even humans (Dale and Irwin 1995). Living modified organisms (LMOs for short, sometime referred to as

TABLE 3. Perils and promise of genetic engineering for biodiversity.

Beneficial

1. More productive plants may lessen encroachment on natural areas.
2. More resistant plants and creation of crop symbionts should reduce need for agrochemicals.
3. Organisms will be created that clean up pollution.
4. All wild species are now potentially useful as sources of valuable genes, so the perceived value of wild biodiversity is increased.

Detrimental

1. Adapting crops to agriculturally marginal areas may mean more sacrifice of natural areas.
2. Danger of unintended creation of superpests and consequent reduction or elimination of natural biota.
3. Crops engineered to be herbicide resistant may encourage use of herbicides.
4. Escape of genes to wild plants may change natural genetic balance and so modify natural biodiversity.
5. Danger of toxins being produced and affecting wildlife.
6. Mankind's manipulation of nature often produces unforeseen problems, sometimes disastrously.
7. Some people will mistakenly believe that the capacity to create genes in the laboratory means that wild germplasm and hence wild biodiversity are no longer needed.

genetically modified organisms or GMOs) are thought to have considerable potential for good and at least some potential for harm (Edge 1994). Conceivably, all plant species can contribute genes to crops, and thus in a sense modern genetic engineering is associated with a greatly increased significance for all wild plants. A vision of "molecular farms" has emerged, with crops genetically engineered to produce industrial enzymes, biodegradable plastics, lubricants, specialty fibers, biofuels, drugs and vaccines - indeed, a very wide range of pharmaceutical, industrial, and food products (McCormick 1992; Brown 1996). There is potential for development of extremely useful organisms that would assist agriculture, including crop symbionts (such as especially efficient mycorrhizas) and biological control agents (Hoffman and Carroll 1995). The major application of biotechnology to agriculture is currently transgenic crops (Rissler and Mellon 1996), and hundreds of different transgenic plants have already been released (Kahl and Winter 1995). Transgenic crops have been synthesized which incorporate traits for disease resistance, longer shelf life, and tolerance to herbicides. While this greatly increased capacity to create novel forms of life has inspired some to visualize the benefits of creating healthier and more productive crops and livestock, at the same time it has raised prospects of negative impact, particularly on biodiversity. "As often happens... the momentum of commerce overtakes society's ability to fully discuss the risks and benefits of a new technology... the genie of agricultural biotechnology is out of the bottle" (Rissler and Mellon 1996). Table 3 summarizes the good and bad potential of genetic engineering for biodiversity, and the following expands on some of these points.

Some individuals object on principle to the creation of LMOs. Their argument is that transferring genes between highly unrelated organisms - for example between plants and animals, is unnatural,

and since at least some LMOs are bound to find their way into nature, this represents a kind of unacceptable contamination of biodiversity. Aside from philosophical problems, there is fear that the creation of LMOs will have dangerous results for biodiversity. Duvick (1996) posed the question of whether or not such biotechnology will have consequences for nature as dangerous as the ozone hole. He wrote "Mistakes certainly will be made in applications of biotechnology, just because of the unpredictability of nature with its manifold interactive facets. Undesirable consequences of molecular tinkering indeed will ensue, somewhere, sometime."

An alarming, if improbable, possibility is that plants engineered to contain virus particles might facilitate the creation of new viruses pathogenic on crops and wild plants. When viral genes are transferred to confer virus resistance, the virus could become "encapsidated" in the coat protein synthesized by the transgenic plant, which may in turn result in the virus being transmitted to new host plants (Dale and Irwin 1995; see page 64 in Rissler and Mellon 1996 for a good presentation). Furthermore, it is conceivable that recombination could generate a virus with an altered host range, and hence with unpredictable consequences for biodiversity.

One concern is that transgenic crops will simply be able to grow in a considerably wider range of habitats or circumstances from which they were previously excluded (e.g., saline soils, arid lands, cold climates), and so crops would displace areas currently supporting wild biodiversity. As pointed out in the introduction, most of Canada is considered unsuitable for agriculture, and so widening the adaptive range of crops offers particular economic benefits. Keighery (1995) concluded that transgenic plants developed to survive in many of the agriculturally marginal areas of Australia pose a serious threat to Australia's biodiversity. Australia, with more than

25 000 species of indigenous flowering plants, is considerably more diverse than Canada, with less than 4 000 indigenous species, and so the problem of endangering biodiversity is less serious. Nevertheless, as Canada's limited good agricultural areas succumb to urbanization, the possibility of growing productive crops in places currently considered marginal will inevitably increase pressure on the biodiversity of wildlands.

Perhaps the most troubling possibility is that of creating new "superweeds." A simple scenario is that some transgenic plants could become more invasive. However, our most important crops are usually so highly modified from their wild ancestors that single gene transfers are most unlikely to confer the ability to thrive outside of cultivation. A more plausible situation is that hybridization between a crop and a weedy relative could invigorate the latter. Gene transfer to wild populations could significantly displace natural genetic variation in populations of some wild species. This could be particularly harmful in centres of diversity of wild crop relatives. Before this era of sophisticated gene transfer, some weeds became invigorated genetically by natural hybridization with a related crop (for examples see Small 1984). The possibility of even more dramatic invigoration from gene transfer from LMOs to weeds needs to be examined seriously. Herbicide tolerance has been bred into some crops by genetic engineering. However, a herbicide-resistant oat (*Avena fatua*) could be dangerous, as wild oats, already a difficult to control weed, could suddenly acquire herbicide tolerance and be extremely problematical. Transgenic crops have acquired genes for resistance to diseases and pests, and tolerance to such conditions as drought, salinity, cold and heat, and these traits also if transferred to weeds could in theory result in superweeds.

Another potential problem is that transgenics could become toxic to wildlife (as well, as course, to humans). Hypothetically, for example, a potato (*Solanum tuberosum*) variety transformed with a gene for disease resistance might trigger a dormant gene for alkaloid production. If that gene is transferred to wild *Solanum* species, these could, at least theoretically, poison herbivores feeding on those species. Plants that are deliberately engineered to express toxic drugs and pesticides are more likely to pose problems for wildlife. For example, corn plants designed to produce toxins would be an obvious danger to birds. The use of designer crops to produce pharmaceuticals, vaccines, drugs, enzymes and other chemicals important to health and nutrition is both exciting and frightening. The importance of crops that improve the welfare of humans is obvious, but the potential impact on biodiversity of the inevitable increase of such chemicals in the environment is very difficult to assess.

Still another perceived danger is that the creation of herbicide-resistant crops could lead to increased use of herbicides. Since herbicide firms have a vested interest in increasing sales of their particular brands, they would support gene technology requiring the use of their herbicides, and this might detract from the overall effort to reduce herbicide use. Furthermore, such advanced biotechnology might make large farming operations even more profitable than at present, at the expense of small family farms, reducing social well-being.

To date, genetic engineering of crops has been carried out for high-profile crops that are grown in confined areas, but much less so for plants that may have value in open pastures and rangelands, and that are able to grow in marginal areas. Range and pasture species are usually much harderier than field and orchard crops, and consequently more competitive genetically-engineered range and pasture species would almost certainly tend to become even more feral and aggressive than their non-engineered counterparts.

The above discussion stresses potential of genetic engineering of plants for adverse consequences for natural biodiversity. However, there is also potential for benefit. Critically endangered species have almost always become genetically depauperate, and therefore are especially vulnerable to pests and diseases. Just as genetic engineering transfers genes for resistance to pests and diseases to crops, the same could be done for selected endangered species. Atmospheric pollution is of growing concern, and is thought to be a frequent cause of die-back of many species. Perhaps it is possible to transfer pollutant-resistant genes to wild species (of course, it would be preferable to eliminate atmospheric pollution). Living modified organisms could be valuable for biodiversity for such uses as treating industrial wastewater and air emissions and to degrade toxic compounds or take up toxic metals at contaminated waste sites, thus restoring habitats for biodiversity (Edge 1994).

Transgenic plants do not currently pose a significant problem for biodiversity in North America. Public suspicion of bio-engineered organisms is very high, and there are international attempts underway to develop protocols for safely introducing transgenic species. Discussion (some would say debate) of the issue is sometimes polarized, and unfortunately sometimes based on ignorance. It is essential that appropriate research be conducted into the impact of transgenic plants in Canada where there is a possibility of threatening biodiversity. It is also important that biologists in Canada become knowledgeable about the issue, since the public will increasingly demand informed opinion. Genetic engineering epitomizes mankind's search for technological fixes for the world's problems, and many proponents of biotechnology have concluded "that the development

of transgenic crops should be the primary response to the challenges of twenty-first century agriculture" (Rissler and Mellon 1996). "An important question

for the future is whether engineered crops will facilitate or retard a global transition to a sustainable agriculture" (Rissler and Mellon 1996).

Issue 8: Sustainability

Thou shalt maintain biodiversity through sustainable agriculture.



Ideally, human society should be an integral part of nature, respecting and preserving the diversity of life, consuming no more than can be replenished, and leaving a heritage of a healthy world to future generations. This is the essence of sustainability, which finds its chief expression today in agriculture. Although "sustainable agriculture" (or occasionally "ecological agriculture") was popularized in the 1980s, it traces some of its roots to the conservation movement of the 1920s, the "limits to growth" thinking of the 1960s and 1970s, and the antitechnology orientation of environmental activists (Lu and Kelly 1995). The adverse side effects of some aspects of conventional agriculture had become painfully evident by the 1980s. Modern agricultural practices often make intensive use of advanced technologies and highly specialized, mechanized and capital- and chemical-intensive inputs dependent on nonrenewable stocks of fossil fuels. Negative impacts on society have included threats to human health and food safety. Negative impacts on the environment have included soil erosion, depletion of natural resources, environmental contamination, and loss of biodiversity.

Biologists need to understand the very recent historical context in which the word sustainability has been used. A seminal event was the release of the highly influential report of The World Commission on Environment and Development set up by the United Nations (Brundtland Commission 1987). This referred to "sustainable development," and combined ecological issues with problems of economics and social justice. Thus while environmental

sustainability may be a straightforward concept, sustainable development and its derivatives, including sustainable agriculture, are not (Goodland 1995). The concept of sustainability is considered by some to be inherently flawed (e.g. Gatto 1995). At least in theory, one can envision human society organized and operating to provide social justice to all while limiting its consumption of space and resources in ways that do not compromise biodiversity in all of its senses. On the other hand, there are those who believe that sustainable development is a concept that serves to camouflage the necessary and inevitable sacrifices that humankind must institute to avoid degrading the world to an unacceptable level. Indeed, "sustainable growth" is an oxymoron (Daly 1990a, 1990b), since the world's resources and carrying capacity are limited. However, a concept of "development" as transformation towards desired objectives can be consistent with genuine sustainability. Working towards a practical implementation of the concept of sustainability is obviously necessary, as is the need for collective actions among all scientists, economists, technologists, and indeed all citizens.

The phrase sustainable agriculture is contentious, and variously defined (Keeney 1990; Science Council 1991). To ecologists, sustainability means just what it says, an ecologically balanced, natural, stable system which is buffered against long-term degradation. To most agriculturists, however, "sustainable agriculture" implies more than just the sustainability of agriculture: also included are social and economic concerns, particularly quality of life, equity

TABLE 4. A vision of agricultural sustainability for Canada (Leblond 1990).

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1. A secure and well-managed resource base of agricultural land and soil to support the long-term productivity and competitiveness of the Canadian agri-food industry.
 2. An agri-food sector that contributes to improved surface and groundwater quality through the use of environmentally sustainable production and processing practices.
 3. An agri-food sector that has adapted itself to, and manages on a sustainable basis, the surface and groundwater resources available to it.
 4. Canada's agri-food sector and wildlife resources to be managed for sustainability and long-term mutual benefits.
 5. An agri-food sector that is able to respond to air and climate change and which does not itself contribute to air and climate problems.
 6. An agri-food sector that is more energy efficient, less polluting and less dependent on non-renewable energy resources.
 7. A major reduction in the impact of pollution on air, soil and water resources used by the agri-food sector. An agri-food sector that has minimized its contribution to air, soil and water degradation and pollution.
 8. Canada to have an accessible and sufficiently diversified genetic resource base that can be effectively utilized to assure the sustainability of agriculture for future generations.
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of benefits for various interest groups and, most particularly, the economic viability of farming systems (Lu and Kelly 1995). At present, abandoning the use of agrochemicals (so-called organic agriculture) in North America could result in yield reductions of 50 to 100% depending on the crop (Lu and Kelly 1995). Most advocates of sustainable agriculture hold that by reducing the use of agrochemicals and adopting various alternative environmentally-friendly agriculture strategies it is possible to achieve an acceptable compromise between degree of environmental and biodiversity damage on the one hand, and profitability of agriculture on the other. Idealists would hold that it is even possible to eliminate all environmental damage associated with agriculture, and so genuinely have a stable agro-ecosystem comparable to natural, healthy self-sustaining ecosystems. Pessimists would hold that growth of agricultural yield efficiency, particularly for food, cannot keep pace with population increase, and so genuine long-term sustainability is not achievable under the present circumstances.

The Rio Convention on Biological Diversity defined "sustainable use" as: "the use of components of biological diversity in a way and at a rate that does not lead to the long-term decline of biological diversity, thereby maintaining its potential to meet the needs and aspirations of present and future gen-

erations" (Heywood et al. 1995). As pointed out by Heywood et al. (1995), however, most uses of biodiversity lead to at least some change or loss.

Although variously defined, sustainable agriculture is generally understood as a compromise of efficiency and profitability of production of quality products on the one hand, and on the other, conservation of nonrenewable resources and respect for biological, physical and social environments (Geng et al. 1990; Keeney 1990). Elements of concern include environmental sustainability (air, water, soil, biodiversity), economic sustainability (particularly for the agri-food sector), and social sustainability (particularly for farmers). The working definition of sustainable agriculture agreed upon by a Canadian federal and provincial ministers committee (Leblond 1990) is: "Sustainable agri-food systems are those that are economically viable, and meet society's need for safe and nutritious food, while conserving or enhancing Canada's natural resources and the quality of the environment for future generations."

Interest in sustainable agriculture has been growing in the last decade in Canada (Hill and MacRae 1992). An excellent analysis of agricultural sustainability in Canada, with numerous recommendations, was produced by a federal-provincial committee (Leblond 1990). The principal goals envisioned by this committee are given in Table 4.

Issue 9: Profitability as a Key to Harmony Between Agriculture and Environmentalism

Thou shalt promote harmony between agriculture and environmentalism.



Biodiversity is economically important because it provides biological resources (Beattie 1991). The Earth's biota is an indispensable agricultural resource, furnishing germplasm for presently cultivated species, a wealth of species exploitable in the future as cultivated plants, pollinators, and biocontrol agents, and essential functions in the maintenance of ecosystems supporting agriculture (Ehrlich and Wilson 1991). The concept of biodiversity, and the underlying habitat preservation upon which the maintenance of biodiversity is dependent, has become the heart of an economic argument. As stated by Webb (1991) "how much does wildlife have to be worth before it will generate more income per unit area than can come from conventional agriculture?" Paul Hawken (1993), however, has pointed out at great length the hidden costs that must be considered in exploiting bioresources. As he has stated, "Our human destiny is inextricably linked to the actions of all other living things. Respecting this principle is the fundamental challenge in changing the nature of business."

Up until the present, human activities destructive of biodiversity have appeared to be highly profitable — at least in the short term. Thus agriculture, ranching, urbanization and forestry, which have often degraded biodiversity, have resulted in economic prosperity for Canadians. It is human nature to oppose policies that reduce one's wealth, and not surprisingly the environmental movement has been opposed by many vested interests concerned that policies good for biodiversity were bad for them. As discussed by Montgomery and Pollack (1996), the most contentious environmental issue is simply who will pay for conservation of biodiversity (the "public good/ private cost" dilemma). Increasingly in Canada, efforts are underway to obtain the cooperation of industry and business in protecting biodiversity (see Schultz et al. 1994 for good examples). In particular, given the immense importance of agri-

business in Canada, it is vital wherever possible to enlist agricultural industries as allies rather than as enemies. With appropriate policies, this is feasible.

Farmers are in fact the principal managers of a portion of Canada's rural environment, hence of appreciable biodiversity. A frequently advanced policy is to enlist farmers as trustees of the environment over which they have control, and provide them with compensation for the valuable functions of their property. In maintaining agricultural land, and its associated soil, water, and in some cases wetlands and wildlife shelterbelts, farmers are in fact providing free services to society, and doing so under conditions of increasing economic duress. Many farmers have a special affinity for nature, and can be appropriate stewards of their land given the existence of a supportive social contract that recognizes the dual roles that should be played: provision of agricultural commodities and maintenance of a healthy environment. Canadians spend over \$5 billion annually on wildlife activities (Science Council 1991), and it would be appropriate for more of these leisure dollars to go towards encouraging farmers to maintain the environment for nature recreation.

Another suggestion relates to agricultural land occupied by hobby farms. Such land is not lost to agriculture, constituting a kind of land bank, saving farmland for possible future use. Appropriate policies, such as tax concessions coupled with discouragement of development, are needed (Science Council 1991).

A trend that needs to be assessed for its impact on biodiversity is the increase in Canada of large-scale agriculture, as corporations take over and amalgamate thousands of small farms into larger operations. In 1941 there were 732 832 farms in Canada, but by the last census (1986) this had declined to 293 089, and the reduction has continued (Reid 1995). In Canada, the corporate concentration of the agrifood sector is greater than in the

United States (MacRae et al. 1993). The resulting exodus from rural environments is disturbing from a social perspective, but also disquieting from the point of view of biodiversity and sustainability, since small farms by their nature are friendlier to nature than the huge monocultures of corporate farms. Moreover, there is the human factor. Can a

competitive profit-driven corporation afford to adopt environmentally-friendly techniques? A welcome trend is so-called "corporate greening" — a movement by corporations to provide merchandise that has been produced in an environmentally benign fashion, such as organic products (MacRae et al. 1993).

Issue 10: Biodiversity Research as an Agricultural Priority

Thou shalt support
biodiversity
research.



As stated by Tisdell (1995), "our current knowledge about biodiversity conservation lags far behind our capacity to destroy Nature." There is widespread recognition of the lack of adequate knowledge regarding biodiversity and the urgent need to increase research in Canada (e.g., Biodiversity Science Assessment Team 1994). "Ecosystem research in Canada is scattered, fragmented or for many ecosystems, non-existent. Hence, our understanding of how both modified and natural ecosystems work is too superficial to formulate and support scientifically based programs of ecological sustainability for the country and the planet" (Mosquin and Whiting 1992).

The total annual expenditure on research and development for the Canadian agri-food sector has exceeded a half billion dollars in some years, about two-thirds of this provided by the federal government (Science Council 1991). However, the current trend of shrinking resources, staff reductions and short-term mandates is a concern. Associated with this "funding crunch" is an increased reliance on the private sector for contract work, most of which is necessarily narrowly profit-oriented. "There is widespread agreement that sustainable agriculture cannot be adequately studied by short-term, piecemeal projects. The nature of the questions demands long-term research drawing on the expertise of multidisciplinary teams and broadly grounded generalists" (Science Council 1991). Moreover, there is a need for novel approaches to examine environmentally-friendly agricultural systems, and unfortunately

in a climate of downsizing and focusing on core activities, it is very difficult to obtain the necessary support for new endeavours.

Taxonomy, ecology, population genetics and conservation biology are the disciplines essential for the study of biodiversity, but the number of specialists in these fields is shrinking in Canada. Expertise in these fields is distributed in Canada in various federal and provincial government departments, the universities, and the private sector. It is imperative to coordinate and concentrate these activities to maximize benefits for biodiversity (Small et al. 1995). As pointed out above, the welfare of biodiversity and agriculture in Canada are inextricably linked and, from both an economic and a human viewpoint, research investment in the interrelationships of agriculture and biodiversity should be of the highest priority.

Final Word

Commercial agriculture today is commonly blamed for much of the negative impact on biodiversity caused by humans. This needs to be kept in perspective, however. Agriculture has allowed the huge human population of the world to be fed. More than that, the efficiency of modern agriculture, that is its ability to produce large yields on relatively small acreages, saves much of the landscape, which otherwise would have to be used to grow food. In Canada, our very high standard of living is substantially attributable to agriculture. The challenge today is to adopt practices that will allow us to continue to prosper while reversing the unacceptable and potentially

catastrophic decline of all of the components of biodiversity, without which the quality and perhaps even the possibility of human survival is in doubt. Fortunately there are many initiatives currently underway, both within Canada and as international ventures, that are intended to address the problems raised in this review. Three key Agriculture and Agri-Food documents currently at the advanced draft stage deserve mention: Agriculture and Agri-Food Canada (AAFC) three-year action plan for biodiversity; AAFC initiatives relating to biodiversity; and Biodiversity initiatives involving Canadian agricultural producers. As well, a draft strategy entitled Sustainable agriculture and agri-food development in Canada is in preparation.

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Rare and Endangered Plants and Their Habitats in Canada¹

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Approximately one-third of the native vascular plant taxa known to occur in Canada (1009 of 3269 taxa) were classified as being nationally rare by Argus and Pryer (1990). Of these, 147 taxa are endemics, and 68 are in urgent need of conservation. Most provinces and territories also have lists of species that are considered to be rare within those jurisdictions. Where Natural Heritage Programs exist (e.g., British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, Quebec), detailed work on the status, distribution, demographics, ecological requirements, and threats is being conducted, and this work, in conjunction with that by interested field botanists and researchers, has resulted in revisions to the provincial lists of rarities. Refinements have also occurred in the criteria by which rarity is assessed, with the trends being toward increased quantification of status, inclusion of more ecological information, fuller consideration of threats to populations, and standardization among jurisdictions within North America. However, legislative tools for ensuring the protection of these rare species and their habitats are generally inadequate. Very little work has been done on determining the status of non-vascular plants anywhere in Canada. Also, far less work has been done on rare habitats than on their constituent species. This situation is changing slowly (e.g., extensive work on alvar communities in Ontario, Lake Athabasca dunes in Alberta and Saskatchewan, Atlantic Coastal Plain shoreline communities in Nova Scotia and Ontario). However, there are numerous habitats that require detailed attention, some of these being rare or diminishing (tall-grass prairies), while others are more common but support populations of rare plant species (calcareous cliffs, flats, shores, and peatlands).

Key Words: Rare plants, rare habitats, conservation, biodiversity, Canada.

Rare plants and their habitats, as well as rare habitats *per se*, comprise integral components of the biodiversity of any geographically defined area. The original focus for concern over the reduction of biodiversity came from the depauperization of biotas in the tropical forests, where land use practices are jeopardizing the continued existence of numerous species, many of which have not even been described. Even in north temperate, boreal, and Arctic floras, which are better known taxonomically, new species are discovered occasionally (e.g., *Carex juniperorum*, Catling et al. 1993). The level of knowledge about most species (even the common ones), especially with regard to ecological requirements and life history attributes, is very limited.

The Canadian Biodiversity Strategy (Environment Canada 1995b) takes a broad view of the concept of biodiversity, including not only the traditional idea of species richness, but also encompassing ecosystem diversity at all scales, along with the ecological processes that enable those systems and their component species to function and interact. Rare species constitute a part of this concept, as do the habitats and landscapes in which they occur. At least two of the Strategy's goals have direct bearing on the conservation of rare plants and rare habitats; i.e., to

“conserve biodiversity and use biological resources in a sustainable manner”, and to “improve our understanding of ecosystems and increase our resource management capability” (Environment Canada 1995b, page 3). Conservation actions require knowledge, often at several scales of ecological organization (e.g., population, species, vegetation community, landscape). The cataloguing of the elements of diversity that may be at risk, followed by studies of their ecological requirements and/or composition/structure/function, are the first steps toward generating credible conservation actions.

Over the past two decades, considerable progress has been made in the determination of the status of many species in the Canadian vascular plant flora. This has been due, in large part, to the efforts of dedicated staff members at the National Museum of Natural Sciences in Ottawa (now, the Canadian Museum of Nature), led by George Argus, who initiated the Rare and Endangered Plants Project, and facilitated the completion of the provincial/territorial and national lists (see Table 1). The importance of this work should not be underestimated. These lists have resulted in concerted efforts to rediscover historical populations, search for additional populations of the listed species, and study the demo-

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Table 1. Numbers of rare vascular plant taxa in Canadian provinces and territories.

Province/Territory	Number of Rare Species	Source
Alberta (AB)	350;	Argus and White 1978;
	360	Packer and Bradley 1984
British Columbia (BC)	816	Straley et al. 1985
Manitoba (MB)	291	White and Johnson 1980
New Brunswick (NB)	207	Hinds 1983
Newfoundland-island (NF)	271	Bouchard et al. 1991
Northwest Territories (NT)	206	McJannet et al. 1995
Nova Scotia (NS)	219	Maher et al. 1978
Ontario (ON)	542	Argus et al. 1982-1987
Prince Edward Island (PE)	191	Day and Catling 1991
Quebec (QC)	408	Bouchard et al. 1983
Saskatchewan (SK)	300	Maher et al. 1979
Yukon Territory (YT)	313	Douglas et al. 1981
Canada	1009	Argus and Pryer 1990

graphics and ecological requirements of some listed species.

There are several groups of plants that have not received the same level of attention, however, including the mosses, liverworts, and algae. Fungi and lichens also lack sufficient data to enable the determination of their species' status, with rare exceptions (see Appendix I, which contains four species of lichens for which national status has been determined). Recent phytogeographical research in some regions of Canada [e.g., the Gulf of St. Lawrence (Belland 1987), Ontario (Ireland and Ley 1992)] has begun to lay the groundwork for an understanding of the status and ecology of mosses. Preliminary or provisional lists of rare mosses have now been prepared for Ontario (Ontario Ministry of Natural Resources 1996*) and Alberta (J. Gould, personal communication), and similar lists of probable or potential rarities are being prepared for the macrolichens and liverworts of Alberta (J. Gould, personal communication). However, much work remains to be done before a set of provincial/territorial lists of rarities can be produced for these elements of the flora.

Some provinces have recently established Conservation Data Centres or Natural Heritage Information Centres to track and coordinate information on the status of rare species and habitats. British Columbia, Alberta, Saskatchewan, Manitoba, Ontario, and Quebec have established (or are in the process of establishing) such agencies. These agencies assign a status ranking to each organism and community type for which there is sufficient data. They also form part of a continent-wide network that also includes all of the state Natural Heritage Programs. The Nature Conservancy (USA) is a major partner with the Canadian Conservation Data Centres, having established database standards, and coordi-

nated the designation of global ranks for all species. The subnational (in our case, provincial) ranks for each species are determined by the individual Conservation Data Centres, with their collaborators.

In many ways, the determination of the status of habitats is more difficult than the determination of the status of species. This is due, in large part, to the lack of a single comprehensive classification system for vegetation communities. Because communities reflect responses of multiple species to multiple abiotic and biotic factors and interactions, the development of classification schemes for communities is a highly complex, and somewhat subjective, task. Nevertheless, at regional scales, it is possible to produce classification schemes that encompass the range of variation in vegetation. Analytical tools that facilitate the mathematical/statistical analysis of large data sets have been used to accomplish this task in various parts of Canada. Classification schemes now exist for forest communities in various provinces, and wetlands have been classified in some areas, as well. Preliminary comprehensive classification schemes for all known vegetation types have been developed for southern Ontario, with the aim of ranking those community types that are rare and in need of conservation attention (Wasył Bakowsky, personal communication). As long as the infrequently occurring community types are recognized and included in the sampling phase of ecosystem classification studies, their attributes can be compared with those of more common community types. As a result, clues regarding the reasons for their rarity (perhaps including such features as unusual species associations, infrequent substrate types, localized microclimatic conditions, etc.) will emerge. However, even in areas where no vegetation analysis has been conducted, or where no ecosystem classification system exists, certain community types stand out as being unusual or rare. Usually, this is due to the presence of infrequent but characteristic and consistent landform/species associations. Long before detailed studies of such communities had occurred, the remnant tall-grass prairies of southwestern Ontario and the alvars of southern Ontario were recognized as infrequent to rare, and also endangered, community types. The same is true for limestone, dolomite, and serpentine cliff, talus, and slope communities in many parts of Canada.

Determination of Rarity

Until recently, the definition of rarity has been qualitative. This is due, at least in part, to the fact that there are several mechanisms by which a species or vegetation type might have achieved its current distribution. Rarity may be either an inherent characteristic of a species or vegetation community, or induced by extrinsic factors, such as incompatible land uses that change the features needed for sur-

vival. Early attempts to arrive at general and comprehensive hypotheses to explain rarity were too simplistic. These invoked historical biogeographic explanations or genetic impoverishment mechanisms, which, however, were rarely supported by much data. Drury (1980), Stebbins (1980), and Brouillet (1985) have provided useful reviews of these early hypotheses. In fact, except in cases where the habitat itself is rare, and therefore, by extension, species adapted to those habitat conditions are also rare, each case of rarity has some unique attributes. Even in cases where communities of rare species appear to share general habitat preferences and requirements, and a common biogeographic history (e.g., Atlantic Coastal Plain communities in Nova Scotia and Ontario), the individual species in those communities differ substantially in their abundances, and in their inter- and intra-site microdistributions. Thus, it has been difficult to develop a general set of rules that can be applied to all rarity patterns.

Rarity is also a relative concept that must be defined in a geographic context. In the present discussion, rarity has been dealt with at a provincial/territorial and national scale. A species or vegetation community that is rare in Saskatchewan, for example, may be common (at least locally) in an adjacent geographical area, such as Alberta or Montana. However, this does not detract from the fact that the species or community is an important component of the biodiversity of Saskatchewan, and may require conservation attention there (cf. Wilson 1993).

The series of provincial/territorial and national lists of rare plants serves as a starting point for more formalized recognition of the status of these plants. A national committee (Committee on the Status of Endangered Wildlife in Canada; COSEWIC), composed of representatives from each of the provincial and territorial government wildlife agencies, four federal agencies (Canadian Museum of Nature, Canadian Parks Service, Canadian Wildlife Service, Canadian Department of Fisheries and Oceans), and three national conservation agencies (Canadian Nature Federation, Canadian Wildlife Federation, World Wildlife Fund Canada), deliberates on the national status of plants (and other wildlife, in the broad sense), and also plays a major role in allocating funds for the preparation of status reports that provide the background data necessary for these deliberations. An annual update on Canadian species at risk is issued by COSEWIC (Anonymous 1996*; see Appendix I for the current status assessments for plants). COSEWIC uses a simple qualitative scale of rarity categories. The "extinct" and "extirpated" categories are self-explanatory. The three categories with which we are most concerned here are "endangered", "threatened", and "vulnerable" (synonymous with their earlier use of the term "rare"). "Endangered" species are those "... facing imminent

extirpation or extinction". "Threatened" species are "... likely to become endangered if limiting factors are not reversed". "Vulnerable" species are "... of special concern because of characteristics that make it [them] particularly sensitive to human activities or natural events" (Anonymous 1996*). This committee also designates species as "Not at Risk" when, after a status report has been completed, the evidence indicates that there are more and/or larger populations than previously thought, and that those populations are not under threat from exploitation or incompatible land uses. After such studies, the status of some species still cannot be determined adequately, because of insufficient data, and they are placed in an "Indeterminate" category. Such species are candidates for future re-assessment.

At present, COSEWIC designations have no force in law. However, federal protection of endangered species may be realized through legislation such as the Wild Animal and Plant Protection Act (Environment Canada 1991), and the Canadian Endangered Species Protection Act (Environment Canada 1995a). Canada is also a signatory nation to the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Argus (1978) summarized the plant species regulated under this convention. All Canadian species covered by CITES are within its Appendix II, which requires export permits from the country of origin. All native Canadian cacti (Cactaceae) and orchids (Orchidaceae) are contained within that Appendix, as is American Ginseng (*Panax quinquefolium*). However, CITES does not regulate intra- or inter-provincial trade in any of these species.

Recently, with the establishment of Conservation Data Centres (also known as Natural Heritage Information Centres) in some provinces, there has been a trend toward increasing quantification of status assessments. These agencies assign status ranks at both a global scale [in concert with The Nature Conservancy (USA) and the other North American Natural Heritage Programs (as the equivalent American agencies are called)] and a provincial scale. Three categories of relevance here are used to designate degrees of rarity. The rarest species in a province (subnational region), ranked as "S1", are usually found in five or fewer extant populations within that province, or have very few remaining individuals within the populations that are known to exist. "S1" can be considered to be roughly equivalent to 'Endangered' as used by COSEWIC. These species are extremely susceptible to extirpation (or in the case of endemics, extinction). Species classed as "S2" are very rare, usually with between 6 and 20 extant occurrences in the province, or with large populations in fewer than 6 sites. These taxa may also be susceptible to extirpation or extinction, and may be considered analogous to "Threatened"

species in non-quantitative ranking systems. Species listed as "S3" occur in 21 to 100 locations within the province, or they have large populations in cases where fewer than 21 locations are known. These species are rare to uncommon, but are not in immediate danger of extirpation.

Some provinces, such as Ontario, have also established technical committees, composed of biologists, to assist with the determination of status, for the purpose of official listing or regulation of species under appropriate legislation. It is important to note that the status lists prepared by the Conservation Data Centres do not automatically enter into regulation. On occasion, the status rankings assigned by specialists are not reflected in legislative regulations. Regulation requires vetting through a political process.

Rare Plants

Preliminary inventories of the rare vascular plants of each province and territory (with the exception of Labrador), and for Canada as a whole, have been completed (Table 1). These lists provide a point of departure for detailed work on the ecology and conservation requirements for the rare species, and the data on which they are based enable priority-setting for conservation actions. The list of nationally rare vascular plants contains 1009 taxa, a relatively high proportion of the 3269 species comprising the native vascular plant flora of Canada (Argus and Pryer 1990). Roughly similar proportions of the native floras of each province and territory have been considered to be rare in those jurisdictions. In most cases, species that have been included on these lists have been found to be legitimately rare, in spite of increased field activity. Only in a few cases have species been found to be significantly more common than originally thought, and these cases often involve taxonomic groups that are perceived to be difficult. One such example is Drooping Sedge, *Carex prasina*, which was known from only two recent Ontario locations in 1982 (Ball and White 1982). It was also considered to be rare in Quebec (Bouchard et al. 1983), and was considered to be nationally rare as recently as 1990 (Argus and Pryer 1990). Subsequent to the publication of the rare plant lists and atlases, a flurry of field activity resulted in the discovery of numerous populations of this species, such that it is no longer considered to be rare (Oldham 1996; J. Gagnon, personal communication).

One hundred and forty-seven of the nationally rare vascular plant taxa are endemics, restricted in their distributions to small geographic areas (e.g., Queen Charlotte Islands, Lake Athabaska sand dunes, High Arctic islands, Newfoundland's Northern Peninsula, Great Lakes near-shore swales). Forty of these endemic taxa are considered to be of top conservation priority (Argus and Pryer 1990), implying that they may be in imminent danger of extinction with-

out conservation efforts. It is likely that many of these taxa have always been rare and restricted in distribution. However, there are situations where endemic taxa are being endangered by human actions, such as the drainage or development of Great Lakes marshes. These situations require immediate remedial action to prevent the extirpation of populations, or the ultimate extinction of these taxa.

Many of the rare species on the national list occur near the edges of their ranges in Canada. These are often referred to as peripheral species. This, however, does not diminish their importance as components of biodiversity. British Columbia and Ontario are particularly rich in nationally rare species (426 and 355, respectively). Large proportions of these rare species are peripheral in their distributions. These include British Columbia species with affinities to the California Floristic Province, including the Cascade Ranges [portions of the Coast Forest Region (Rowe 1972); Hickman 1993]. They also include Ontario species of the Deciduous Forest Region (also known as Southern Deciduous Forest or Carolinian Forest), with affinities to the northeastern and north-central United States, the upper Mississippi Valley, and the northern Appalachian Mountains (Allen et al. 1990; Maycock 1963; Rowe 1972). Substantial proportions of the other provincial/territorial sets of rare species also are comprised of species near the limits of their geographic distributions.

Habitats of Rare Plants

In order to ascertain patterns among the habitat preferences of Canadian rare vascular plants, each provincial and territorial rare plant list was examined, and the habitat descriptions contained therein were scored for each species. There are inherent difficulties with this approach. Habitat descriptions generally are derived from specimen labels. Thus, variability in detail on the labels will lead to a substantial level of generalization in the habitat descriptions published in the lists. Also, the various authors of the provincial and territorial lists will have had different concepts of some habitat or community types (this was especially evident in wetland types, such as bogs, fens, and conifer swamps). The approach taken here has been, again, to generalize as much as possible, while maintaining habitat categories that will still provide some insight into habitat preferences of rare species. Where highly specific ecological conditions are known to be required by a species, these have been maintained as distinct habitat categories (e.g., margins of hot springs, snowbeds, calcareous substrates). Because of the variability in detail in the data sources, a scale (1-3) has been used in Table 2, to indicate the relative frequency of rare species' habitat preferences within a province or territory. The range in number of habitat occurrences within each category in this scale is

TABLE 2. Habitats of the rare vascular plants of the provinces and territories of Canada.

Habitat Description	Province/Territory of Occurrence*											
	AB	BC	MB	NB	NF	NT	NS	ON	PE	QC	SK	YT
ARCTIC/SUBARCTIC												
Arctic/subarctic beaches/meadows	-	-	3	-	-	3	-	3	-	2	-	2
Arctic/subarctic/alpine tundra	1	3	3	-	-	3	-	1	-	2	1	3
ALPINE/SUBALPINE/MONTANE												
Alpine/subalpine meadows	3	3	-	1	1	3	-	-	-	1	-	3
Alpine/subalpine cliffs/rocky slopes/ talus/scree/outcrops	3	3	-	1	1	3	-	-	-	1	-	3
Alpine seepage areas	-	1	-	-	-	-	-	-	-	-	-	1
Snowfields/snowbeds	1	1	-	-	2	1	-	-	-	1	-	1
Margins of mineral springs	-	-	-	1	-	-	-	-	-	-	-	3
Margins of hot springs	1	1	-	-	-	1	-	-	-	-	-	1
Montane meadows/prairies	-	1	-	-	-	-	-	-	-	-	-	2
Montane slopes/outcrops	2	2	-	-	-	1	-	-	-	-	-	1
Montane/subalpine forests	2	1	-	-	-	-	-	-	-	1	-	-
OUTCROPS/BARRENS												
Rocky slopes/ridges/outcrops/barrens	3	3	3	3	3	3	3	3	1	3	3	2
Rocky slopes/ridges/outcrops/ barrens - dry	2	3	2	-	1	-	-	3	-	-	3	1
Rocky slopes/ridges/outcrops/ barrens - moist	1	2	1	-	-	1	3	1	-	-	1	1
Rocky slopes/ridges/outcrops/ barrens - calcareous	1	1	1	3	3	2	1	3	-	3	1	1
Rocky slopes/ridges/outcrops/ barrens - gypsum	-	-	-	1	-	-	1	-	-	-	-	-
Lava talus	-	1	-	-	-	-	-	-	-	-	-	-
Granite/gneiss cliffs/outcrops	1	-	-	-	1	-	1	1	-	1	1	1
Serpentine	-	1	-	-	1	-	-	-	-	1	-	-
Basalt	-	1	-	-	-	-	-	-	-	-	-	-
Shale	1	1	-	-	-	1	-	1	-	1	1	1
Schist	-	-	1	-	-	-	-	-	-	-	-	-
Sandstone	-	-	-	-	1	-	-	1	1	1	-	-
Slate	-	-	-	-	1	-	-	-	-	-	-	-
Quartzite	-	-	-	-	1	-	-	-	-	-	-	-
Siliceous rocks/soils	-	-	-	-	1	-	-	-	1	1	-	-
MEADOWS/PRAIRIES												
Open sandy/gravelly slopes/hills	3	3	3	1	1	1	1	2	1	1	3	1
Fields/meadows - dry	1	1	1	2	1	1	1	1	3	2	-	-
Fields/meadows - moist to wet	3	3	3	3	2	3	3	3	3	3	3	3
Fields/meadows - calcareous	1	1	1	1	1	1	1	-	1	1	1	1
Sagebrush hillsides	-	3	-	-	-	-	-	-	-	-	-	-
Dry prairies/grasslands/steppes	3	3	3	-	-	1	-	3	-	-	3	-
Moist prairies	-	-	1	-	-	-	-	3	-	-	1	-
Dry gravel	-	1	1	-	-	-	-	1	-	1	1	1
Dry acidic soil	1	-	-	-	-	-	-	1	-	-	-	-
MOIST TO WET, OPEN HABITATS, WETLANDS												
Moist to wet calcareous gravels/shores	1	1	1	2	2	-	1	1	-	1	1	1
Clay soil	1	1	1	-	1	-	-	1	-	1	1	-
Muddy shores/mudflats	2	2	1	-	-	-	-	1	-	1	1	1
Fresh-water marshes	2	2	1	1	1	2	1	2	1	2	1	1
Salt/brackish marshes	1	2	2	2	1	1	1	1	2	1	1	1
Saline/alkaline flats/floodplains/ meadows	2	2	1	-	-	3	-	1	-	-	1	2
Seepage areas/springs	1	1	1	-	1	-	1	1	1	1	1	-
Lakeshores/shorelines	3	3	3	3	3	3	3	3	3	3	3	2
Seashores/coastal beaches	-	2	-	2	3	1	1	-	2	2	-	-
Sea cliffs/bluffs/headlands	-	2	-	1	2	1	1	-	1	-	-	-
Shallow water (lakes, ponds, streams)	3	3	3	3	3	3	2	3	3	3	3	2

Continued

TABLE 2. (Continued).

Habitat Description	Province/Territory of Occurrence*											
	AB	BC	MB	NB	NF	NT	NS	ON	PE	QC	SK	YT
Shallow water - calcareous	1	-	1	1	1	-	1	1	1	-	1	1
Vernal pools	-	1	-	-	-	-	-	-	-	-	-	-
Coastal waters	-	1	-	-	-	-	-	-	-	-	-	-
Streamsides/sandbars/riparian floodplains	3	3	2	3	3	3	2	3	1	3	3	3
Waterfalls	-	1	-	-	-	-	-	1	-	-	-	-
Rapids	-	-	-	1	-	-	1	1	-	1	-	-
Ditches	1	1	1	1	-	1	1	1	1	1	1	-
Fens/sedge meadows	1	1	1	2	3	2	1	1	1	1	3	2
Swamps/wet woods	1	2	1	2	1	1	2	3	3	1	1	1
Bogs/muskeg/wet Black Spruce woods	2	3	3	2	1	2	2	2	2	3	3	3
DRY, OPEN HABITATS												
Sand dunes	1	2	1	1	1	1	1	2	2	1	2	1
Sand barrens/blow-outs	1	1	1	-	-	1	-	1	-	-	1	-
Burns	-	-	-	-	-	-	-	-	1	1	1	-
Thickets/brush/scrub	2	2	2	1	3	1	1	3	3	3	1	2
FORESTS AND SAVANNAHS												
Boreal forest (Jack Pine/upland Black Spruce/White Spruce)	-	1	-	1	1	1	1	1	1	1	2	-
Dry aspen woods	-	-	1	-	-	1	-	-	-	-	1	-
Moist coniferous forest	3	3	1	-	2	2	-	1	-	-	2	2
Moist/rich deciduous forest	1	1	1	3	1	-	3	3	1	3	2	1
Calcareous woods/hardwoods	-	-	1	1	-	-	-	1	-	1	-	-
Moist/rich mixed forest	-	-	2	1	-	-	1	2	1	1	2	-
Dry oak/oak-hickory woods	-	1	-	-	-	-	1	1	-	1	1	-
Oak-pine woods	-	-	-	-	-	-	-	1	-	1	-	-
Pine woods	1	1	-	-	1	-	-	1	1	1	2	-
Pine plantations	-	-	-	-	-	-	-	1	-	-	-	-
Red Juniper savannah	-	-	-	-	-	-	-	1	-	-	-	-
Oak savannah	-	-	-	-	-	-	-	2	-	-	-	-
Dry open woods	3	3	2	3	-	1	2	3	3	3	2	1
Moist/rich woods	3	2	2	-	-	1	-	2	2	-	1	-
Dry deciduous forest	-	-	-	1	-	-	-	1	1	1	-	-
EPIPHYTES AND PARASITES												
Epiphyte	-	1	-	-	-	-	-	-	-	-	-	-
Parasitic on <i>Alnus</i>	1	1	-	-	-	-	-	-	-	-	-	-
Parasitic on Apiaceae	-	-	-	-	-	-	-	1	-	-	-	-
Parasitic on <i>Arctostaphylos</i>	-	1	-	-	-	-	-	-	-	-	-	-
Parasitic on Asteraceae	1	1	1	-	-	-	-	1	-	-	-	-
Parasitic on Chenopodiaceae	-	1	-	-	-	-	-	-	-	-	-	-
Parasitic on Convolvulaceae	-	1	-	-	-	-	-	-	-	-	-	-
Parasitic on Fabaceae	-	1	-	-	-	-	-	1	-	-	-	-
Parasitic on <i>Fagus</i>	-	-	-	-	-	-	-	-	1	-	-	-
Parasitic on Lamiaceae	-	-	-	-	-	-	-	1	-	-	-	-
Parasitic on Linaceae	-	-	-	-	-	-	-	1	-	-	-	-
Parasitic on Lythraceae	-	-	-	-	-	-	-	1	-	-	-	-
Parasitic on Malvaceae	-	-	-	-	-	-	-	1	-	-	-	-
Parasitic on Onagraceae	-	-	-	-	-	-	-	1	-	-	-	-
Parasitic on <i>Picea</i>	-	-	-	-	1	-	-	-	-	-	-	-
Parasitic on Poaceae	-	-	-	-	-	-	-	1	-	-	-	-
Parasitic on Polygonaceae	-	-	-	-	-	-	-	1	-	-	-	-
Parasitic on <i>Quercus</i>	-	-	-	-	-	-	-	-	-	1	-	-
Parasitic on Rosaceae	-	-	-	-	-	-	-	1	-	-	-	-
Parasitic on conifers	-	1	-	-	-	-	-	-	-	-	-	-

*provincial and territorial abbreviations as in Table 1. Relative rankings (1-3) for habitat preferences of rare species are based on the following ranges (NB, NT: 1-7 reports [tallies] = 1; 8-14 = 2; 15+ = 3. AB, MB, NF, NS, PE, SK, YT: 1-9 = 1; 10-19 = 2; 20+ = 3. BC, ON, QC: 1-14 = 1; 15-29 = 2; 30+ = 3). See text.

province-dependent. Thus, a province with relatively few rare species, such as Prince Edward Island, required fewer rare species habitat preferences to achieve a score of "3", than did a province such as British Columbia, with a large number of rare species. The scale was applied after tallying of habitat preferences was completed. This approach allowed for each province and territory to be dealt with equally. Although somewhat subjective, it is hoped that this approach provides insights into both regional and national trends in habitat preferences, and that it may assist in priority-setting with regard to habitats that may be in need of conservation actions (because of the concentrations of rare species within them).

Certain patterns are immediately evident and easily explained. The regions that contain mountains (British Columbia, Alberta, Northwest Territories, Yukon Territory) have a preponderance of rare species in the alpine, subalpine, and montane habitat types, but particularly in moist meadows. Alpine and subalpine, open, rocky habitats are also concentration points for rare plants in these regions. There is not necessarily a concentration on calcareous sites, although this may be an artefact of how habitats were characterized in the provincial/territorial lists, or of the lack of detail at the source (specimen labels). It is interesting to note that montane and subalpine forests are not habitats with major concentrations of rare vascular plants. However, open, rocky montane slopes and outcrops support more rare species. In fact, open, rocky habitats of all sorts, at all elevations and latitudes, are extremely important for their concentrations of rare vascular plants (Table 2). Although the more specialized habitats within these rock outcrops/slopes/barrens have not been consistently described in the provincial/territorial lists, it is apparent from Table 2 that there are many specialized niches to which rare species have become adapted. Some examples of such specialized habitats include lava talus (British Columbia), gypsum outcrops (New Brunswick, Nova Scotia), serpentine outcrops (British Columbia, Newfoundland, Quebec), and alvars (included within calcareous barrens; Ontario). Drury (1969) suggested that specialization on limestone or serpentine substrates might be a response to competition, rather than physical stress. However, this may be too simplistic an explanation, since Kruckeberg (1984) has noted a wide range of evolutionary responses to the serpentines in California. Brunton (1979) provided an informative example of how three closely related taxa of cliff-brake ferns were partitioned among microsites on limestone substrates in Alberta. Western Cliff-brake, *Pellaea occidentalis*, is found on dry, exposed, southwest-facing sites; Smooth Cliff-brake, *P. suksdorfiana*, occurs on shaded, cool, east- or north-facing cliffs by water; and Purple

Cliff-brake, *P. atropurpurea*, is located on dry, partially shaded, southwest-facing sites.

Another obvious pattern relates to arctic/subarctic habitats. In provinces with limited arctic/subarctic area (relative to their total areas), many species occurring in these areas are considered to be provincially rare. In some cases, this may be due to a lack of botanical exploration. However, such areas in Manitoba, Ontario, and Quebec also contain many species that reach the limits of their ranges in these arctic/subarctic fringes (i.e., they are at the peripheries of their ranges). Nevertheless, they are naturally occurring components of the biodiversity of these jurisdictions. The Northwest Territories and Yukon Territory contain abundant habitat in the arctic/subarctic zones. It has been difficult, however, to further subdivide the habitat types in these areas, because the lists of rare plants for these regions contain general habitat descriptions, for the most part. It is evident, however, that both coastal beaches and meadows, as well as tundra further inland, are important habitats for both territorial and provincial arctic/subarctic rarities.

Natural meadows, fields, and grasslands form another nucleus of important habitat types for rare vascular plants in Canada. Moist to wet meadows support far more rare species in almost all jurisdictions, than do dry meadows. Again, calcareous meadows constitute a subset of the field/meadow category that is important for some species. There may be some inconsistency among authors in the distinction between calcareous meadows, fens, and sedge meadows. When the fen/sedge meadow category is examined, the importance of these minerotrophic, moist to wet habitats is accentuated. Several provinces and territories have high scores for this vegetation class (Table 2). Moist to wet, open, calcareous gravels and shores also support rare species in most jurisdictions.

Although wet, open meadows predominate in the field/meadow category, some dry grassland communities also contain numerous rare vascular plant species. This is particularly true of dry prairies, probably because most of them have been converted to agricultural uses. British Columbia, Alberta, Saskatchewan, Manitoba, and Ontario all have many rare species that are associated with dry prairie conditions. Another rare habitat rich in rare species is the xeric sagebrush hillside/slope, which is restricted to southern interior British Columbia.

Moist prairies have also dwindled to a small fraction of their former extent. The rare species categorized as preferring moist prairies in the provincial lists tend to be associated with tall-grass prairies. Southwestern Ontario is the focal point for these remnant habitats, but southeastern Manitoba also contains significant amounts of this vegetation type. These moist prairies generally are not excessively

alkaline. In the prairie provinces, alkaline flats, floodplains, and meadows, which usually are moist in the spring, and desiccate during the summer, support substantial numbers of rarities, as well. The Northwest Territories, Yukon Territory, British Columbia, and Alberta are rich in species preferring these habitats.

Several other moist to wet habitats consistently support many rare species in all jurisdictions. The shores of lakes, ponds, rivers, and streams fall into this category, as do riparian habitats (open and shaded). Each jurisdiction also contains several rare aquatic macrophytes. Some of these clearly are associated with calcareous waters. Two of the specialized aquatic habitats occupied by rare plants are vernal pools [northern limit of a threatened habitat type characteristic of the California Floristic Province (Holland and Jain 1988); British Columbia], and rapids (which contain the nationally rare Riverweed, *Podostemum ceratophyllum*, in Ontario, Quebec, New Brunswick, and Nova Scotia). Open and wooded wetlands of several types, including coniferous and hardwood swamps, ombrotrophic bogs, muskeg, and fens (noted above), all support several rare vascular plant species in most or all jurisdictions. Moist woodlands support more rare species than do dry woodlands (a situation parallel to that for open habitats; however, see below). Rich, moist hardwood forests, especially in Ontario, Quebec, New Brunswick, and Nova Scotia, are particularly important. Moist coniferous forests are important habitats for rare species in boreal and montane regions.

Dry woodland communities appear to be less rich in terms of their rare species content. However, certain provinces contain concentrations of rare species in such habitats. Ontario is one case where numerous species rely on dry hardwood forests with southern affinities. This includes both closed-canopy oak-hickory and maple-beech forests, as well as more open oak savannahs. Dry coniferous forests are far less diverse, but some rare species do require dry pine- or spruce-dominated forests.

It is also important to recognize that there are a few groups of rare vascular plants that are highly specialized in the sense that they require specific hosts. A rather long list of hosts is found in Table 2. The parasitic species are found mainly within the Dodder family (Cuscutaceae) and the Mistletoe family (Viscaceae). British Columbia and Ontario have the most rare parasitic species. This is consistent with their having the largest floras and the highest numbers of rare species in their floras (Table 1).

Rare Habitats

The previous discussion focussed on the habitats of the provincially/territorially rare vascular plants. Not all of the habitats in which rare species occur are themselves rare. The factors that lead to rarity in a

species are frequently unknown. Some habitat types, especially those related to localized substrate outcroppings or unusual hydrological features, are rare in their own right. Other habitat types may have been widespread at one time, but are now rare due to land use activities, such as ploughing, grazing, clearing, mining, flooding, draining, logging, and urbanization/development. Examples in the latter category include some types of old-growth forests, Great Lakes marshes, and all types of prairies. Although no national (or even provincial) inventory of rare habitats exists, a brief discussion of a few habitat types that are generally considered to be rare will assist in explaining some of their features, and perhaps also provide some clues as to the reasons for their rarity.

The Atlantic Coastal Plain vegetation of Nova Scotia and Ontario has been studied intensively by Paul Keddy and his colleagues. In these infertile sand and gravel shoreline habitats, subject to fluctuating water levels and intense wave exposure, individual species vary in their responses to the exposure. Water depth and wave energy are both important factors in determining within-lake distributions of species. Species with Atlantic Coastal Plain affinities tend to be most abundant where exposure to waves is most intense. The wave action serves to reduce soil fertility by washing away the finest sand particles, as well as organic matter, and also serves to limit the establishment of shrubs and coarse herbaceous vegetation (P. A. Keddy 1981, 1983; P. A. Keddy and Wisheu 1989). Some of the species with this floristic affinity are locally abundant within a small geographic area (e.g., Virginia Meadow-beauty, *Rhexia virginica*, and Southern Yellow-eyed Grass, *Xyris difformis*), in the Muskoka-Parry Sound area of central Ontario. Others, with the same floristic affinity, are extremely rare within the same area (e.g., Screw-stem, *Bartonia paniculata*, and Engelmann's Quillwort, *Isoetes engelmannii*). These Atlantic Coastal Plain shoreline habitats may be threatened in various ways. In many cases, these communities have developed on the shorelines of lakes that are also considered to be prime sites for cottage development. The pressures on such sites in both Nova Scotia and Ontario are intense (C. J. Keddy and Sharp 1989*; P. A. Keddy and Wisheu 1989; personal observations). Another source of potential damage to these communities is from water-level alteration and control. The gradual reduction in water levels through the summer is an essential attribute for the annual and short-lived perennial species that occupy the emergent shoreline communities (P. A. Keddy and Reznicek 1982; Reznicek 1994; Sharp and Keddy 1993*). Water level control is likely to have an adverse effect, unless water-level fluctuations are managed in accordance with the ecological requirements of the species that make up these rare communities (Sharp and Keddy 1993*).

Tall-grass prairies and oak savannahs provide examples of community types that are both rare in their own right, and that contain numerous provincially (and nationally) rare species. These vegetation types formerly were much more extensive than they are today; perhaps less than 1% of the pre-settlement tall-grass prairie and savannah remain in southern Ontario (Bakowsky and Riley 1994). The coincidence of some of the remaining prairies with portages, ancient lake bluffs, and other traditional campsites, suggests that aboriginal use of fire as a tool, as well as natural fires, and warmer- and drier-than-normal site conditions, played an important role in the persistence of these habitats (Bakowsky and Riley 1994; Catling et al. 1992). Faber-Langendoen and Maycock (1994) described six prairie types in Ontario (dry; dry mesic; mesic sandy loam; wet mesic; wet mesic sandy; wet mesic sandy loam), which have characteristic vegetation patterns correlated with site differences. All of these types are now rare. Agricultural and, to some extent, suburban/urban land uses have resulted in the rarity of these vegetation types. Another threat to the remaining fragments of these habitats is fire suppression. Without proper fire management, the remaining sites will become overgrown or close in with fuller canopy development, resulting in the probable loss of some rare species, as well as the communities themselves.

Rarity due to the localized occurrence of unusual or uncommon edaphic/geological features is well known. This has been alluded to above (**Habitats of Rare Plants**). A few additional examples are helpful in understanding the patterns and causes of rarity. Areas of endemism often coincide with unusual substrate conditions. A good example is found in the active sand dune systems along the south shore of Lake Athabasca, in northern Saskatchewan and Alberta. This area extends for approximately 90 km along the shore, and for up to 20 km inland (Argus and Steele 1979; Raup and Argus 1982). Argus and Steele (1979) have studied the morphology and phenolic glycosides of the endemic Tyrrell's Willow, *Salix planifolia* subsp. *tyrrellii*, on these dunes, and have found that this taxon has adapted to the active dune conditions by developing genetically controlled prolonged apical dominance, which enables shoots to continue growing upward through the constantly accreting sand, so that portions of the plant can remain exposed on the crests and flanks of these dunes. A different adaptation to the same conditions has evolved in another endemic, Sand Dune Long-stalked Chickweed, *Stellaria longipes* subsp. *arenicola*. In the typical subspecies, cross-pollination is the normal breeding system. However, in the sand dune endemic, the breeding system has switched to self-pollination. In addition, the capsules of the endemic

subspecies dehisce to release their seeds soon after maturity, unlike the widespread typical subspecies (Ramamoorthy and Chinnappa 1995).

Another example of a rare (and threatened) vegetation complex is the alvars of the Great Lakes region. Alvars are naturally open areas of thin soil over relatively flat Ordovician and Silurian limestone and dolomite (and sometimes Precambrian marble) pavement, that support relatively sparse vegetation. They remain open because of seasonal extremes in soil moisture content (wet in spring, desiccated in summer), extremely thin, poorly developed soils, and, at least historically, occasional fires. Ontario contains over 90% of the total Great Lakes alvar landscape (Catling and Brownell 1995; Catling et al. 1975). Alvars support a rich diversity of provincially and nationally rare vascular plants, including at least one endemic, Lakeside Daisy, *Hymenoxys herbacea* (Catling 1995; Catling and Brownell 1995; Catling et al. 1975; Cusick 1991). Catling and Brownell (1995) described two major types of alvars (shoreline and plateau), the latter having various expressions depending on the nature of the rock exposures and the degree of soil development. They characterized these variants as alvar grassland, alvar pavement, alvar savannah, and pavement ridge. The highest diversity of alvar specialists is found on the alvars of the western Lake Erie region, Manitoulin Island, and the Napanee Plain. Alvar-like communities on marble substrates are not nearly as species-rich, but do contain a few of the characteristic limestone/dolomite alvar specialists (personal observations). The major threats to alvars arise from conversion to alternative uses. A major current use of alvars is as pastureland. This form of land use has variable effects. On one hand, grazing may serve to keep woody vegetation from invading sites with better than usual soil development. However, some of the alvar species may suffer from overgrazing. These effects are not yet known. Lands that are being used for pastures are also likely to be protected from fire more diligently than are inactive alvars. Catling et al. (1975) also noted that some of the alvars they studied were being used as unauthorized dumps. Perhaps the most serious threat to alvars is from mining and aggregate production. Given the close proximity of many of the alvars to the Greater Toronto Area, and the easy access to crushable limestone for gravel and cement, because of the negligible overburden, some of the major alvars are undergoing extraction at an increasing rate. Thus, an already geographically limited habitat type is under threat from a non-renewable resource extraction activity. Similar threats face other limestone-, gypsum-, and sandstone-based habitats in many parts of Canada (e.g., Fahselt et al. 1979).

Conclusion – Future Priorities

A considerable amount of progress has been made over the past 20 years in our understanding of the status, distribution, and ecology of the rare vascular plants and their habitats in Canada. Having said that, however, there is still an enormous amount to be learned before effective conservation measures can be applied for more than a handful of species. Unfortunately, botanists often are requested to recommend conservation actions in the absence of adequate data. For this reason, it may be necessary to find new ways of generating status reports, or of dealing with conservation requirements of vulnerable, threatened, and endangered plants and communities. This is not to say that the traditional single-species approach should not continue. However, it seems necessary to find new, more efficient ways of obtaining the necessary data on more species and vegetation communities in less time. Also, efforts should be focussed on the taxa or communities with the most pressing conservation needs. This requires a priority-setting mechanism(s). COSEWIC has a process for determining priorities for funding allocations for status reports, which appears to combine an assessment of submitted proposals with an assessment of threats to each taxon. Argus and Pryer (1990) developed a priority-rating system for the nationally rare vascular plants that takes into account each taxon's Canadian range, population sizes, threats, and rarity in all jurisdictions of occurrence. Using this system, they ranked 68 species as having top priority for conservation action. This set of 68 vascular plants should serve as a starting point for further studies, not only on status and demographics, but also on ecological requirements. A quick perusal of these 68 species indicates that approximately half have had status reports prepared (see Appendix I). Approximately 35 of these species still require assessments. Several of the other species assessed by COSEWIC fall within the second priority category of Argus and Pryer (1990).

An alternative approach to priority-setting for conservation has been referred to as "species triage" (McIntyre et al. 1992). This approach is rooted in the philosophy that it is not possible to protect all species from extinction, and that focussing efforts on the rarest of the rare is often both cost- and time-intensive. Rather, they suggest that a primary goal of conservation efforts should be to provide habitat and landscape diversity that maximizes the range of selective pressures and the number of species that are able to exist. Another way of thinking about this concept is to ensure the provision of as broad a range of niches or site conditions as possible for the most species. This approach may lean too far in the other direction. However, some intermediate approach, which combines single-species and habi-

tat approaches, should be feasible. An adaptation of the "species triage" concept that enables an assessment of the probability that conservation actions will provide the desired result (i.e., maintenance of viable populations in the wild) may be worthy of further consideration. This could be thought of as a form of risk/benefit assessment.

The idea of focussing on habitats rather than species is not new. Most conservation agencies realize that there are far too many rare species to deal with effectively, individually. One concept that has been suggested in Ontario, but not yet attempted, was the idea of multi-species status reports, for situations where assemblages of rare species occur together (Bowman 1991). Such status reports could include selected demographic data on the individual rare species, but would focus on the status of the habitat in which they occurred. Some of the habitats of rare species in which this approach might be feasible have been discussed above, and include tall-grass prairies, alvars, Atlantic Coastal Plain communities, snowbeds in certain mountain ranges, serpentine outcrops, etc. This approach would be analogous to the "guild" approach sometimes advocated in species monitoring programs.

For certain plant groups, such alternative approaches are not yet feasible, because little is known about the target organisms or their ecological requirements. In the case of such groups (bryophytes, algae, lichens, fungi), attempts must first be made to address the question of which taxa (and which habitat attributes) require conservation attention. As noted earlier, some work has been done on compiling data on the rare species in some of these groups, in some jurisdictions, but much more work is needed. It may well be that some of the rarities in these groups co-occur with the rare vascular plants. However, at the present time, we do not know.

The move to establish Conservation Data Centres in several provinces is positive, and should continue. The staffs in these Centres have the specific task of tracking and updating knowledge on rare organisms and ecosystems in their jurisdictions. Ultimately, each province and territory should establish such agencies.

There also is a need for diversified and strengthened legislative tools to promote conservation of both rare species and significant habitats and landscapes. Most legislative tools that exist at the present time appear to be too weak. These weaknesses are manifested in several ways. Invariably, Canadian legislation contains incomplete and inadequate lists of rare species. In some cases, the regulations attached to these acts easily can be circumvented, or are overly permissive in terms of allowances for land uses that may not be compatible with the goal of sustaining healthy ecosystems and populations of the listed or regulated species. Enforcement of the

regulations in these acts also is problematic in several ways. There are insufficient personnel to enforce the regulations, evidence often is difficult to obtain for prosecution, and in some cases, upon conviction, penalties are trivial.

Canada, along with its provinces and territories, has made significant progress in cataloguing rare vascular plants, and has begun to develop tools and mechanisms to conserve these elements of its biodiversity. Continued efforts at the species level, but also especially on ecosystems, are now needed to ensure that as much of the natural diversity as possible is conserved for future generations.

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APPENDIX I. Status designations for flowering plants and lichens, assessed through the auspices of the Committee on the Status of Endangered Wildlife in Canada, as of September 1996 (Anonymous 1996; Erich Haber, personal communication; Sylvia Normand, personal communication). Provincial and territorial acronyms are the same as those used in Table 1.

Species	Common Name	Canadian Occurrence	Status	Year
Flowering Plants, Ferns and Allies				
<i>Abronia micrantha</i>	Sand Verbena	AB, SK	Threatened	1992
<i>Adiantum capillus-veneris</i>	Southern Maidenhair Fern	BC	Endangered	1984
<i>Agalinis gattingeri</i>	Gattinger's Agalinis	ON	Endangered	1988
<i>Agalinis skinneriana</i>	Skinner's Agalinis	ON	Endangered	1988
<i>Aletris farinosa</i>	Colicroot	ON	Threatened	1988
<i>Arisaema dracontium</i>	Green Dragon	ON, QC	Vulnerable	1984
<i>Armeria maritima</i> ssp. <i>interior</i>	Athabaska Thrift	SK	Threatened	1981
<i>Aster anticostensis</i>	Anticosti Aster	NB, QC	Threatened	1990
<i>Aster curtus</i>	White-top Aster	BC	Threatened	1996
<i>Aster divaricatus</i>	White Wood Aster	ON, QC	Threatened	1995
<i>Aster laurentianus</i>	Gulf of St. Lawrence Aster	NB, PE, QC	Vulnerable	1989
<i>Aster subulatus</i> var. <i>obtusifolius</i>	Bathurst Aster	NB	Vulnerable	1992
<i>Aster yukonensis</i>	Yukon Aster	NT, YT	Not at Risk	1996
<i>Azolla mexicana</i>	Mosquito Fern	BC	Threatened	1984
<i>Balsamorhiza deltoidea</i>	Deltoid Balsamroot	BC	Endangered	1996
<i>Bartonia paniculata</i>	Branched Bartonia	ON	Vulnerable	1992
<i>Brickellia grandiflora</i>	Large-flowered Brickellia	AB, BC	Not at Risk	1996
<i>Buchnera americana</i>	Bluehearts	ON	Threatened	1985
<i>Cacalia plantaginea</i>	Indian Plantain	ON	Vulnerable	1988
<i>Camassia scilloides</i>	Wild Hyacinth	ON	Vulnerable	1990
<i>Carex nebrascensis</i>	Nebraska Sedge	AB	Not at Risk	1995
<i>Castanea dentata</i>	American Chestnut	ON	Threatened	1987
<i>Castilleja levisecta</i>	Golden Paintbrush	BC	Threatened	1995
<i>Celtis tenuifolia</i>	Dwarf Hackberry	ON	Vulnerable	1985
<i>Cephalanthera austinae</i>	Phantom Orchid	BC	Vulnerable	1992
<i>Chenopodium subglabrum</i>	Smooth Goosefoot	AB, MB, SK	Vulnerable	1992
<i>Chimaphila maculata</i>	Spotted Wintergreen	ON	Endangered	1987
<i>Cicuta maculata</i> var. <i>victorinii</i>	Victorin's Water-hemlock	QC	Vulnerable	1987
<i>Cirsium pitcheri</i>	Pitcher's Thistle	ON	Threatened	1988
<i>Clethra alnifolia</i>	Sweet Pepperbush	NS	Threatened	1986
<i>Collinsia verna</i>	Blue-eyed Mary	ON	Extirpated	1987
<i>Coreopsis rosea</i>	Pink Coreopsis	NS	Endangered	1984
<i>Cypripedium candidum</i>	Small White Lady's-slipper	ON, MB	Endangered	1981
<i>Desmodium illinoense</i>	Illinois Tick-trefoil	ON	Extirpated	1991
<i>Draba kananaskis</i>	Kananaskis Whitlow-cress	AB	Indeterminate	1992
<i>Drosera filiformis</i>	Thread-leaved Sundew	NS	Endangered	1991
<i>Epipactis gigantea</i>	Giant Helleborine	BC	Threatened	1984
<i>Erigeron philadelphicus</i> ssp. <i>provancheri</i>	Provancher's Fleabane	QC	Vulnerable	1992
<i>Erigeron radicans</i>	Dwarf Fleabane	AB, BC, SK	Not at Risk	1996
<i>Erysimum angustatum</i>	Narrow-leaved Wallflower	YT	Not at Risk	1993
<i>Floerkea proserpinacoides</i>	False Mermaid	NS, ON, QC	Not at Risk	1984
<i>Frasera caroliniensis</i>	American Columbo	ON	Vulnerable	1993
<i>Fraxinus quadrangulata</i>	Blue Ash	ON	Threatened	1983
<i>Gentiana alba</i>	White Prairie Gentian	ON	Endangered	1991
<i>Gentiana victorinii</i>	Victorin's Gentian	QC	Vulnerable	1987
<i>Geum peckii</i>	Eastern Mountain Avens	NS	Endangered	1986
<i>Gymnocladus dioica</i>	Kentucky Coffee-tree	ON	Threatened	1983
<i>Halimolobos virgata</i>	Slender Mouse-ear Cress	AB, SK	Endangered	1992
<i>Hibiscus moscheutos</i>	Swamp Rose-mallow	ON	Vulnerable	1987
<i>Hordeum pusillum</i>	Little Barley	AB	Indeterminate	1993
<i>Hydrastis canadensis</i>	Golden Seal	ON	Threatened	1991
<i>Hydrocotyle umbellata</i>	Water Pennywort	NS	Endangered	1985
<i>Iris missouriensis</i>	Western Blue Flag	AB, BC	Threatened	1990
<i>Isoetes bolanderi</i>	Bolander's Quillwort	AB	Vulnerable	1995
<i>Isoetes engelmannii</i>	Engelmann's Quillwort	ON	Endangered	1992
<i>Isopyrum biternatum</i>	False Rue-anemone	ON	Vulnerable	1990
<i>Isotria medeoloides</i>	Small Whorled Pogonia	ON	Endangered	1982

Continued

APPENDIX I. *Continued.*

Species	Common Name	Canadian Occurrence	Status	Year
<i>Isotria verticillata</i>	Large Whorled Pogonia	ON	Endangered	1985
<i>Juncus caesariensis</i>	New Jersey Rush	NS	Vulnerable	1992
<i>Justicia americana</i>	American Water-willow	ON, QC	Threatened	1984
<i>Lachnanthes caroliniana</i>	Redroot	NS	Threatened	1994
<i>Lespedeza virginica</i>	Slender Bush-clover	ON	Endangered	1986
<i>Liatris spicata</i>	Dense Blazing Star	ON	Vulnerable	1988
<i>Lilaeopsis chinensis</i>	Lilaeopsis	NS	Vulnerable	1987
<i>Limnanthes macounii</i>	Macoun's Meadowfoam	BC	Vulnerable	1988
<i>Liparis liliifolia</i>	Purple Twayblade	ON	Threatened	1989
<i>Lipocarpha micrantha</i>	Small-flowered Lipocarpha	BC, ON	Threatened	1992
<i>Lophiola aurea</i>	Golden Crest	NS	Threatened	1987
<i>Lotus formosissimus</i>	Seaside Bird's-foot Lotus	BC	Endangered	1996
<i>Lupinus lepidus</i> var. <i>lepidus</i>	Prairie Lupine	BC	Endangered	1996
<i>Magnolia acuminata</i>	Cucumber-tree	ON	Endangered	1984
<i>Morus rubra</i>	Red Mulberry	ON	Threatened	1987
<i>Opuntia humifusa</i>	Eastern Prickly-pear Cactus	ON	Endangered	1985
<i>Oxytropis lagopus</i>	Hare-footed Locoweed	AB	Vulnerable	1995
<i>Panax quinquefolius</i>	American Ginseng	ON, QC	Threatened	1988
<i>Pedicularis furbishiae</i>	Furbish's Lousewort	NB	Endangered	1980
<i>Phegopteris hexagonoptera</i>	Broad Beech Fern	ON, QC	Vulnerable	1983
<i>Phlox alyssifolia</i>	Blue Phlox	AB, SK	Not at Risk	1996
<i>Plantago cordata</i>	Heart-leaved Plantain	ON	Endangered	1985
<i>Platanthera leucophaea</i>	East. Prairie White-fringed Orchid	ON	Vulnerable	1986
<i>Platanthera praeclara</i>	West. Prairie White-fringed Orchid	MB	Endangered	1993
<i>Polemonium van-bruntiae</i>	van Brunt's Jacob's Ladder	QC	Threatened	1994
<i>Polygala incarnata</i>	Pink Milkwort	ON	Endangered	1984
<i>Potamogeton hillii</i>	Hill's Pondweed	ON	Vulnerable	1986
<i>Psilocarphus tenellus</i> var. <i>tenellus</i>	Slender Woolly-heads	BC	Not at Risk	1996
<i>Ptelea trifoliata</i>	Hop Tree	ON, QC	Vulnerable	1984
<i>Pycnanthemum incanum</i>	Hoary Mountain-mint	ON	Endangered	1986
<i>Quercus shumardii</i>	Shumard's Oak	ON	Vulnerable	1984
<i>Ranunculus alismaefolius</i> var. <i>alismaefolius</i>	Water-plantain Buttercup	BC	Endangered	1996
<i>Rosa setigera</i>	Climbing Prairie Rose	ON	Vulnerable	1986
<i>Sabatia kennedyana</i>	Plymouth Gentian	NS	Threatened	1984
<i>Salix planifolia</i> ssp. <i>tyrrellii</i>	Tyrrell's Willow	SK	Threatened	1981
<i>Scirpus longii</i>	Long's Bulrush	NS	Vulnerable	1994
<i>Scirpus vecundus</i>	Few-flowered Club-rush	ON	Vulnerable	1986
<i>Smilax rotundifolia</i>	Round-leaved Greenbrier	ON (Carolinian population)	Threatened	1994
<i>Stellaria arenicola</i>	Sand Stitchwort	AB, SK	Not at Risk	1992
<i>Stephanomeria runcinata</i>	Pink Rush	BC	Not at Risk	1996
<i>Stylophorum diphyllum</i>	Wood Poppy	ON	Endangered	1993
<i>Talinum sediforme</i>	Fameflower	BC	Not at Risk	1990
<i>Tephrosia virginiana</i>	Goat's-rue	ON	Threatened	1996
<i>Tradescantia occidentalis</i>	Western Spiderwort	AB, MB	Threatened	1992
<i>Trillium flexipes</i>	Drooping Trillium	ON	Endangered	1996
<i>Triphora trianthophora</i>	Nodding Pogonia	ON	Threatened	1988
<i>Vaccinium stamineum</i>	Deerberry	ON	Threatened	1994
<i>Viola pedata</i>	Bird's-foot Violet	ON	Threatened	1990
<i>Viola praemorsa</i> ssp. <i>praemorsa</i>	Yellow Montane Violet	BC	Threatened	1995
<i>Virgulus sericeus</i>	Western Silver-leaf Aster	MB, ON	Vulnerable	1988
<i>Woodsia obtusa</i>	Blunt-lobed Woodsia	ON, QC	Threatened	1994
<i>Yucca glauca</i>	Soapweed	AB	Vulnerable	1985
Lichens				
<i>Heterodermia sitchensis</i>	Seaside Centipede	BC	Endangered	1996
<i>Hypogymnia heterophylla</i>	Seaside Bone	BC	Vulnerable	1996
<i>Nephroma occultum</i>	Cryptic Paw	BC	Vulnerable	1995
<i>Pseudocyphellaria rainierensis</i>	Oldgrowth Specklebelly	BC	Vulnerable	1996

Book Reviews

ZOOLOGY

Birds of the Besnard Lake Area

By J. Gerrard, G. Bortolotti, and K. Wiebe. 1996. Special Publication Number 20, Saskatchewan Natural History Society, Regina, Saskatchewan. 456 pp., illus. \$12.00

Much of Saskatchewan's limited population and a large portion of its visitors see only the southern prairie region. This leaves a vision of grain fields, ranches and open grasslands. We need to be reminded that over 50 percent of the Province is woodland. A flight to one of the northern communities will reveal just how extensive is that woodland region. About a quarter of a million square kilometres of the Northern Boreal Forest lies north of LaRonge and this area is essentially traversed by only three roads. Needless to say there is a lack of data for this region.

Besnard Lake lies to the north and west of La Ronge and is just at the edge of the northern boreal forest. It has been used as an ornithological study area for many years, primarily to research raptor biology. The researchers kept more extensive notes than just for the birds of prey under study and these data form the basis of this book. Although they did undertake some specific surveys, the data are largely anecdotal. This may result in some bias creeping into the results but it is difficult to judge as there are no other databases with which to make a comparison.

There are a number of surprises in their findings. For example, on a spring census of hooting owls they found 25 Boreal Owls giving an average density of one per kilometre. Earlier this year I was pleased to find one singing Boreal on a route just north of

Prince Albert. On the other side of the ledger they found one Pine Grosbeak and that was 18 years ago! Another surprise was the midsummer record of a Green-tailed Towhee – the first in almost fifty years. How many other interesting vagrants are missed in this large region?

Less surprising, but as interesting, were the changes due to habitat. The prairie species of duck (Mallard, Shoveler, and Pintail) are replaced by the cavity nesters (mergansers, Common Goldeneye, and Bufflehead). Similarly, the sparrows swing from Vesper and Clay-coloured to White-throated and Swamp. Other birds like Grey Jay and Raven remind the reader the book is set in the northern forest. It is these records that are the real value of this work. So little has been published for this area that every contribution is important. This book is a well-organized summary of the over 25 years of data collection coupled with some thoughtful introductory notes and commentary. It will be a useful addition to your birding library.

One other aspect of this book that I found remarkable (unique!) is that one of the authors (Gerrard) is a politician and an ex-member of the federal cabinet. The public vision of politicians in recent years has not been one of dedicated, hard working scientists!

ROY JOHN

#1 613 McPherson Avenue, Saskatoon, Saskatchewan S7N 0X7.

Birds of the Elbow

By J. Frank Roy. 1996. Special Publication Number 21, Saskatchewan Natural History Society, Regina, Saskatchewan. 325 pp., illus. \$30.00.

Frank Roy is a well known naturalist in Saskatchewan and in demand as a speaker. This is due in part to his personality. He is charming, humorous and very knowledgeable and not surprisingly these traits permeate this book. He transmits the essential raw data in an easy, comfortable fashion and he adds numerous anecdotes that bring a special prairie flavour to the book. Through these vignettes the reader gets to know some of the people as well as the birds. Most of these individuals are farmers, trying to make a living under often difficult conditions. That they took the time to study and help

the environment is to their credit and this book is a tribute to them too.

Roy is in a unique position to write about the birds of southern Saskatchewan. He was born and raised during the formative years of the province. He had the foresight to document the human and natural history and its many changes. From his own data and those of his many friends he has pulled together a summation and given us this chronicle of prairie bird life. Although he has written specifically about birds of the Elbow region, much of what he says applies to the southern Saskatchewan prairie in general. Indeed, a visitor wishing to get an appreciation of prairie birdlife would be advised to visit this area; accompanied by this book of course.

The author, through a series of excellent maps and a description of the land and climate, gives the reader a clear understanding of the Elbow region. He adds a more detailed portrait of the most productive birding areas. Following these descriptions a visitor should be able to find the locality and be aware of what species and numbers to expect at a given date. I recently tried the directions for Gardiner Dam and Luck Lake and found they worked well. At Luck Lake I saw the first few Hudsonian Godwits of this year's migration.

By reading the species accounts, the reader will get an understanding of how and why birds are found in this area. The accounts are an exhaustive examination of a bird species, history, its interaction with human activity, current status, and distribution. The data will provide a sense of the current numbers to be expected and how this may change with time. Last year I made several trips to the Elbow and saw spectacular gatherings as three-quarters of a million White-fronted Geese (along with large numbers of other geese, ducks, and cranes) and many thousands of Hudsonian Godwits (plus other shore birds).

Roy includes a summary of his observation of that prairie phenomenon, the shelterbelt, and adds a note on the current wildlife conservation program; the Heritage Farmstead Program. These are part of the changes in the prairie ecosystem brought on by human activity. He includes a more substantial commentary on the backgrounds of the contributors than most authors, a characteristic to be expected from his people-oriented nature. In the appendices Roy gives

a detailed table of occurrences by area, a list of Christmas Bird Count results, and, my favourite, a status and abundance bar chart. At the appropriate places Roy adds a reasoned discussion of topics like lumping and splitting or difficult to identify species.

If you believe that Saskatchewan is an uninteresting tableland of grainfields then examine the 22 photographs Roy has selected. The wheatfields are there but so are the other landscapes that make this province, for those prepared to look, a fascinating place. Indeed the jumbled sculpture of the coulees seems more dramatic after leaving the wheatfields or sloughs. The text is also illustrated by line drawings of some of the birds species.

By combining the initial chapters, the anecdotal vignettes, the supplementary information, and the species accounts, the reader should have a good concept of the southern Saskatchewan prairie and its birdlife. My recommendation is to acquire a copy of this book this winter (it could solve a lot of Christmas present woes!) and read it while the snow flies. Then plan a trip (or two) for next year to see the birds of your choice. If you see a name on a mail box that matches one of the contributors – drop in. You will discover prairie hospitality to add to your sightings of birds.

ROY JOHN

#1 613 McPherson Avenue, Saskatoon, Saskatchewan S7N 0X7

Atlas of Saskatchewan Birds

By Alan R. Smith. 1996. Special Publication Number 22, Saskatchewan Natural History Society, Regina, Saskatchewan. 456 pp., illus. \$45.00.

I instinctively knew there was something different about this bird distribution atlas from those in which I had been involved. I did not understand what prompted this reaction until I began looking for the names of the participants. I then realised that this book was not created by a body of volunteers systematically combing individual squares but by the collation of historical data. This gives the range maps some odd biases. For example, Great Horned Owl, Swainson's Hawk, and Ferruginous Hawk have almost complete coverage in southern Saskatchewan. This reflects the 40-year banding work of the tireless Stuart Houston (he recently banded his 7000th Great Horned Owl) more than the overall owl distribution. Similarly there is an area west of Outlook that shows more confirmations of breeding for several species. This is the area studied by an indefatigable record keeper, J. Frank Roy, who has roamed and chronicled his home range since childhood. Naturally there

are numerous records clustered around Saskatoon and Regina, the centres of population.

Once I understood this difference in approach the anomalies in the distribution maps became more understandable. Northern Saskatchewan is clearly under represented (compare the distribution maps of Great Horned Owl and Barred Owl – a northern species) and this area needs a campaign similar to that used in Northern Ontario. There are better records for rare birds, especially if they are big and showy, like Whooping Crane. A common bird such as the American Goldfinch does proportionately less well. In southern Saskatchewan (there are few records for the north) the Goldfinch has been recorded in only 50% of the area. Just 10% of these records are confirmed breeding with 70% rated as possible breeding. While these data may indicate there are some localities with unsuitable habitat I think a more significant factor is lack of coverage and the extra effort to track down and confirm nests. This is part of the impetus and discipline provided by a "square-bashing" atlas project.

Al Smith's approach does bring one major advantage. As this is not a breeding bird atlas he has included *all* collected data. Through the use of 14 different symbols, used alone and in combination, the author has mapped breeding, migratory transients, and wintering birds. The plethora of symbols I found confusing at first but with practice I now find the maps fairly easy to read. Smith also uses "peripheral screens" around the provincial border. These area narrow bands of cross-hatching in various densities that indicate the status of a bird in the adjacent province or state. I have already found this to be a novel and useful feature.

In addition to the species accounts Smith gives a fine summary of the biotic regions. This shows that the province has more forest coverage than the grassland that makes it famous. He has included a set of three overlays; one of which is the biotic regions and shows this fact clearly. The author's chapter on the human history and how it has impacted the flora and fauna is both thoughtful and thought provoking. It leads into the currently accepted checklist of Saskatchewan birds. The author has attached appendices that summarises rarities and hypothetical birds, Christmas Bird Counts, Breeding Bird Surveys, and other useful information.

This book is a good source of information for the southern end of the province. It does take more

effort, however, on the part of reader, to be sure they are interpreting the data in the best fashion, than with other atlases. For the northern area it is less directly informative but will still be a useful guide. Visitors to the province will also need at least a good road map as a locality map is not included. The reader will also need some local help for the more obscure places (many prairie towns have disappeared but people still use their names to designate a locality).

When I closed this atlas I was left with a sense that Saskatchewan needed a formal breeding bird atlas (BBA) project to close the obvious gaps in Al Smith's work. I recognize that overcoming the problems of atlassing the northern half of the province would be a major challenge. However a BBA would result, not in a replacement for this book but in a complement to it; using it as a stepping stone to a new, different output. This is not to take away from the monumental effort by this author but a call to all the other Saskatchewan (Canadian?) birders to rally to his aid. Meanwhile, I have already begun to use this atlas as a reference and a guide and, I am sure, will use it even more so in the coming months.

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The Whooping Crane: North America's Symbol of Conservation

By Jerome J. Pratt. 1996. Castle Rock Publishing, c/o 3000 Meadowlark Drive, Sierra Vista, Arizona 85635. 171 pp., illus. \$17.75 Canadian.

Thirty years after Faith McNulty's superb 1966 account, *The Whooping Crane: The bird that defies extinction* (E. P. Dutton), this aptly-titled sequel is most timely. No one is better qualified for this difficult assignment than Jerome J. Pratt, who has been intimately involved as the driving force behind the small but influential Whooping Crane Conservation Association. The book has a great deal of Canadian content and the Foreword is by Saskatchewan's Minister of the Environment, the Hon. Lorne Scott.

Pratt begins with a recapitulation of the near-demise of this striking bird, with only 14 or 15 birds left by 1939 in what we now call the Aransas – Wood Buffalo population. Pratt provides much more information than did McNulty about the contributions of two Canadians from the Saskatchewan Museum of Natural History, Fred Bradshaw and Fred Bard, and of one American, Dr. Lawrence H. Walkinshaw of Battle Creek Michigan.

Pratt has wisely included important historic material. Chapter Two is reprinted from Walkinshaw's 1973 book, *Cranes of the World*, with a few updates as appropriate, and there are three appendices, writ-

ten by the late Clarence Cottam in 1958, by Dayton O. Hyde in 1961, and by Elwood G. Bizeau in 1975.

Pratt's own background as an aviculturist and as commander of a Signal Pigeon Company in Europe during World War II makes him highly critical of early fumbling efforts by government authorities, who were slow to hire individuals with the necessary avicultural expertise. He is, however, less incisive and less detailed than he might have been in analysing the reasons for failure of the expensive, 1975–1988 experiment of substituting 288 Whooping Crane eggs into natural nests of the Sandhill Crane at Gray's Lake Refuge, Idaho. He does not tell us that although 210 eggs hatched in spite of predation, chick mortality was high (Kuyt, *Bird Conservation International* 6: 3–10, 1996), with later disproportionate mortality of the females. As a result only four birds remained in the Rocky Mountain flock by 1994, though in 1984 this flock had numbered at least 31 Whooping Cranes, including 12 young of the year.

Another chapter is devoted to Whooping Cranes in captivity; although there were 88 adult and 41 young Whooping Cranes in captivity in December 1995, not one example of successful breeding in the wild by progeny of such cranes has yet occurred.

Perhaps this will yet happen now that a new, non-migratory population has been established on the Kissimmee Prairie in Florida, where the first 33 juveniles were released in 1993–1994.

This inexpensive, informative book should be in the library of all those interested in this endangered species, still at great risk from any possible local catastrophe occurring either in the relatively small breeding area in Wood Buffalo National Park, or on the even smaller wintering grounds on the Aransas

National Wildlife Refuge in Texas. I like Pratt's quotation from U.S. Secretary of the Interior, Stewart L. Udall, who described the effort to save the Whooping Crane as "... a love affair — between a civilized, sophisticated nation and an enormous, elusive bird."

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Fossils of the Burgess Shale

By D. E. Briggs, D. H. Erwin, and F. J. Collier. 1996. Smithsonian Institution Press, Washington, D.C. xvii + 239 pp., illus.

The importance of the fossils from the Burgess Shale in Yoho National Park, British Columbia, need not be repeated here at any great length. The capturing of soft bodied organisms as a thin organic film on a dark grey-black shale is truly unique. Yet in many ways *Fossils of the Burgess Shale* is a tribute not only to the rarity of the fauna but to Charles Walcott who discovered the fossils and recognized them for what they were. Walcott, then secretary for the Smithsonian Institute in Washington, viewed these fossils as related to major contemporary groups but as Stephen J. Gould has colourfully pointed out in his 1989 book *Wonderful Life*, the interpretation of the past does not always survive the passages of time.

The first 50 pages of *Fossils from the Burgess Shale* provide context for the reader with a brief history of Walcott's early adventures at the turn of the century up to more recent Royal Ontario Museum activities under the direction of Desmond Collins. Following this is an equally brief outline of the complex nature of how the fossils ended up there in the first place and the nature of their surrounding sedimentary tomb. In overviewing the large sample of specimens that have been collected (and there are thousands) the uniqueness of the fauna is found not only in the simple tabulation of specimens but that 86% of the creatures found are soft bodied; creatures that normally don't fossilize at the best of times. The context of Cambrian life over 500 million years ago is briefly taken up before the page turns to the remainder and bulk of the book.

For the most part this book is a photographic and text essay on the individual groups (at the generic

level) found in the fauna: a simple and familiar format. Generally, a full page black and white photograph of a representative specimen (which at times can be a little bit difficult to interpret; for example see *Halichondrites* on page 70) followed by a page of interpretive text (including historical changes) is used. The format is familiar because in many ways it follows Conway Morris and Harry Wittington's 1985 Geological Survey of Canada's publication (Miscellaneous Report 43) by the similar title, *Fossils of the Burgess Shale, A National Treasure in Yoho National Park, British Columbia*. The difference being is that the more recent publication provides more photographs of the genera and artist rendering of each.

The discovery, interpretation, reconstruction, and eventual meaning of any fossil specimen or fauna is flavoured with the eventual humility of our own ignorance (whether *Hallucigenia* walked on its feet as first described or its tentacles need not matter to those who find the creature truly bizarre either upside down or black to front). Not only do we stand on the shoulders of the pioneers of yesteryear, like Walcott, but we stand on the shoulders of the not so giants of the more distant past: creatures like the alien-like *Opabimia* or *Anomalocaris*; or *Pikaia*, one of the oldest chordates known: our oldest ancestor.

The fauna is truly interesting to any who ponder our wandering planet's earliest creatures. This book, if for only the illustrations, enhances this sense of wonder.

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Mammals of the Canadian Rockies

By George W. Scoter and Tom J. Ulrich. 1995. Fifth House Ltd., Saskatoon, Saskatchewan. 185 pp., illus. \$22.95

Canada's national parks in the Rocky Mountains offer some outstanding opportunities for viewing mammals. The mammals of the region have been covered in various technical reports and general natural history guides. However, *Mammals of the Canadian Rockies* is the first popular book that is dedicated solely to the mammalian fauna of this region.

Introductory sections cover the geology and ecology of the Canadian Rockies and provide a general review of mammalian biology. The Rocky Mountain region is defined and the locations of national and provincial parks are illustrated in three black-and-white maps. The overview of mammalian biology is concise and non technical and rather heavily weighted towards the large hoofed mammals and carnivores. Most of the book is dedicated to accounts of the 75 species found in the region. Species are grouped by mammalian order and arranged by decreasing size and familiarity with the hoofed mammals and carnivores followed by the smaller and more obscure rodents, bats, and insectivores. The accounts of the larger mammals include four or five colour photographs, a description of the species, and a relatively detailed summary of their basic natural history. Accounts for the smaller species, particularly bats and shrews, have a single colour photo and a sketchy outline of their life history. Distribution is coded into seven areas: five national parks and two broad regions (Kananaskis country and northern British Columbia). I found the letter codes used to summarize distribution in the species accounts slightly awkward. However, a checklist clearly lists each species, occurrence in the seven areas.

The colour photographs especially for the larger species are generally superb. If I have a criticism, it

is that there too many redundant photos for many species. The book could have used a stronger editorial hand for selecting the most effective colour illustrations. For example, I question that five photos are required to illustrate the cougar. Three of the five illustrations of the Thinhorn Sheep are of the Dall's subspecies, a race that technically does not inhabit the northern Rocky Mountains. Eliminating some colour photographs and adding more drawings to illustrate identification traits similar to the figure that compares the external characteristics and tracks of the Grizzly and Black Bear would have enhanced the book. Curiously a black-and-white drawing contrasts the features of the Plains and Wood Bison subspecies yet the Wood Bison is a race is not found in the wild in the Canadian Rockies. Drawings of tracks at least for the hoofed mammals and some of the larger carnivores would have also been useful for the reader.

The authors' objectives defined in the introduction are to "identify the mammals you are most likely to see and describe their life histories". They have generally succeeded with their second objective. However, the book has more limited value as an identification tool. The non technical writing style, attractive photos, pleasing layout, and pocket size are all features of this book that will appeal to the novice naturalist and general user. Serious naturalists may find the book too general and they may want to consult the standard provincial mammal references for British Columbia and Alberta or the excellent mammal section in Ben Gadd's *Handbook of the Canadian Rockies*.

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The Snow Geese of La Pérouse Bay: Natural Selection in the Wild

By Fred Cooke, Robert F. Rockwell, and David B. Lank. Oxford University Press, Oxford. xii + 297 pp., illus. Canadian \$106.95.

In this book, one of the world's most extensive long-term studies of a single species is analysed with great care. The Snow/Blue Goose complex at the La Pérouse Bay colony on the coast of Hudson Bay, east of Churchill, Manitoba, has innumerable genetic and ecologic facets of unusual interest.

Each of the thirteen chapters begins with a problem or hypothesis, then presents the results (which are often unexpected), and concludes with a summary. Clear writing and an unusually well-organized

text, supported by maps, graphs, and tables, allows one to digest a formidable mass of material. Few biologists have achieved this standard of clarity. Adjectives such as succinct, logical, sequential, encyclopedic apply. Superlatives such as superb and prodigious are appropriate. Everything one might wish to know about the biology and ecology of this species is here.

The history of the Snow Goose is well presented. At the turn of this century, the white and blue morphs remained separate during breeding, migration, and wintering. The blue morph was restricted to the eastern arctic, particularly Baffin Island, and

wintered in Louisiana. The white morph bred farther west, and wintered in Texas. This situation still pertained when Dewey Soper discovered the nesting grounds of the Blue Goose in 1925, and found not one mixed pair. In 1930 Sutton found 2% mixed pairs on Southampton Island. Intermingling over the subsequent 60 years has resulted in the present situation where there are substantial admixtures on both the breeding and wintering grounds, the blue morph forming an ever-larger percentage. The total Snow Goose population at La Pérouse Bay has increased by a factor of ten, from 2000 breeding pairs in the 1950s to the present 20 000. Similar explosions in number have occurred across northern Canada.

Bird banding has provided much of the information about migration routes and longevity; 97% of the Snow Goose recoveries are from hunted birds. Four to eight thousand geese are banded annually. The place and date of death, from banding recoveries, becomes known for 12%, though the recovery rate has gradually decreased to less than 3%. Monthly maps of recoveries plot the progress of migration.

Sample sizes in this 25-year study (1968–1992) are large; 35 468 nests survived through incubation. Each year several hundred nests are studied during laying and several thousand nests at hatching. The average survival rate of young in their first year is 42.4%, in the second year, 75.6%, and in adult years, 83%, a figure that might rise to 94% if hunting ceased. In different years, hunting accounts for between 14 and 85% of immature deaths and 75% of adult deaths. In part because they do not breed until two to four years of age, an amazing 77% of geese have zero progeny in their lifetime. The other 23% and immigrants are responsible for a population that has increased ten-fold! Females return to their natal colony to nest, but they mate on the wintering grounds and bring males that are almost entirely from other colonies. Once established, pair bonds are maintained until the death of a partner.

Some of the facts established by this study pretty well conform to our expectations. For example, pre-laying foraging success affects clutch size. Goslings of either sex weigh an average of 85 g at hatch; the larger males have a fledging weight of 1600 g and the females, 1500 g. Eggs are laid at 33 hour intervals. Incubation lasts only 23.7 days. First-time breeders are less successful. Eggs laid in the nest of other geese have a lower hatchability.

Yet nothing is static. Goslings at the La Pérouse colony are eating themselves out of house and home, by overgrazing the surrounding sedge and goose grass, thereby lowering the per capita nutrient availability. Total brood failure, which stayed below 10% throughout the 1970s, skyrocketed to over 30% in 1988 and 1989, and 60% in 1990. The clutch size,

size of individual eggs, growth rates of goslings, and mean body weights have all declined significantly. But nature, perhaps simply by chance, seems to have ways of compensating. Once geese reach adulthood, the annual adult survival increased from 78% in 1978 to 88% in 1987, equivalent to a doubling of the expected mean adult life span from 4.0 to 7.8 years. Biological facts such as these are made easy to comprehend.

Complexities of biology are everywhere apparent. Whether a hypothesis is based upon genetic or environmental theory or common-sense, many predictions go embarrassingly awry, and are proved to be wrong. Here are a few examples. Since numbers of the blue morph are increasing disproportionately, one would expect studies to confirm greater fitness of the blue morph. Wrong! White and blue morphs each have the same adult survival rate of 82.6%. With an increasing population, one might expect clutch sizes to increase over time. Wrong! Clutch size is decreasing. Should one expect smaller eggs to produce smaller goslings with a lower chance of survival? Wrong! There are no fitness differences among birds of different mean egg mass. Might one expect the fittest geese to be largest? Wrong! Adult annual survival is not correlated with body size. On theoretical grounds an increase of 0.1 egg per clutch was expected in a study of this duration, but instead the clutch size declined by 0.4 egg. There is some selection for larger females in better condition that nest early and have a larger-than-average clutch, but the advantage is dissipated in part because there is increased predation of the early nests. And so it goes.

My praise does not apply to Chapter 8, "Heritability of quantitative traits," obviously the one chapter not written by Fred Cooke and David Lank. I could not understand the first two pages of this chapter. Perhaps genetic theorizing is more difficult to follow than environmental effects from cold or wet years? Terminology used in this book in general is not overly technical, though *epistasis* and *iteroparous* slipped through; the former is defined, the latter is not.

This book sets an extremely high standard for future studies, and is a model for anyone contemplating long-term research. The price seems unreasonably high on a per page basis, and out of reach for the average individual, but is competitive if one considers the amount of data provided per dollar. Do your best to persuade your librarian to use part of her ever-declining budget for this classic. The professors and graduate students of Queen's University have done a superb job. Canadians should be proud of this landmark study.

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A Critical Review of the Aerial and Ground Surveys of Breeding Waterfowl in North America

Graham W. Smith. 1995. Biological Science Report 5, National Biological Service, Washington, D.C. 251 pp., 1 map, 12 graphs. Free.

Each May, ducks are counted, by species, from morning aerial surveys of the same 77 waterfowl producing areas in central and northern North America, east of the Rockies, from Montana and the Dakotas north, and in Alaska. Fifty-seven of the 77 strata are in western and northern Canada. The pilot and the observer are both biologists trained to count birds. Ground studies by a two to four-person crew, who walk around or through the same transect strip, but at a different time (to allow for the ducks flushed by the aircraft to return), allow calculation of Visibility Correction Factors, which are calculated for each species and for each aerial crew. The aerial observer counts ponds as well as waterfowl, only on his side of the plane, but the pilot does not, so that the number of ponds the observer records is doubled. This survey is claimed to be the most extensive anywhere in the world.

Each well-distributed species has 11 pages of tables showing changes in numbers recorded over 40 years, from 1955 to 1994. In addition to variable fluctuations over the years, Northern Pintail numbers have declined through 1991, low numbers of American Wigeon were associated with droughts in the mid-1960s and 1980s, and Gadwall increased through the late 1950s and 1960s. Changes in numbers of ponds are also graphed, and allow an understanding of some of the vacillations observed for certain species. Data are presented for the American Coot, but not for geese (though numbers were recorded!).

There is no better reference source for changes in numbers of western Canadian waterfowl; 1955–1994.

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Proceedings of the 6th International Grouse Symposium

Edited by David Jenkins. 1995. World Pheasant Association, P.O. Box 5, Lower Basildon, Reading, Berks RG8 9PF, U.K. iv + 175 pp. £15.

The 6th International Grouse Symposium was held in Udine, Italy, 20–24 September 1993. These proceedings contain 27 papers and 12 abstracts of presentations from that symposium representing 14 countries. The predominance of papers are European with Germany (8) and Italy (5) dominating.

Topics covered during the symposium include all aspects of the ecology and management of grouse. Several important papers are included here such as J. F. Bendell and L. I. Bendell-Young "Populations and habitats of snowshoe hares, ruffed and spruce grouse in the southern boreal pine forest of Ontario." This paper should be of special interest to North American grouse workers.

The proceedings have been carefully edited. English usage is relatively uniform between papers. Some symposia volumes make no attempt to provide

such consistency of English usage. The papers in this volume read smoothly and are easily understood.

The International Grouse Symposia are an important contribution to grouse ecology and management. The World Pheasant Association is commended for sponsoring these meetings every three years. All scientists, naturalists, and sportspersons interested in grouse should attend one of these symposia. The 7th symposium was held in August 1996 in Ft. Collins, Colorado.

The Proceedings of the 6th are recommended for the breadth of valuable information on grouse that transcends species and continents. The coverage in this volume is decidedly Eurasian, but the topics are just as relevant in Canada and the U.S.

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Leks

By Jacob Höglund and Rauno V. Alatalo. 1995. Princeton University Press, Princeton. xiii + 248 pp., illus. Cloth U.S. \$49.50; Paper U.S. \$24.95.

In the words of the authors, leks are "aggregated male displays that females attend primarily for the purpose of fertilization". The word "lek" is of

Scandinavian origin and although leks are popular subjects of study all over the world, it is fitting that this book was written by two Scandinavian experts. Moreover, the popularity of the topic means that the timing is right for this, the first book devoted solely to leks.

The first part of the book (two chapters) is an introduction to the phenomenon of lekking and especially to the great diversity that can be found in lek organization throughout the animal kingdom. Although leks are most often studied in birds, they can be found in all vertebrates and in insects, and the authors give descriptions of leks in these various groups. They also discuss the variation in the extent of aggregation, in the relative importance of fertilization and resources as the reason for females to visit the lek, and in the prerequisites for leks to evolve (e.g., potential for female choice, external fertilization, absence of male parental care). A second part (four chapters) looks at the occurrence of sexual selection in lekking species first from the point of view of the males (e.g., what are the male attributes that contribute to mating success?) and then from that of the females (do females visit leks because it allows them to choose the "best genes" for their offspring, or are benefits more direct, such as reduced search costs, the possibility to copy other females' choice, reduced risk of injury, or reduced risk of disease transmission?). The details of a case study on Black Grouse are given, as well as a comparative analysis of lekking birds.

A third part (three chapters) asks the question: How did leks come to evolve? Many hypotheses are given, with supporting evidence when available, some of which relate to intraspecific variation and its ecological correlates. The last part of the book is a

short conclusion that recapitulates the important points, and presents the best prospects for future studies, with emphasis on the need for experimentation rather than description or the search for correlations.

The book is very well researched: an impressive 603 references are listed. Many facts are conveniently summarized in the form of tables that refer to previous work. But do not think that this book is a mere collection of empirical findings. Theories are expounded, and the authors do not shy away from conceptual and mathematical models to explain the evolution of leks or some of their characteristics. They also do not hesitate to admit to the existence of debate around many questions. Indeed, I got the impression that most questions about sexual selection in lekking species and the evolution of leks have not yet been satisfactorily answered.

This is the latest in a series of 13 monographs in behavior and ecology edited by John R. Krebs and Tim Clutton-Brock. The high standards of the previous books are maintained, in terms of both contents and presentation, and I think that people who appreciated these previous monographs will also like this one.

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Animal Evolution: Interrelationships of the Living Phyla

By Claus Nielsen. 1995. Oxford University Press, New York. ix + 467 pp. Cloth U.S. \$137.50; Paper U.S. \$54.00.

Claus Nielsen has compiled an extremely impressive review of the major features of animal phyla, and within a phylogenetic framework. This masterpiece integrates both developmental and adult characteristics into a synthesis that will form THE fundamental reference for the evolution of animal phyla for at least the next decade – a truly impressive accomplishment. This work not only offers a complete phylogenetic analysis of all animal phyla, it contains new hypotheses of relationships where such rearrangements are supported by clear, unambiguous synapomorphies. Each chapter of the book illustrates a summary of hypothesized relationships by noting the shared derived character states on the phylogenetic tree. There can be no misunderstanding about hypotheses. Where genealogical relationships are unclear, such as in the relationships of the Oligochaeta and Polychaeta relative to one another

and to other Annelida, the tree branching sequences are left unresolved. Five taxa are simply considered as "enigmatic". The analysis is sound, and not at all speculative. Each chapter has a list of critical references from which the character states were derived.

This book has great potential as a university classroom text. Although this does not appear to be the intention of the text, learning about the progression of animal complexities could not be presented in a more lucid manner for students. For the first time, this exceptional work integrates phylogenetic theory into describing the main features of all animal groups. I would highly recommend this book for anyone with an interest in the evolution of animal phyla; you will not be disappointed.

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Bird Song: Identification Made Easy

By Ernie Jardine. 1996. Natural Heritage/Natural History, Toronto, Ontario. 207 pp., illus. \$14.95.

This small book is an excellent introduction to identifying bird song. My first impression is to go out and try it out to see how well it works. The book has a straightforward introduction to categories of bird song which are based on the type of song. Songs are divided up into very short song, repeated notes, short songs with varying notes, and long songs with varying notes. A symbology for how songs sound is presented, which is obvious and requires little prior understanding to follow. The song is also explained in the text with the familiar word representations such as kee-kee-kee-kee or wick-wick-wick-wick for the northern flicker. Some delightful sketches of birds identify sections in the text.

The book is divided into two main sections, one dealing with the main types of song following a species by species account and the second organized by major habitats in which birds may be found. This

seems to me to be particularly sensible and will allow a person to identify a song easily. The book does not attempt to cover all the species, but rather 125 of the commoner ones. This should be sufficient for people to try out birding by ear and see if they enjoy it. The book provides some useful references though I was surprised that no reference was made to the complete songs and calls which accompanies Godfrey's *Birds of Canada*. This set of discs or tapes provides one of the best references of bird song and would be a must for someone wishing to expand their listening skills. For anyone who is not very good at identifying bird songs and wants to get into improving their skills, I would heartily recommend this little guide.

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A Century of Avifaunal Change in Western North America

Edited by Joseph R. Jehl, Jr. and Ned K. Johnson. 1994. Studies in Avian Biology Number 15, Cooper Ornithological Society, Camarillo, California. viii + 348 pp., illus. U.S. \$40.00.

The Cooper Ornithological Society was devoted in its early years almost entirely to western North America and although papers published in its journal, *The Condor*, now encompass the entire continent and beyond, the society still tends to meet in western U.S. states. Thus, a symposium of avifaunal changes in western portions of the continent was a particularly appropriate aspect of the society's 1993 centennial anniversary celebrations in Sacramento, California. This 27-chapter book puts the presentations made during that symposium on record.

A brief overview by the editors outlines the generation of the symposium and contents of the book. The editors note the profound changes brought by humans to the habitats of western North America over the last century, emphasizing the fact that these have been detrimental to many native species, but beneficial to others. The rest of the book is divided into five sections: "regional avifaunal change" (eight chapters), "population trends" of broad groups of birds (eight chapters), "effects of human-induced environmental change on avian populations" (four chapters), "case histories" (five chapters), and "prospects" of preservation and restoration (one chapter). Each chapter contains its own list of literature cited.

Although the title describes the contents of most of the book, it is slightly misleading in two ways.

First, the geographic area encompassed differs somewhat from that suggested by it. The editors comment that "essays on exploration and avifaunal change in western Canada and Mexico, including their offshore islands, could not be included." There is a chapter, by C. Stuart Houston, on "the unlikely 18th century naturalists of Hudson's Bay" and a chapter on current status of wetlands avifauna in Mexico's Baja California, but these are the only two chapters exclusively on these two countries. Canadian content in other chapters that encompass Canadian populations is highly variable. Johnson's chapter on "pioneering and natural expansion of breeding distributions in western North America" includes extreme southern portions of British Columbia, but excludes most of that province and all of the other western provinces and territories. Chapters on shorebirds, population trends of landbirds, changes in wintering populations and population trends of introduced birds and Marbled Murrelets contain considerable Canadian content, though mostly with notable omissions. For example, although Christmas bird counts published in *The Canadian Field-Naturalist* were part of the data set on which the chapter on changing winter populations is based, the many Saskatchewan counts published in *The Blue Jay*, were not. Papers on Spotted Owl and Brown-headed Cowbird include general information on British Columbia, but few details. Others on seabirds, waterfowl, raptors, "native pest species," coniferous forest birds, grassland birds, changes in avifauna of saline and alkaline lakes, and avifauna of western riparian habitats con-

tain either brief examples from Canada or no Canadian content whatever in spite of a rich array of Canadian literature. One paper (that of Terry L. Root and Jason D. Weckstein) covers all of the continental U.S. and the eight "southernmost" Canadian provinces (including Ontario, Quebec and two Maritime provinces), rather than western North America. Houston's paper, covering the former Hudson's Bay Territory, covers northern central North America, with about as much eastern as western area. Two papers are on Hawaii, politically part of the U.S.A., but biologically not part of North America. The second deviation from the title is that two papers, Houston's on Hudson's Bay explorers and one of the papers on Hawaii, cover early ornithological history on the areas covered, mostly before the century covered by the book, with little information in them on avifaunal changes. While I found both chapters very interesting, I wondered why they were in this particular book.

Although Canadian content *per se* is lacking or sparse in several of the chapters of direct concern to Canada, the book is full of information relevant to us. The chapters are written well on the whole, with numerous references in most. Thus, the book should serve as an important information source for researchers working on ecological aspects and conservation of bird species in western Canada. I found about 50 errors, mostly minor grammatical flaws and misspelled or outdated species names. The latter are puzzling, considering that both editors are well known for taxonomic studies. A few references vary slightly between text and the literature cited section and a few others are missing entirely.

Biological errors are few and mostly a matter of omission or outdated information. Wild Turkeys have definitely (not just "probably") been reintroduced to Ontario (page 194). Although the increase and range expansion of Barred Owl is well documented, it is not true that there were "no northern populations... reported west of the 100th meridian, and only one individual north of the 50th parallel –

in Pinawa, Manitoba" between 1963 and 1972 (page 198). That statement may well apply to the Christmas bird count data in the data base examined, but there are published records in all three prairie provinces during that period. Manitoba populations of Gray Partridge are missing from the table of successful introductions (page 222), as are both Manitoba and Saskatchewan populations of Rock Dove. Although I would have agreed with the statement that Winter Wrens are "associated with continuous forest" (page 239) until recently, my colleagues and I working in the Nimpkish Valley of northern Vancouver Island in 1995 and 1996 also found them to be abundant on logged areas, where old stumps and upturned roots provide plenty of nesting sites.

Many of the conclusions and hypotheses based primarily on U.S. populations also apply (or potentially apply) to Canadian populations, such as the effects of fishing pressure and techniques on seabird populations, and the effect of shrinking riparian habitat on the parasitism rate by cowbirds on some of their host species. Michael Scott's comment in the closing chapter that the environmental demands of expanding human populations constitute "the ultimate cause of extinction and jeopardy" (page 342) applies to most troubled species in all areas, and his final admonition that "the best time to save a species is when it is common" should be drilled into the minds of all wildlife managers and budget-slashing finance ministers!

The authors, editors and the Cooper Ornithological Society can be proud to have produced an outstanding anniversary volume that will long serve as a valuable reference source, although Canadian readers will need to supplement it with bibliographies, other books and journal papers from British Columbia, the prairie provinces, and the northern territories.

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The Red-winged Blackbird

By Les Beletsky. 1996. Academic Press, San Diego, California. 314 pp., illus. U.S. \$40.00.

This new book about one of my favorite birds, the Red-winged Blackbird or "Redwing", is subtitled *The Biology of a Strongly Polygynous Songbird*. It is the conspicuous male that gives rise to the name; its habit of acquiring several mates is one of the features attracting behaviourists. Instead of a dust jacket, this book has a striking colour photo – of a male Redwing feeding nestlings – on the hard-bound cover, a pleasing feature. Otherwise, the book lacks colour photos, relying on 28 black-and-white illus-

trations by David Beadle. These aptly portray several aspects of both male and female Redwing behaviour. This is a fairly detailed account of research studies of behavioural ecology of Redwings and related birds conducted mainly by university professors and their graduate students over the past 30 years.

Beletsky has studied the Redwing for more than two decades, working in New York, Michigan, and Washington state. Much of this book deals with his post-doctoral studies in Washington where he collaborated with professor Gordon H. Orians, a major figure in blackbird research.

Although this comprehensive review of Redwing biology deals primarily with academic studies, the author writes with enthusiasm and clarity. For a student, or a professor, wishing to embark on a research project, this book offers a wide range of possibilities, a guide to what's been learned, and which avenues provide further opportunities for study. For naturalists, or birders with an enquiring mind, this book will reveal a new world of ornithological endeavour. Whether laypersons, as suggested on the back cover, will find this book appealing is less clear.

The author states: "Although there are other books that feature Redwings, there is no other that covers so broad a range of topics, nor one that synthesizes as much information; thus this book supplements more narrowly-focused publications." Female "bill-up" display, however, though fairly common and related to male bill-up display, seems to have been overlooked, though it was mentioned in a recent publication (Yasukawa and Searcy 1995). A few minor errors were noted, e.g., part of the last word on page 52 is missing; caps appear on three species (one misspelled), page 104; information omitted, first line of table, page 129; typos, page 126, 286, 291.

BOTANY

Flore Laurentienne

Par Frère Marie-Victorin, 3^e édition, 1995, mise à jour et annotée par Luc Brouillet et Isabelle Goulet. Presses de l'Université de Montréal, Montréal, Québec. xv + 1083 p., illus. \$58.

Les auteurs de cette troisième édition se sont donné pour objectif de «fournir une synthèse des travaux (taxonomiques et floristiques) la plus exacte possible» concernant les espèces recensées au Québec tout en conservant le texte original de la seconde édition, devenue quelque peu désuète depuis sa parution en 1964. De cette deuxième édition, le livre reprend intégralement les préfaces, l'abrégé historique et bibliographique, l'esquisse de la flore laurentienne, la clé générale, la flore proprement dite, le résumé et le tableau statistique, le glossaire et l'index. L'avant-propos, signé par Pierre Dansereau, traite avec éloquence de la contribution et de l'influence du frère Marie-Victorin sur l'évolution des sciences au Québec et présente un portrait des progrès récents de la biosystématique et des sciences naturelles en Amérique du Nord. Les auteurs ont utilisé des chiffres placés en marge du texte original qui renvoient à 881 notes et références, à près de 700 photos couleurs ainsi qu'à une liste comprenant 325 taxons nouveaux ou présentant un intérêt sur le plan de la conservation. Ces additions portent le nombre total d'espèces vasculaires du Québec, décrites ou citées dans la nouvelle édition, à environ 2800.

There is now an astonishing volume of technical material published on the Redwing, much of which, as described in this book, is at the forefront of behavioural ecology. Dr. Beletsky cites more than 400 titles, including about 240 which specifically mention the Redwing; 28 are by the author. Beletsky, who hasn't lost any of his interest in the species, notes: "given what information is already available and what these birds have to offer, I am surprised that even more biologists do not study them... the Red-winged Blackbird has contributed mightily to several fields of research and should continue to do so for some time to come."

Reference

Yasukawa, K., and W. A. Searcy. 1995. Red-winged Blackbird (*Agelaius phoeniceus*). In *The Birds of North America*, Number 184. Edited by A. Poole and F. Gill. The Academy of Natural Sciences, Philadelphia, and the American Ornithologists' Union, Washington, D.C.

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Le format du livre est un peu plus grand que celui de l'édition précédente mais son utilisation demeure pratique sur le terrain. La qualité de la réimpression des planches est bonne. Les photos couleurs, dont plusieurs sont magnifiques, les notes et les références ajoutent un attrait au volume. En dépit de cela, le résultat est à mon avis décevant. Contrairement à l'annonce du communiqué de lancement émis par l'éditeur, la mise à jour de la nomenclature est incomplète et la répartition des espèces n'a pas été revue. La section des notes et références comporte beaucoup d'erreurs et des omissions importantes. Il en résulte un ensemble inégal où se retrouvent des travaux d'importance mineure en ce qui concerne la connaissance de notre flore et d'où sont absentes des contributions majeures de contemporains de Marie-Victorin et de botanistes de la génération actuelle, plusieurs flores locales ou régionales et des monographies comme celles de Benson sur les *Ranunculi* (*American Midland Naturalist* 1948) ou de Barkley sur les *Senecio* (*North American Flora* 1978). Certaines notes portent à confusion ou sont exprimées de façon maladroite: «L'épinette du Colorado (*P. pungens* Engelm.) fut également plantée [au Québec]. Son indigénat demeure ainsi discutabile» (note 217); «cette espèce agressive [*Lythrum salicaria*] déplace les milieux naturels» (note 455). D'autres sont

erronées ou ne tiennent pas compte des changements taxonomiques récents: «*Saxifraga gaspensis* Fern. n'a pas été répertorié au Québec» (note 402) alors que le type provient de la Gaspésie; *Solidago racemosa* et *S. randii* sont regroupés sous *S. spathulata* plutôt que sous *S. simplex* (note 662); *Alnus crispa* est regroupé sous *A. mollis* plutôt que sous *A. viridis* (note 251) en dépit des changements proposés par l'étude biosystématique à laquelle nous renvoyent les auteurs (note 249). Il est aussi mentionné que la taxonomie de certains genres, notamment celle des *Ranunculus* et des *Rubus*, est problématique. Cette remarque aurait pu être appliquée à d'autres genres au moins tout aussi problématiques (*Antennaria*, *Euphrasia*, *Crataegus*, etc.). Parmi les 700 photos présentées, une vingtaine sont mal identifiées (*Sedum purpureum*, *Hieracium pratense*, ...), au moins 60 ne permettent pas (ou difficilement) d'identifier la plante à l'espèce soit parce qu'elles sont de piètre qualité, soit parce que la plante se distingue mal de son environnement (*Myriophyllum exalbescens*, *Juniperus communis*, ...) et une dizaine sont mal orientées.

La liste des nouvelles espèces comprend plusieurs entités dont la valeur taxonomique n'est plus reconnue (*Ranunculus aquatilis* var. *calvescens*, *Lathyrus hultenii*, *Betula saxophila*, *Eriocaulon rollandii*, ...) et omet de signaler des additions telles que *Salix alaxensis*, *Saxifraga tenuis*, *Iris virginica* et *Cerastium arcticum*. Plusieurs espèces mentionnées comme nouvelles sont déjà citées dans le texte (ex.: *Astragalus aboriginum* var. *major* sous *A. forwoodii*, *Erigeron philadelphicus* ssp. *provancheri* sous *E. provancheri*, *Minuartia biflora* sous *Arenaria saja-*

nensis). On peut aussi s'interroger sur l'inclusion dans cette liste d'*Antennaria boecheriana*, *A. ekmaniana*, *A. sornborgeri* et *A. straminea* (ces deux dernières citées dans l'esquisse générale de la flore) puisqu'elles sont maintenant considérées comme synonymes d'espèces déjà mentionnées dans le texte. Par ailleurs, *Antennaria eucosma*, reconnu dans les traitements récents, n'y figure pas. Quelques erreurs d'indigénat se sont aussi glissées dans la liste (ex.: *Artemisia tilesii* et *Carex preagrabilis*). Dans plusieurs cas, la nomenclature des espèces de la liste n'est pas à jour (*Cystopteris fragilis* var. *laurentiana*, *Lonicera prolifera*, ...). En parallèle, les auteurs auraient dû dresser la liste des espèces à exclure de la flore du Québec ou dont la présence est à confirmer (*Carex lyngbyei*, *Arnica louiseana*, *Betula lenta*, ...). Enfin, il aurait été beaucoup plus pratique de faire figurer ces entités nouvelles en marge du texte à la hauteur des genres concernés.

En conclusion, un volume dont la présentation est soignée, comportant peu d'erreurs typographiques mais dont la mise à jour, sans doute précipitée, est incomplète et comporte trop d'erreurs et d'omissions. La Flore laurentienne restant un ouvrage incontournable tant pour les amateurs que pour les professionnels, je suggère tout de même à ceux qui voudront en faire l'acquisition d'attendre une réimpression dans laquelle les corrections nécessaires auront été apportées.

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Greenland Lichens

Eric Steen Hansen. 1995. Rhodos, Copenhagen. 124 pp. DK 150

Greenland Lichens is a thorough compilation of the lichen species found in Greenland. After many years of collecting in Greenland, Eric Steen Hansen has compiled this guide which includes 300 species of characteristically circumpolar lichens. The text has an introductory section which includes "Ecology and Plant Communities", "Practical Uses of Lichens", and "Collection, Identification and Conservation of Lichens". This section is well written but all too short. The methods for identifying lichens such as testing with KOH, for example, are casually mentioned and too briefly explained. Unfortunately, for the beginner, references are also missing from these sections.

There are no taxonomic keys to be found in the book. The lichens are divided into the macrolichens and microlichens and are presented in alphabetical order within each group. The *Cladinas* are distinct

from the *Cladonias* although the *Parmelia* group has been brought together under "*Parmelia*" with genera such as *Xanthoparmelia* and *Arctoparmelia* found in brackets following the old name. However, the synonyms are inconsistent. For example, *Bryocaulon divergens* is one species whose changing nomenclature has been hard to follow and here it is given without either of the synonyms.

Photographer Jørgen Andersen has provided a full colour photograph of each and every species. The plates are clearly printed and the colours are excellent. A very few of the darkest lichens such as *Cetraria andrejevii* are a little dark but not significantly so. Some shots are very close, focusing on the thallus, while others are further away and have been chosen to reveal associative patterns. Sometimes the type of shot doesn't work. For example, the photograph of *Cetraria sepincola* is too distant. The scales change quite a bit from species to species and the pictures lack a reference scale which can be confus-

ing. Further, a few specimens are mixed with other species and this could be confusing such as the *Cetraria cucullata* which has some prominent *Alectoria ochroleuca* mixed in. The specimens are from the Danish collection and most specimens look representative although a few specimens like the generally angular, *Cladina arbuscula*, appear too rounded.

Each lichen is described using terminology that is partially supplemented by a brief glossary but again this is not for the beginner. The specimens are generally well described but need comparison. For example, if I had trouble sorting *Umbilicaria arctica* from *U. hyperborea* in the field, these descriptions would not clarify the situation. Each description of a species is accompanied by a brief discussion of the range that it is found within Greenland and throughout the circumpolar area including Russia.

This is not an introduction to lichenology in the field and in that context it should be thought of as a companion to other texts such as Hale (1979), Thomson (1984), or other regional guides. *Greenland Lichens* is an exciting publication for sev-

eral reasons. This is an inexpensive (approximately \$35 CDN) little book (21 x 14 cm) with a plastic coating, superb photographs, and good descriptions of lichens which makes it feasible and very tempting to accompany you in the field. It has been written with considerable economy to make it that way and it will be excellent for the experienced field scientist in Greenland. There is nothing like it currently available in North America either. With these photographs and descriptions of the species, this is the book that will confirm or refute your original identification of a specimen. It is a gem for anyone who is planning to spend time anywhere in the arctic and it will cost less than 12¢ a photograph.

References

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 Thomson, J. W. 1984. *American Arctic Lichens: 1. The macrolichens*. Columbia University Press, New York.

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***Bromus* L. of North America**

By Leon E. Pavlick. 1995. Royal British Columbia Museum, Victoria, British Columbia. 160 pp.

The grasses placed in the genus *Bromus* are referred to as Bromes or Bromegrasses. Collectively they are ecologically and economically a very important part of the Canadian flora. The genus is distributed throughout Canada below the tree-line, both altitudinally and latitudinally. Smooth Brome (*B. inermis*) is a very important forage species introduced from Eurasia. Its aggressive growth habit, which makes it an excellent forage grass, is also causing problems as it invades and degrades native habitats. Among the half dozen weedy annual species of significance in Canada, Downy Brome (*B. tectorum*) is one of the most serious weeds of arable fields and rangelands in the Prairie Provinces. It is even a legally regulated weed in Manitoba, Saskatchewan, and Alberta. Some of the perennial species are important as wildlife forage in forested regions and rangelands (e.g., *B. ciliatus*, *B. porteri*), while others are considered rare plants in certain jurisdictions (e.g., *B. kalmii*).

This book represents a rather classical monograph of the genus and provides a updated review of the group throughout North America. The author's style and approach is, however, useful and readable to a wider audience other than just the classical taxonomist. A brief introduction outlines the background, scope and *modus operandi* of the work. The species concepts (which differ among taxonomists)

adopted are briefly discussed. The approach is one of recognizing overlapping morphological variation when it can be largely (if not completely) correlated with ecological and/or geographic patterns. The author states that "No new species are proposed but a number of sometimes neglected taxa are resurrected [to the species level]". A description of the genus is followed by a brief discussion of the classification within the grass tribe and the infrageneric taxonomy of the Sections.

The identification aids begin with a key to the five Sections recognized. Each Section then has a separate key to the recognized species and varieties (sub-specific taxa). The species descriptions are consistent and highly readable considering the dry nature of such information. After the main description there is a discussion of variation and key or description of any recognized varieties. Extensive details of the distribution and habitat are frequently given. A list of "major references" concludes the species accounts and is of exceptional utility as it gives users access to a broad range of taxonomic literature including original descriptions, differing taxonomic opinions (and taxonomic problems) and further keys, drawings, descriptions and other biological information.

After the species accounts is a section, referred to as "Nomenclature", where the synonymy and complex nomenclature is given for each recognized taxon in tabular format. This is particularly useful

to those interested in studying *Bromus* as the sources of all published names applying to North American taxa and their synonyms are given. It is also very useful to those less ardent students as it allows easy comparison with the nomenclature and species concepts of other regional floristic and taxonomic works.

Of particular note is the glossary which admirably explains, in direct and unadorned language, the specific and often obscure terminology used to describe the anatomical, morphological and ecological conditions which are often specific to the grass family. The overall format of the book is pleasing and utilitarian. Species accounts begin on the top of a left-hand page with the illustrations on the right-hand page. Exceptions occur only when there is no illus-

tration available for the taxon. Distribution maps are generally on the lower left and are large enough to be easily readable. Some of the maps of species of limited distribution are hard to read because of the light shading and some illustrations have fared poorly during printing.

This book is the first comprehensive treatment of *Bromus* in North America since that of C. L. Shear in 1900. It is a welcome modern synthesis as well as a carefully and articulately constructed account of a major element in the flora of the Northwestern Hemisphere.

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Plants of Southern Interior of British Columbia

By R. Parish, R. Coupé, and D. Lloyd. 1996. Lone Star Publishing, Vancouver, British Columbia. 462 pp., illus. \$24.95, U.S. \$19.95.

Plants of southern interior of British Columbia is the third in a series of field guides of the flora of British Columbia. This book is divided into eight easy-to-find color-coded sections. Rather than adopting the traditional Englerian system of classification commonly used in most floras, the authors have opted to classify the plants into seven distinct life-form groupings that include: trees; shrubs; wildflowers; grasses and grass-like plants; ferns and their allies; mosses and liverworts; and lichens. Although their system of classification may at first seem unconventional, its simplicity has made this book very accessible to the non-professional.

The introduction includes a brief overview of the climate, vegetation zones, and habitats encountered within the province's southern interior and provides the reader with a sense of the region's climatic, ecological, and floral diversity. Useful maps depicting the geographic extent of the area covered in this book and vegetation zones one would encounter within its boundaries are provided on the inside front and back covers. The section on aboriginal plant use and knowledge provides an interesting ethnobotanical perspective.

The bulk of the book is comprised of species descriptions. Each of the seven life-form groupings begins with a general description of the plants included in each within group, followed by a dichotomous key and line drawings or photographs. The more than 1000 photographs and 700 line drawings are of good quality and illustrate the plant's general appearance, and often, one or more of the diagnostic characters. Dichotomous keys usually precede some of the larger, more complex plant families within each group (e.g., Compositae, Fabaceae).

Each species described includes: a common and scientific name; a description of its appearance and habitat; diagnostic features of the leaves, fruits, and flowers (these are commonly boldfaced); ecology; and notes on important taxonomic, ecological, and ethnobotanical features. However, I did notice that the names of the validating authors for the specific epithets were not included. Although this omission is not critical to the overall utility of the book, inclusion of these names would have made this volume a much more useful source of information for students of plant taxonomy and systematics. Nonetheless, the authors provide a reference list where such information can be obtained. While the authors have made a valiant attempt to reduce the often unnecessary terminology found in most floras, the inherent nature of floras is such that terminology cannot completely be avoided. They have therefore included an illustrated glossary for the terms that were deemed necessary.

It is immediately evident that the authors have put considerable time and effort into the research and preparation of this book. They have successfully woven elements of taxonomy, ethnobotany, and ecology into a beautifully illustrated and informative volume. The only error that I noticed was the inclusion of the Lycopodiaceae (club mosses) and Selaginellaceae (spike mosses) with the mosses rather than the ferns and their allies. Although most floras and field guides commonly neglect to include the mosses, liverworts, and lichens, their inclusion (at least those species common to the region) here provide the reader with a relatively comprehensive overview of the regional vegetation.

The publishers ought to be congratulated on producing a book that is handsomely bound, compact, and appears durable enough to withstand the rigors of field work. More importantly, they have kept its price low which makes it an attractive alternative to some

of the more expensive professional floras. I highly recommend this book not only as a source of information for the specialists, but to the non-specialists interested in southern British Columbia's flora.

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ENVIRONMENT

Wild Thailand

By Belinda Stewart-Cox, photographs by Gerald Cubitt.
MIT Press, Cambridge, Massachusetts. 208 pp., illus.
U.S. \$40.00.

Bangkok is a city of extremes: beautiful buildings and ugly poverty, but the photographs in *Wild Thailand* show a lush countryside, hundreds of orchid species, exotic animals, and curious insects. There has been a reduction in undisturbed forest from 70% in the 1930s to 15% of the land area of Thailand today. The author fluctuates between lyrical praise of what still remains of the original countryside, and despair at the loss of so much of it to make way for development and provide raw materials (particularly wood) to the rest of the world. In spite of a population explosion and the consequent need for housing and agricultural land, efforts have been made to conserve what is left: there are 77 national parks, 36 wildlife sanctuaries, and 40 non-hunting areas.

Wild Thailand is a lavishly illustrated overview of the country's natural history, and the photographs are superb. However, the text has more depth than usual in this genre, and also chronicles the efforts of both Thais and dedicated western ecologists to prevent further degradation. Government support dates from the 1970s and there are several effective indigenous non-governmental organizations working within the country, often in partnership with world conservation organizations such as UNESCO.

The index is unusually comprehensive, and the bibliography has a high proportion of Thai authors. Reading this lovely book leaves one feeling optimistic that Thailand will succeed in halting the devastation of the past century and conserve the rich flora and fauna.

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Ecology of Infectious Diseases in Natural Populations

Edited by B. T. Grenfell and A. P. Dobson. 1995.
Cambridge University Press, Cambridge, Massachusetts.
xii + 521 pp., illus. U.S. \$59.95.

The Isaac Newton Institute brought together experts from 11 countries for a workshop in March 1993. The four working groups dealt with population biology, genetics, evolutionary issues, and the spatial dynamics of parasitism. The result provides a synthesis of current knowledge about the quantitative ecology and epidemiology of infections in both animal and plant host populations. As the introduction states, "The epidemiology of infectious diseases is one of the great triumphs of applied ecology."

A few facts of general interest emerge. Brucellosis has been present for 75 years among Elk in Yellowstone National Park, but tests that are accurate in cattle, when extrapolated to Bison or Elk, give large numbers of both false negative and false positive results for this disease. Rabies, even as it spreads, is increasing in prevalence among Striped Skunks and Raccoons. The introduction of the myxoma virus to Australia initially led to widespread reductions in rabbit populations – until the virus became less virulent and the rabbits became more resistant. An effective vaccine for rinderpest led to

its eradication throughout much of East Africa. Do parasites regulate host populations? Yes, though as yet *Trichostrongylus tenuis* in Red Grouse is one of the few well-documented examples.

Macroparasites, such as lice, fleas, ticks, and various worms, have a diversity of antigens, cause morbidity more often than mortality, and may live in equilibrium with their host. Others may reduce host survival, increase susceptibility to predation, decrease the ability to defend resources, or affect host fecundity and even cause host castration. There are complicated relationships between parasites and hosts, between parasites, and between host nutrition, immune responses, infection intensity and disease prevalence. Many problems are spatial: tuberculosis among possums in New Zealand assumed great importance because it posed a potential threat to that country's lucrative cattle export market.

Most problems and their possible analyses and solutions are tested by sophisticated mathematical models. Each chapter has an unusually extensive bibliography. There is a useful glossary, but clearly if the reader needs help with some of the simpler terms, he or she should not be attempting to read this book.

In summary, this book is another example of the complexity of biological interactions, which can be understood only by highly specialized experts. This book on occasion should be a useful reference, whereby reading of the introduction and conclusion of one or two chapters might provide the needed

answer to someone's problem. Almost no one will read it from cover to cover.

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The Environmental Impacts of Lead Shotshell Ammunition and Lead Fishing Weights in Canada

By A. M. Scheuhammer and S. L. Norris. 1995. Occasional Paper 88. Canadian Wildlife Service, Ottawa, Ontario 54 pp.

Classical Mediterranean civilization is said to have collapsed in part through the toxicity of lead ingested by many routes (though a perusal of Plutarch suggests that the lack of nonlethal methods of political succession may also have been important); modern North America has recently banned its use in gasoline and paint. This easily-manipulated element has many attractive physical and chemical properties, but it can easily get out of control.

All pollution teaches us that insignificant actions endlessly repeated add up to significant problems. One shotgun shell may bring home a meal, while stray pellets disappear instantly into illimitable marsh and waters. A snapped fishing line is regretted mostly for the \$5 lure. As decades of shot rain down on ever-decreasing wetlands, and curtains of gear festoon telephone cables at bridges, the insignificant accumulates. Lost lead is swallowed for gizzard gravel by water birds, embedded and fallen pellets dissolve, and herbivores, scavengers, and predators consume lead with their food. As many as 200 pellets per square metre accumulate in marshes; 40% of North American waterfowl ingest sporting lead every season; and half the mortality of Common Loons (*Gavia immer*) may be due to ingested sinkers.

This clearly written document does what it sets out to do. Anyone interested in a brief review of the

history, production, environmental chemistry, and toxicology of sporting lead on Canadian birds should consult it. If, however, the reviewer is prepared to be astonished, it can also be read as a critique of many facets of Commercial Society: Thirty percent of carcasses of Loons, never legal targets, carry embedded pellets (page 30). Six shots are fired for every duck retrieved (page 10) and 20-45% of ducks hit are crippled rather than retrieved (page 37); I do not hunt waterfowl, but as a museum bird collector, such dismal marksmanship would have led me to seek remedial training or another method of obtaining specimens. Despite the 20 years of furore over this problem, without regulation only a tiny fraction of shot or sinker sales are of alternative materials (page 39). Almost all manufacturers queried by the authors considered Commercial ritual to be more important than the welfare of Canada's fauna, and none would disclose the amount of lead they currently use in these products (pages 12, 15).

Individuals and the market have had two decades to adjust to the knowledge that it is evil to shoot lead over marshes. Evidently only increased government regulation can save the hundreds of thousands of waterbirds killed or debilitated by sporting lead every year.

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Biological Checklist of the Kemptonville Creek Drainage Basin, RR#2, Oxford Station, Ontario K0G 1T0

An Ecosystem Approach to Living Sustainably – A Perspective for the Ministry of Natural Resources

By Paul A. Gray, Leslie Demal, Dave Hogg, Don Greer, Dave Euler, and Dave DeYoe. 1995. Ontario Ministry of Natural Resources, Peterborough, Ontario. vi + 77 pp., illus. Free.

Contrary to what the title suggests, this Discussion Paper (it is not a book) does not outline an ecosystem approach to living sustainably - by the authors' own admission, this document is intended "to serve as a catalyst for discussion and debate". In fact, in only one brief section (which is itself cited from another source), are any guidelines to living sustain-

ably listed. The rest of the document outlines a framework to organize the Ecosystem Approach, but no part of the framework is unique to this issue. Cooperation, shunning the me-generation, a citizen's approach, incorporating policies that reach beyond politicians' terms of office, effective communications, learn from history - all of these are useful ideas, but none is elaborated upon in the context of an ecosystem approach to sustainable living.

The paper emphasizes several themes throughout. The most refreshing one is contrary to the

“man and nature” symbolism (which implies mutual exclusivity) but rather “man as part of nature”. Rarely do the authors refer to *nature*, rather *ecosystem* is used throughout to emphasize the inter-relatedness of all organisms. Unfortunately, *ecosystem* and *ecology* are only defined in Chapter 5. Ironically, *ecosystem approach* is defined prior to the defining of *ecosystem*.

The history of the ecosystem approach is well researched. The body of the paper is only 59 pages yet the authors cite over 140 other documents. The ecosystem approach to sustainable living is contrasted with the conventional approaches, and a management framework is also discussed. The document ends with a program checklist that is intended to assist in the management of the ecosystem approach. The authors recognize a serious consequence of the ecosystem approach from the management (political) perspective. Current political boundaries are useless for this approach. Ontario (the province of the authors' residence) for example, has several ecosystems, none of which is enclosed by its current

boundaries - will we be redrawing maps so political and ecosystem boundaries are the same?

In several places in the document, common sense is delivered to the reader in a way that suggests that the item is novel. “Understand and effectively use knowledge...” is a suggestion that one hopes is not new to government! Even though graphics are supposed to help the reader better understand the text, many of the figures are complex and non-intuitive. Only a limited number of field naturalists would find this document useful, but that in itself is no criticism as the intended audience (and thus the writing style) is for managers and policy makers. The naturalists that are interested in policy making will find this useful, just as much (if not more) as a great bibliographic source as for the content of the paper itself.

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Ocean Forests: The Diversity and Value of Kelp Forest Ecosystems

By Carrie Konig. 1995 [1996]. Canada Biodiversity Associates Report 1: 13 pp. Free from Biodiversity Convention Office, Environment Canada, Ottawa, Ontario.

This pleasant pamphlet does not contain a description of the series of which it is to be the first, but since it comes from the Biodiversity Convention Office I assume that it is supposed to inform Canadians about the biotic diversity of their land and waters. How is public education under the rubric of ‘biodiversity’ supposed to differ from general ecological or conservation education? Such education should emphasise the identity and characteristics of particular taxa, and teach the reader to identify easily recognizable taxa which he has not previously distinguished. A document for Canadians should try to generalize its subject matter as widely as possible across Canada. It is on the basis of these assumptions that I review the first of this series (the work-term project of a co-op undergraduate), hoping that these principles can direct the production of future booklets in this series.

Canada: One theme of any Canada-wide treatment of a marine subject must be the oceanographic and biogeographic similarities and differences among the coasts. Here the text treats kelp forests as a purely Pacific phenomenon, and it is only through the map on the last page that Atlantic Canadians learn that their kelp-dominated ecosystems are ever considered forests.

Biodiversity: Learning to recognize previously unknown taxa depends on good biological illustration, but most drawings here are unlabelled decorations. One small drawing names nine seaweeds but does not distinguish kelps from others, gives no indication of scale, lacks the detail that inspires confident identifications, and labels what is apparently *Laminaria setchellii* as *L. saccharina*. There are no labelled drawings of the invertebrates, fish, birds, and marine mammals listed as residents of kelp forests. If the Biodiversity Office cannot afford to have good new drawings made for these booklets, they should be able to get permission to use published authoritative drawings if they advertise the sources in captions.

The text is well-written and accurate enough that a ruthless peer-review and editing would have purged it of errors. It's a good idea to have students work up this kind of document, but they should learn that such reviews are part of scientific publication, and government offices should see that the reviews are solicited and fully heeded.

FREDERICK W. SCHUELER

Biological Checklist of the Kemptville Creek Drainage Basin, RR#2, Oxford Station, Ontario K0G 1T0

Human Ecology: Fragments of Anti-fragmentary Views of the World

Edited by Dieter Steiner and Marcus Nauser. 1993. Routledge, London and New York. xxv + 365 pp.

This is another multi-authored volume in which workers in a field which ought to have been ecologically premised try to come to grips with the fact that they have slighted the ecological basis of the phenomena they study. Here Swiss geographers face the danger that impressive neologisms will arrive at a commonplace reading of the daily headlines in a convoluted rehearsal of what every naturalist has long known.

There is nothing here that is much like ecology, and if geography is not already, or does not already contain, human ecology, then geographers should try out existing ecological theories and practices, rather than inventing over-elaborate theories which give the impression that the social sciences are an exercise in flawed assumptions. Scientific ecology is no panacea, but geography will not be ecologically grounded by infusing quasiecological concepts into the arcane conceptualizations and unneeded classifications of social pseudosciences. *A priori* descriptive theories of society will always prove too artificial, complex, and self-referenced to predict future events.

Would-be eco-reformers should review the literature of other fields to see who first made suggestions similar to theirs, and study the success of previous usages before proposing new terminology. Is "the ethico-political articulation of ecosophia" (page 333) an improvement on the preservation of the world in wildness, wise use of natural resources, the land ethic, ecophilia, sustainability, biophilia, sense of place, or the many other names by which ecological responsibility has been known? The struggle for a human ecology is not so much with facts and events but against the ease with which ideas can be narrowed, professionalized, and co-opted. There are good and valid ideas here, but we need clear, simple language, not jargon-bound fragmented scholarship, to describe and confront ecological change.

In the chapters of the first of four parts, *Human Ecology*, S. Boyden uses new-made words to seek trans-disciplinary understanding; D. Steiner reinvents historical contingency in the arbitrary formalism of triangular interactions among Person-Society-Environment; P. Weichart reflects on human nature, finding that in ecological interactions, actions are a more appropriate unit of study than the interacting individuals; and M. Hupperbauer finds philosophies of the ahistorical sciences inadequate for dealing with the "ecological crisis," but does not invoke existing philosophies of the historical sciences.

Part II, *The implicit and the explicit*, deals with People's knowledge of their environment. C. Carello tries to break down artificial limitations on the academic study of phenomena; I. Josefson makes preci-

sion rather than falsifiability the criterion of scientific discourse; G. Pillet reinvents economics with additional non-monetary currencies; H.-J. Mosler proposes that a phase-shift towards ecologically benign behaviour may come through a combination of government incentives and individual commitment; and finally D. Reichert channels streams of consciousness about the philosophy of subject-object relationships into diverse fonts. Part III considers structuration theory, which in R. J. Lawrence's exposition seems to be a formalization of political discourse, ignoring the wider realms where such discourse is known to break down; while M. Nauser points out that People have differing access to, and abilities to evaluate, "environmental" information; and A. Lang disparages vaguely described, "traditional" theories of the mind, and then applies basic ethological principles to human memory, culture, and architecture.

Part IV, *The regional dimension*, seeks to apply these ideas to "the environmental crisis." G. Bahrenberg and M. Dutkowski present a brief for a decentralized post-commercial society with "fault-tolerance," which seems mostly an epiphenomenon of local scale; B. Werlen develops the notion that People associate events with the places where they happened; D. Steiner, G. Durrenburger, and H. Ernste counter the fragmentation of personal roles in modern commercial society with commonplaces of the back-to-the-land, home-schooling, feminist, and regional development movements. O. Soderstrom wavers between multiple theories, all of which seem too abstract to handle data which might bear on them, and when data finally are considered by P. Gould, spatial "analysis" is isopleth maps of the spread of AIDS, without correction for population density or other plausibly explanatory factors.

In general these essays are more decorated with references to the literature than documented by them. There is no attempt to falsify alternative theories with data, and the discussions occasionally break down into ecofreak whining. There is little of the recognition one would expect from Swiss authors of traditional public democratic deliberation, among People who understand the long-term ecological consequences of their actions, in appropriately bioregional jurisdictions, as a means of settling ecological problems. Perhaps there is more among these admitted fragments than "think globally, act locally," but if we could implement that admirable slogan we could then test the further geographic theories an ecologically sustainable society would need to guide itself through the millenia.

FREDERICK W. SCHUELER

Biological Checklist of the Kemptville Creek Drainage Basin, RR#2, Oxford Station, Ontario K0G 1T0

Biodiversity and Conservation of Neotropical Montane Forests

Edited by Steven P. Churchill, Henrik Balslev, Enrique Forere, and James L. Luteyn. Proceedings of the Neotropical Montane Forest Biodiversity and Conservation Symposium, The New York Botanical Garden, 21–26 June 1993. Published by The New York Botanical Garden, Bronx, New York 10458-5126, U.S.A. 702 pp., illus. U.S. \$85.

Biodiversity and Conservation of Neotropical Montane Forests is a volume which represents the compilation of works generated through and from the symposium for Biodiversity and Neotropical Forests held 21–26 June 1993 at the New York Botanical Gardens. Over 200 scientists from 16 countries attended the symposium with one goal: to share their information in an effort to better understand the tremendous biodiversity found in the montane regions of the Neotropics. Their goals included helping to educate the public about the increasing deforestation taking place in these areas. The Editors have undertaken a major task and have been successful in

preparing a volume which is both informative and thought provoking. Its usefulness is evident for both the lay person and of course, the field-naturalist.

In order to truly appreciate this volume one must first appreciate the geographic areas known as the Neotropics. Further, we must then side-step our scientific appreciation for such locales and examine their worth from a more global context. In particular the section titles: Plants and Humans; Impact and Utilization in Montane Environments and Montane Forests: Conservation and future are most thought provoking. The text is arranged under several sections and is a useful informative body of work recommended for anyone interested in studying the biodiversity and conservation of the neotropical forests.

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The New Ecological Order

By Luc Ferry. 1995. Translated by Carol Volk. The University of Chicago Press, Chicago, Illinois. 176 pp. Cloth U.S. \$34.95; Paper U.S. \$14.95.

Luc Ferry is a French philosopher who has studied the Deep Ecology Movement and brings his reflections in a presentation showing the origins of deep ecology and current thinking on the subject, as well as significant historical events and thinkers who contributed to the philosophy of deep ecology. Aldo Leopold's *A Sand County Almanac* (1949), and Henry Salt's *Animal Rights Considered in Relation to Human Progress* (1894) to Christopher Stone's *Should Trees Have Standing* (1974), and Bill Deval's *The Deep Ecology Movement* (1980) are just some of the references which Ferry uses to lead us into the ideas of deep ecology as a philosophy of the rights of the environment, animals, birds, reptiles, plants, and rocks.

The question which Luc Ferry puts to us is whether natural things have rights over human beings or whether human beings have all of the rights and natural things have only vicarious rights as a part of the interests of human beings in any situation. The question is both philosophical and timely as we see our resources and the very shape of our planet being altered swiftly. The question is not new, but the nature of questioning has changed from the interests of vinegrowers protecting themselves from infestations of insects in the 16th century, and people wishing to protect themselves and

their children from attacks of domestic dogs in this century, to the interests of a developer in California having been prevented from transforming a natural growth desert canyon into a tourist theme-park.

Ferry tries to explain deep ecology, the idea that the natural world has status and rights which are inviolable by any human beings. He shows the contrast with European traditional understanding of natural things being owned, managed, and disposed of, by any particular human, who at any time has control of the area where the nature happened to be sitting. The question is timely and very important for our life and the future of the planet. Is the natural world to be administered as a resource to be used only on the simplest ethic of production and consumption or can a deep ecologist dictate to the world what the world needs? Are we to follow the voice of a profiteer, or the voice of one who claims to speak for the natural world? Ferry puts these questions before us in a very readable and at times entertaining light, including anecdotes from different political debates, summaries of trials where natural phenomena were in question, and an historical journey through the development of the deep ecology position.

The New Ecological Order tells us from where we have come and gives some ideas, cautions, and signposts. I enjoyed the book and found it to be an easy, and fairly swift read. It is written to a college

level reader and can be managed in a few hours. The material is pertinent and tries to give a balanced view taking material from both sides of the question as well as from history, with the bias being toward conservation of resources. You may not find this book in many bookstores but it is

available from the major chains on special order at the price listed above.

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The Environmental Promise of Democratic Deliberation

By Adolf G. Gunderson. 1995. University of Wisconsin Press, Madison, Wisconsin. xiv + 265 pp.

It's hard to know what to think of this book. At first it seems like a wildly uncontrolled experiment: environmentalist graduate student systematically chats up 46 non-random inhabitants of Wisconsin for 4-12 hrs each, and finds that they develop environmentally responsible views during the interviews. But where might he have found a serious scholar to do the counter-interviews? Is there anybody who could make a plausible case that modern North American society expends too much effort in protecting its "environment?" (Very likely all our many opponents are really NIMBY's who think environmental protection is fine except when it affects themselves or their industry.) It would have been fascinating to see the results of such control interviews, especially since Gunderson finds that individual Wisconsinians are prepared for much stricter government policies than anything that would be imaginably enacted in that country.

He did form a picture of the environmental ideas of his subjects. Many of them haven't thought much about such issues, but they find that they support environmental reforms for many moral, philosophical, economic, personal, social, and religious reasons, but oppose those that they do oppose for a single reason. They think that environmental problems are the consequence of summing individual "sin," rather than seeing the societal structures that make it so hard for an individual to live responsibly. Perhaps the changes in their beliefs after this interview are a

sad commentary on the lack of conversation in a television age, but Gunderson sees the interviews as a model for turning personal beliefs and feelings of Americans into an effective political force for environmental reform.

This is a highly personal Ph.D thesis, cut up into chunks (text, appendix, and end notes) for the book, so one must read the notes with the text to appreciate the argument. No consideration is given to the date of the interviews (sometime before the 1991 date of the youngest references cited), or that Wisconsin is traditionally the most progressive of the United States. The text could have used really severe editing, as it is still turgid with the language of a dissertation, and rich in buzz words that are insufficiently explained for a general audience.

What are the reforms suggested? Gunderson states that to specify their form would contradict the method, which is more democratic deliberation, or political talk. It would have been inconceivable in the last century that there could be a lack of this commodity, and it may be inconceivable to naturalists that there is too little talk about the "environment." but Gunderson suggests that our retreat into privacy is so profound that most People just do not talk about these issues enough to realize how uniformly they feel the need for fundamental environmental reform.

FREDERICK W. SCHUELER

Biological Checklist of the Kemptville Creek Drainage Basin, RR#2, Oxford Station, Ontario K0G 1T0

Wild Ideas

Edited by D. Rothenberg. 1995. University of Minnesota Press. Minneapolis, Minnesota. xxvii + 225 pp., illus. U.S. \$19.95.

Wild Ideas is a collection of 13 essays written by philosophers for philosophers. As such, the book on the whole (though not all of its parts) is a challenging read. The essays' authors challenge the reader's notions of wilderness from a number of perspectives. These range from quite an eye-opening look at the "urban jungle" and its parallel the "untamed wild" to

the contrast between the "wild" and our fenced in, admission required, don't feed the bears "wilderness".

The essays are preambled by an in-depth introduction by the editor who discusses in easy to follow wording, some concepts of wildness and wilderness; he also gives a brief introduction to each of the essays in the collection. The essays are separated into four sections: Whose Wild Idea, Cross-cultural Wild, The Art of Wild and The Wild Revised. The second and third sections (seven essays) are particu-

larly challenging and likely require some experience in philosophy to fully appreciate. The first and last sections (six essays) are easier going and will likely be the most appealing to naturalists. The essayists challenge the reader to think about wilderness in ways that s/he may not have thought of before. Is there such a thing as "wilderness" to people (e.g., pre-European North Americans) who do not segregate themselves from the land? Is setting aside tracts of land good? When we consider conservation areas - places of sanctuary for animals and plants - are we committing cultural genocide by not allowing a rea-

sonable harvest by those who have done so for generations?

This book took me quite some time to get through (I am not a philosopher), but I did read the whole thing out of interest for the material. It is a challenging, yet surmountable collection of essays full of enlightening perspectives on the wild.

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Losing Ground: American Environmentalism at the Close of the Twentieth Century

By Mark Dowie. 1996. MIT Press, Cambridge, Massachusetts. 317 pp., U.S. \$25.00.

Losing Ground is a book about faith – faith in the ability of the irrepressible American spirit to breathe new life into the moribund environmental movement. Hard-fought victories may have been reversed during the Reagan and Bush presidencies, but the American creative imagination, according to award-winning journalist Mark Dowie, may yet lead to the emergence of a more radical, broad-based movement that will pursue environmental justice with an unprecedented vigour. In fact, if Dowie is to be believed, "the real environmental movement has barely begun".

Dowie reaches this conclusion by a curious route. The better part of *Losing Ground* is a stinging indictment of the history of 20th century American environmentalism. With deft precision, Dowie dissects the early conservation movement to reveal that its proponents were largely respectable, white outdoorsmen who sought to preserve their hunting and fishing privileges. He then describes how the inclusive nature of this group came to characterize the promising, new, environmental movement of the 1960s and 1970s. Several pieces of landmark environmental legislation may have been passed, but the people behind the

movement were predominantly white and monied. This "polite revolution" made tree-hugging a safe and popular form of dissent for many Americans. But it had a price. Environmentalism not only evolved into a "mainstream" elitist activity dominated by well-funded Washington lobby groups, but it compromised its defining principles when it chose to negotiate with an unsympathetic Republican White House. In short, the American environmental movement became irrelevant and ineffective at a time when it was needed more than ever before.

That Dowie can find hope in this depressing tale probably says more about the author than the future of the movement. Indeed, if the recent U.S. presidential campaign is any indicator, it will take an ecological disaster of unprecedented proportions to goad the American public into action. Becoming "appropriately rude and decidedly American", in Dowie's words, will not bring about a better world; protest movements take flight only when citizens are motivated to do something about a perceived problem. Hopefully that time will come before it is too late.

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NEW TITLES

Zoology

Bats in question: the Smithsonian answer book. 1997. By D. E. Wilson. Smithsonian Institution Press, Washington. 192 pp., illus. U.S. \$24.95.

Beluga: a farewell to whales. 1996. By P. Beland. Lyons & Burford, New York. 224 pp., illus. U.S. \$25.

***The birds of British Columbia, volume 3: passerines (flycatchers through vireos).** 1997. By R. W. Campbell, N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W.

Kaiser, M. C. E. McNoll, and G. E. J. Smith. University of British Columbia Press, Vancouver. 635 pp., illus. \$95.

†**The ecology, status, and conservation of marine and shoreline birds of the Queen Charlotte Islands.** 1997. Edited by K. Vermeer and K. H. Morgan. Occasional Paper No. 93. Canadian Wildlife Service, Sidney, B.C. 148 pp., illus.

†**King and common eiders of the western Canadian Arctic.** 1997. Edited by D. L. Dickson. Occasional

Paper No. 94. Canadian Wildlife Service, Edmonton. 73 pp., illus.

†**The Kingdon field guide to African mammals.** 1997. By J. Kingdon. Academic Press, Harcourt Brace Sidcup, Kent, United Kingdom. xviii + 464 pp., illus. £29.95.

***A natural history of amphibians.** 1995. By R. C. Stebbins and N. W. Cohen. Princeton University Press, Princeton. xvi + 316 pp., illus. U.S. \$29.95.

The origin and evolution of birds. 1996. By A. Feduccia. Yale University Press, New Haven. x + 420 pp., illus. U.S. \$55.

The private eye: observing snow geese. 1996. By M. Burns. University British Columbia Press, Vancouver. 224 pp., illus. \$29.95

†**Red-winged blackbirds: decision-making and reproductive success.** 1997. By L. D. Beletsky and G. H. Orians. University Chicago Press, Chicago. xxii + 294 pp., illus. Cloth U.S. \$65; paper U.S. \$21.95.

Running wild: dispelling the myths of the Afridan wild dog. 1997. By J. McNutt and L. P. Boggs. Smithsonian Institution Press, Washington. 150 pp., illus. U.S. \$45.

The science of overabundance: deer ecology and population management. 1997. Edited by W. J. McShea, H. B. Underwood, and J. H. Rappole. Smithsonian Institution Press, Washington. 432 pp., illus. U.S. \$37.50.

Sea cucumbers of British Columbia including Puget Sound and southern Alaska. 1997. By P. Lambert. University British Columbia Press, Vancouver. c192 pp., illus. \$24.95.

Snake lovers lifelist and journal. 1996. By C. Scott. University of Texas Press, Austin. 288 pp., illus. U.S. \$19.95.

†**A travel and site guide to birds of Costa Rica with side trips to Panama and Nicaragua.** 1996. By A. D. Sekerak. Lone Star Publishing, Edmonton. 256 pp., illus. \$29.95 in Canada; U.S. \$16.95 in U.S.A.

Western national wildlife refuges. 1996. By D. Wall. Museum of New Mexico Press, Santa Fe. 288 pp., illus. U.S. \$24.95.

Botany

†**The alpine flora of the Rocky Mountains, Volume 1: the middle Rockies.** 1997. By R. W. Scott. University Utah Press, Salt Lake City. 768 pp., illus. U.S. \$110.

Environment

Aiphanes (Palmae) by E. Borchsennius and R. Bernol; **Roystonea (Arecacea: Arecoideae)** by S. Zona; **Euterpe, Prestoea, and Neonicholsonia (Palmae: Euterpeinae)** by A. Henderson and G. Galeano; and **Allagoptera (Palmae)** by Moraes. 1996. New York Botanical Garden, Bronx. Volumes 70–73, Flora neotropica in one volume. 95 + 36 + 90 + 35 pp. U.S. \$50.

Biology of *Populus* and its implications for management and conservation. 1996. Edited by R. F. Settler, H. D. Bradshaw, Jr., P. E. Heilman, and T. M. Hinckley. National Research Council of Canada, Ottawa. 539 pp.

†**Contemporary plant systematics.** 1997. By D. W. Woodland. 2nd edition. Andrews University Press, Berrien Springs, Michigan. xiv + 619 pp., illus. + CDROM.

Ecology and management of sitka spruce emphasizing its natural range in British Columbia. 1997. By E. B. Peterson, N. M. Peterson, G. F. Weetman, and P. J. Martin. University of British Columbia Press, Vancouver. c288 pp., illus. \$75.

A field guide to the families and general of woody plants of northwest South America (Columbia, Ecuador, Peru). 1997. By A. H. Gentry. University of Chicago Press, Chicago. x + 895 pp., illus. Cloth U.S. \$75; paper U.S. \$45.

Flora of St. John, U.S. Virgin Islands. 1996. By P. Acevedo-Rodriguez. New York Botanical Garden, Bronx. 581 pp., illus. U.S. \$49.95.

Geographic variation in forest trees: genetic basis and application of knowledge in silviculture. 1996. By E. K. Morgenstern. University of British Columbia Press, Vancouver. 176 pp., illus. \$75.

The mushroom book. 1996. By T. Laessoe, A. Del Conte, and G. Lincoff. DK Publishing, New York. 256 pp., illus. U.S. \$29.95.

The origin and early diversification of land plants: a cladistic study. 1997. By P. Kenrick and P. R. Crane. Smithsonian Institution Press, Washington. 592 pp., illus. Cloth U.S. \$55; paper U.S. 27.50.

Environment

Alien invaders: the continuing threat of exotic species. 1996. By S. B. Collard, III. Danbury, Watts, Connecticut. 144 pp., illus. U.S. \$17.02

Biodiversity. 1996. By D. H. Patent. Clarion, New York. 109 pp., illus. U.S. \$17.95.

Canadian natural resource policy: from exploitation to management. 1997. By M. Howlett and M. Hessing. University of British Columbia Press, Vancouver. c384 pp. \$65.

Home owner's guide to naturalization. 1996. By L. Lavoie. Thunder Bay 2002, Thunder Bay. 42 pp., illus. \$8.

The language of environment: a new rhetoric. 1996. By G. Myerson and Y. Rydin. University of British Columbia Press, Vancouver. 256 pp. Cloth \$65; paper 24.95.

Manu: the biodiversity of southeastern Peru. 1997. Edited by D. E. Wilson and A. Sandoval. Smithsonian Institution Press, Washington. 672 pp., illus. U.S. \$35.

Natural change and human impact in Madagascar. 1997. Edited by S. M. Goodman and B. D. Patterson. Smithsonian Institution Press, Washington. 448 pp., illus. Cloth U.S. \$75; paper U.S. \$35.

Watching nature: a mid-atlantic natural history. 1997. By M. S. Garland. Smithsonian Institution Press, Washington. 256 pp., illus. U.S. \$15.95.

***Web of life.** 1996. By F. Capra. Anchor/Doubleday, Doubleday Canada, Toronto. xv + 347 pp., illus. \$32.95.

Miscellaneous

The ice-age history of southwestern national parks. 1997. By S. A. Elias. Smithsonian Institute press, Washinton. 216 pp., illus. U.S. \$16.95.

†**Molecular biology made simple and fun.** 1997. By D. R. Clark and L. D. Russell. Cache River Press, Vienne, Illinois, vii + 470., illus. U.S. \$34.95.

***Monad to man: the concept of progress in evolutionary biology.** 1996. By M. Ruse. Harvard University Press. Cambridge. x + 628 pp., illus. U.S. \$49.95.

Park prisoners: the untold story of western Canada's national parks, 1915–1946. 1996. By B. Waiser. Fifth House, Calgary. 296 pp., illus. \$27.59.

Books for Young Naturalists

Above the treeline; and In the forest. 1996. By A. Cooper. Denver Museum of Natural History, Denver. Each 44 pp., illus. U.S. \$7.95.

Animals and their world: biology facts and experiments; Butterflies, bugs, and worms: biology facts and experiments; and Flowers, trees, and fruits: biology facts and experiments. 1996. By S. Morgan. Each 32 pp., illus. U.S. \$6.95.

Animal babies. 1996. By C. Craig. Time-Life Books, Alexandria, Virginia. 32 pp., illus. U.S. \$11.95.

Chaparral; Desert; and Grassland. 1996. By E. R. Ricciuti. Benchmark Books, Tarrytown, New York. Each 64 pp., illus. U.S. \$16.95.

Exotic invaders: killer bees, fire ants, and other alien species are invading America. 1996. By J. M. Lesinski. Walker, New York. 49 pp., illus. U.S. \$16.95.

Guardians of wildlife. 1996. By G. Chandler and K. Graham. Twenty-first Century Books, New Yourk. 64 pp., illus. U.S. \$16.98.

Meat-eating plants. 1996. By N. Aaseng. Enslow, Springfield, New Jersey. 48 pp., illus. U.S. \$15.95.

Plants. 1996. By A., F., and R. Silverstein. Twenty-first Century Books, New York. 64 pp., illus. U.S. \$16.98.

Scaly things. 1996. By K. Lamprell. Time-Life Books, Alexandria, Virginia. 32 pp., illus. U.S. \$11.95.

Sharks. 1996. By S. Parker. Cooper Beech Books, Brookfield, Connecticut. 32 pp., illus. U.S. \$14.40.

Taiga. 1996. By E. Kaplan. Benchmark Books, Tarrytown, New York. 64 pp., illus. U.S. \$16.95.

Things with wings. 1996. By C. Creach. Time-Life Books, Alexandria, Virginia. 32 pp., illus. U.S. \$11.95.

You asked? Over 300 great questions and astounding answers. 1996. Edited by K. Farris. Owl Books, Toronto. 160 pp., illus.

†available for review

*assigned for review

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Cover: Typical aspen, *Populus tremuloides*, stand in Yoho National Park, British Columbia, showing extensive damage to bark by Elk, *Cervus elaphus*, no regeneration, and White Spruce, *Picea glauca*, invasion. Photo courtesy of Charles E. Kay. See article on the condition and trend of aspen in Kootenay and Yoho National Parks; implications for ecological integrity, pages 607–616.

Roost-site Characteristics of Common Poorwills, *Phalaenoptilus nuttallii*, in Saskatchewan

KAILI WANG and R. MARK BRIGHAM

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Wang, Kaili, and R. Mark Brigham. 1997. Roost-site characteristics of Common Poorwills, *Phalaenoptilus nuttallii*, in Saskatchewan. *Canadian Field-Naturalist* 111(4): 543–547.

To determine how vegetation and other characteristics of roost sites for Common Poorwills, *Phalaenoptilus nuttallii*, differed from those at randomly selected sites, we used radio-telemetry to track six individuals to day roosts which, with one exception, were different every day. Nine of the 10 variables we measured differed significantly between roost and random sites. Poorwill roosts had significantly less green vegetation, less overhead cover, more bare ground, and were further away from tall objects than random sites. Our results are consistent with the prediction that roost sites would consist mostly of areas which likely contrast less with poorwill's mottled brown plumage. Birds were regularly found roosting against "backing" objects which we suggest serve as shelter from wind, rain, or sun.

Key Words: Common Poorwills, *Phalaenoptilus nuttallii*, roost site selection, predation, colouration, Saskatchewan.

Common Poorwills (*Phalaenoptilus nuttallii*; hereafter poorwills) are found during the summer months in semi-arid and arid regions of western North America. In southern Canada, near the northern limit of the species' distribution (Csada and Brigham 1992), they occur in the Okanagan Valley of British Columbia and the Cypress Hills of Alberta and Saskatchewan. In Saskatchewan, poorwills reside in open areas, including hillsides and areas where trees have been harvested (Kalcounis et al. 1992).

Limited information is available on roost-site selection by these birds, likely due to the fact that they are generally solitary, nocturnal and highly cryptic. Both male and female poorwills possess plumage with a mixture of colours including brown, buff, black, and white. Published reports of their habitat use are restricted to anecdotal descriptions for single individuals and single sites (Aldrich 1935; Bent 1940; Orr 1948; Sutherland 1984).

Predation is often hypothesized to influence habitat selection by ground-dwelling birds as it is known to be a major source of nest failure (e.g., Lack 1968; Ricklefs 1969; Schieck and Hannon 1993). Predation on roosting adult poorwills by Northern Harriers (*Circus cyaneus*) has been documented in our study area and Coyotes (*Canis latrans*) are also potential predators (Wang et al. 1995). Predation likely imposes selective pressure on this species with respect to roost site selection.

Poorwills are one of the few birds that regularly use torpor (Brigham 1992), characterized by a drop

in metabolic rate resulting in a decline in body temperature, as a physiological means of saving energy. Unlike most small mammals which enter torpor while hidden in a burrow where predation risk is likely minimal, poorwills enter torpor at fully exposed roost sites. Therefore, torpid birds may be especially vulnerable to predation, making choice of day-roost site particularly important. Poorwills regularly use torpor in the Cypress Hills (Csada and Brigham 1994). Even when not torpid, poorwills use a "sit and hide" approach to avoid predators, and may be approached to < 1 m. The objective of our study was to measure features of poorwill roost sites. We predicted that, compared to random sites, roost sites would contain more dead vegetation and bare ground but less live vegetation, which should minimize the contrast between the bird's brown plumage and the substrate thus potentially decreasing the risk of detection by predators.

Materials and Methods

The study was conducted in May through August 1994 in the West Block of Cypress Hills Provincial Park (49°34'N, 109°53'W), in Saskatchewan. As male poorwills are territorial and respond to the calls of other males in their territory, we captured birds by luring them into mist nets using song playbacks. Using an elastic harness slipped over the wings (Brigham 1992), each captured individual was fitted with a 2.4 g radio transmitter (Holohil Systems Ltd., Carp, Ontario) which represented approximately 5%

of body mass. The second member of the pair (usually the female) was mist-netted at a nest or joint roost located by following the individual carrying the transmitter. In total, an area of over 300 km² including all clear-cuts (42 in total) and a large proportion of hillsides in the West Block, was surveyed for birds. We are confident that we captured all males in this area.

We used a Merlin 12 receiver and a hand-held 5-element Yagi antenna to locate the roosts of tagged individuals on a daily basis. When tracking, we tried to avoid flushing birds from their roosts. When a roosting bird was located and not disturbed, we marked the site with natural objects (e.g., sticks and rocks) and returned to make measurements the next day. If the bird was accidentally flushed while tracking, roost site characteristics were measured immediately. Individuals never used the same site as a roost for more than one day except for one male that roosted in the same spot for three consecutive days. This site was included in our analysis only once. There was no evidence that by roosting at a particular site, birds did anything to modify that site.

To quantify roost sites, we measured characteristics of a 1 m × 1 m quadrat centered on each roost (Ryan et al. 1984; Chang and Emlen 1993). The 1 m² area within the quadrat was divided into four equal 0.5 m × 0.5 m sub-quadrats. With the exception of "backing" (e.g., a log, tree, tree stump, or shrub immediately against which the bird was found roosting) and overhead cover (see Table 1 for definition of variables), all variables were measured in each of the four sub-quadrats, and then averaged to give a value for the entire site (Day and Flake 1991). The variables were of two general types: percentage cover variables and distance from the roost spot to objects or patches. Each percentage cover variable was assigned a value using the Daubenmire scale

(Daubenmire 1959) and placed into 1 of 6 classes: 0–4.9%, 5–24.9%, 25–49.9%, 50–74.9%, 75–94.9%, and 95–100%. The midpoints of each class were used in all calculations. For distance variables, we measured the distance from the center of the quadrat to the variable in each sub-quadrat. If the distance was greater than 1 m (< 5% of all cases), then 1 m was recorded.

"Backing" was recorded as present or absent for the quadrat as a whole. Percent overhead cover was determined by placing a poorwill sized plastic bag filled with orange flagging tape at the center of the quadrat and estimating (e.g., Schieck and Hannon 1993) how much of the bag could be seen through overhead vegetation. In no instance was vegetation at a roost site higher than observer eye level.

We used a random-number table to generate a distance (< 100 m) and a random compass direction in order to select a random site in the same clear-cut where a roost was found. Characteristics of random sites were measured in the same manner and on the same day as roost sites. Thus, each random site was "paired" with a roost site in our analysis which allowed us to control for seasonal changes due to vegetation growth.

We obtained data for 60 roost sites used by three male and three female poorwills (1 solitary male, 1 pair of birds and a male paired with two females in temporal succession) roosting in clear-cuts created by logging. We measured the characteristics of 25, 18, and 5 male roosts and 4, 4, and 4 sites used by females respectively. Because many of our data came from two males, and pseudoreplication could be a problem, we compared roost-site variables amongst individual birds to determine if pooling data was reasonable. This was done using one-way ANOVA, except for "backing" which was analysed using a 2 × 6 contingency table. Where there was a

TABLE 1. Variables measured at poorwill roost and random sites in the Cypress Hills.

Variable	Description and Definition
1. Percent trees/shrubs	Percent area of quadrat covered by trees and shrubs. Estimated by vertical observation from 1.6 m.
2. Percent grass	Percent area of quadrat covered by live (green) grass. Estimated by vertical observation from 1.6 m.
3. Percent litter	Percent area of quadrat covered by litter. Estimated by vertical observation from 1.6 m.
4. Percent ground	Percent area of quadrat covered by bare ground. Estimated by vertical observation from 1.6 m.
5. Vegetation distance	Distance from the center of the quadrat to the nearest patch of live vegetation (diameter > 8 cm).
6. Litter distance	Distance from the center of the quadrat to the nearest patch of litter (diameter > 8 cm).
7. Ground distance	Distance from the center of the quadrat to the nearest area of bare ground (diameter > 8 cm).
8. 30 cm object	Distance from the center of the quadrat to the nearest object >30 cm above ground level excluding "backing" (see below).
9. Percent overhead cover	Percent vertical cover of the bird's roost position (see text).
10. Backing	Log, tree, stump, soil ledge, or shrub, immediately against which, poorwill was found roosting (yes or no).

significant difference in site characteristics amongst the six individuals, Tukey's test (Zar 1984) was used to determine where the difference occurred. Prior to analysis, all percentage data were arcsin-transformed and all distances were square root-transformed in an attempt to normalize distributions.

To compare characteristics that were normally distributed after transformation, we used paired *t*-tests. For non-normally distributed data, we used Wilcoxon matched-pair tests on untransformed data (Zar 1984). A 2×2 contingency table was used to test whether backing was found at roost sites more often than expected. Linear regression analysis was used to assess seasonal effects on the amount of tree/shrub and grass cover at roost and random sites. This analysis was restricted to these variables as they would be expected to change most through the growing season when the study was conducted. Statistical tests were taken to be significant when $P < 0.05$.

Results

Only two roost site characteristics differed among individuals, namely, vegetation distance ($F = 4.05$, $P < 0.01$) and overhead cover ($F = 3.15$, $P < 0.01$). In both cases, the differences occurred between one of the females and the other five birds. Consequently, because 8 of the 10 site characteristics were not statistically different between birds, and because for five of six birds, all 10 site characteristics were statistically the same, we pooled all roost site data for comparison with random sites.

Of the 10 variables measured, only percent litter was not significantly different between roost and random sites (Table 2). Relative to random sites, roost sites had less cover by trees/shrubs and live grass, less overhead cover, and more bare ground. Roost sites were farther away from live vegetation

patches and from objects taller than 30 cm, but were closer to patches of litter and bare ground. Also, roosts were more likely to have "backing" than random sites.

The amount of tree/shrub cover at roost sites ($t = 2.40$, $df = 116$, $P < 0.01$) and the amount of live grass at random sites ($t = 3.30$, $df = 116$, $P < 0.01$; Figure 1) changed significantly with season, although the impact of these changes on poorwills was different. Poorwills selected roost sites which had more tree/shrub cover as the season progressed, but used sites with a constant amount of grass cover over the season even though the amount of grass cover declined with season at random sites.

Discussion

Relative to random sites, we found that poorwills roosted in locations with less live vegetation cover, more bare ground, closer to patches of litter and bare ground, and farther away from live vegetation. This combination of characteristics is consistent with the hypothesis that roost sites are chosen to minimize contrast between birds and their surroundings, given the similarity between poorwill's brown plumage and the typical colour of litter and bare ground. It is likely to a bird's advantage to avoid sites with live (green) vegetation as reduced contrast presumably lowers the likelihood of being detected by predators. At nest and roost sites, poorwills typically remain motionless and are very difficult to detect, at least by humans.

Like poorwills, Stone-Curlews (*Burhinus oedipus*), which are also nocturnal, and roost on sparsely vegetated ground, select sites with vegetation that is conducive to the bird remaining concealed (Green and Griffiths 1994). Stone-Curlews will not re-use sites when green vegetation cover increases during

TABLE 2. Results of comparisons between characteristics of poorwill roosts and random sites in the Cypress Hills. N = 60 paired sites from six birds. All *t*-tests were two-tailed.

Variable	Roost site (Mean \pm SE)	Random site (Mean \pm SE)	Test type	Test score
1. % trees /shrubs	28.1 \pm 2.3	38.1 \pm 3.0	paired <i>t</i> -test	$t = 2.90$, $P = 0.005$
2. % green grass	6.1 \pm 1.3	16.8 \pm 2.7	Wilcoxon matched	$T = 616$, pairs test $P = 0.028$
3. % litter	41.1 \pm 2.4	39.6 \pm 3.2	Wilcoxon matched	$T = 776$, pairs test $P > 0.05$
4. % bare ground	35.6 \pm 2.8	14.2 \pm 2.5	paired <i>t</i> -test	$t = 6.41$, $P < 0.001$
5. Vegetation distance (cm)	20.2 \pm 1.9	5.7 \pm 1.0	paired <i>t</i> -test	$t = 8.66$, $P < 0.001$
6. Litter distance (cm)	9.7 \pm 1.9	17.4 \pm 2.3	paired <i>t</i> -test	$t = 2.63$, $P = 0.011$
7. Ground distance (cm)	12.0 \pm 3.4	66.0 \pm 5.0	Wilcoxon matched	$T = 10$, pairs test $P < 0.001$
8. 30 cm object (cm)	48.0 \pm 2.8	36.5 \pm 3.6	Wilcoxon matched	$T = 574$, pairs test $P = 0.019$
9. % overhead cover	7.1 \pm 1.8	22.8 \pm 3.7	Wilcoxon matched	$T = 100$, pairs test $P < 0.001$
10. Backing	46 roost sites with backing	16 random sites with backing	Chi-square	$\chi^2 = 30.03$, $df = 59$, $P < 0.001$

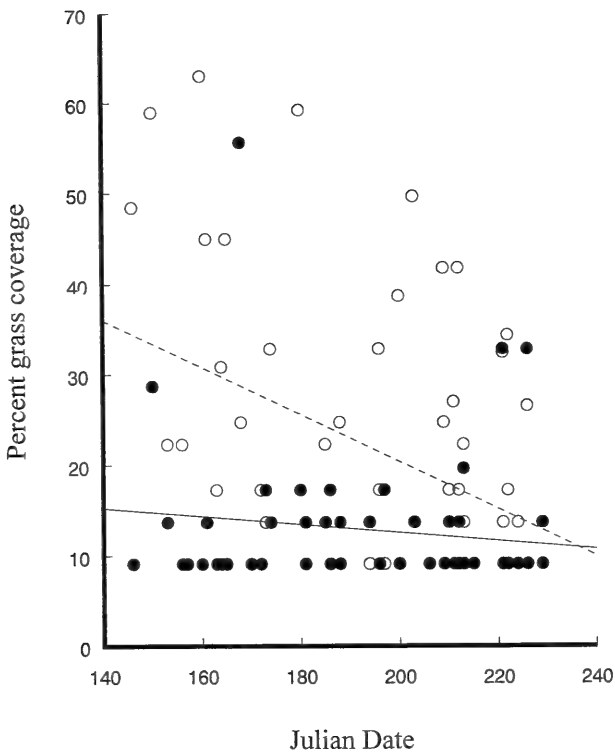


FIGURE 1. Seasonal influence on green grass cover (arcsine-transformed) at poorwill roost and random sites in the Cypress Hills. Roost sites are represented by solid circles and line ($r^2 = 0.020$, $P > 0.25$); random sites by open circles and broken line ($r^2 = 0.179$, $P > 0.01$). Julian dates 140 and 240 represent 20 May and 28 August, respectively.

the growing season. Our results suggest that poorwills tolerate some green vegetation at roost sites, but they apparently select roost sites with a level of green vegetation that does not change with season.

Although overhead "cover" is often equated with an increased degree of concealment from predators (Schieck and Hannon 1993), we found that poorwills avoided locations with overhead cover or surrounded by tall objects. This is also consistent with the hypothesis that thermoregulation may also affect site choice by these birds (French 1993). Poorwills are very tolerant of heat stress (Lasiewski 1969), and thus shade provided by overhead cover may not be critical. Also, a bird roosting on an open unshaded site may derive benefit from being able to use sunlight to rewarm passively after a bout of torpor (Brigham 1992). Overhead cover may also be selected against if it interferes with the bird when it flies away from the site (either flight from a potential predator or when it begins nightly activity) as these birds do not walk well and appear to need a take-off and landing runway (R. M. Brigham, personal observation).

Our analysis indicated that the limited amount of cover provided by trees and shrubs did not change significantly over the summer at random sites, although it did increase slightly at roost sites through

the season. In contrast, and we believe more importantly, poorwills typically selected roost sites with the same amount of grass cover throughout the summer, even though the amount of green vegetation decreased at random sites through time. These results suggest that poorwills may select sites based, at least partially, on the degree of live vegetation cover, especially grass, early in the season.

In conclusion, we believe that poorwills choose roost sites that minimize contrast with their plumage, possibly in order to reduce predation risk. Ours is the first study to assess quantitatively habitat use by poorwills. It remains for further work to determine if the risk of predation, the benefits accrued by roosting at sites exposed to direct sunlight, or some other factor best explains site selection by poorwills.

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Numbers and Seasonal Occurrence of Humpback Whales, *Megaptera novaeangliae*, off Brier Island, Nova Scotia

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Humpback Whales, *Megaptera novaeangliae*, were studied using individual photo-identification in the waters off Brier Island, Nova Scotia, during the years 1984 to 1996. Estimates of the number of whales visiting the area were obtained for each year using mark-recapture methods. The population size has a variance weighted mean of 80 ± 5 (95% CI) for repeated Petersen estimates. There was consistency between estimates from 1984 to 1993 but a decline was seen in 1994 and 1995. These estimates represent approximately 38% of the estimated total population of Humpback Whales of the Gulf of Maine feeding aggregation and approximately 1.8% of the total Western North Atlantic Ocean population. Off Brier Island, a pattern of seasonal variation in sighting rates for half-month periods was observed for the years 1985 to 1989. The results indicate that Humpback Whales arrive slowly in the area during June, reach a population peak around August, the period of greatest plankton abundance, and depart from the area between then and October.

Les Rorquals à Bosse, *Megaptera novaeangliae*, furent l'objet d'une étude de photo-identification dans la région de l'île Brier, Nouvelle-Ecosse, durant les années 1984 à 1996. Le nombre de baleines qui visitent la région chaque année a été estimé à l'aide de la méthode capture-recapture. Le niveau de population a une moyenne pondérée par la variance de 80 ± 5 (95% IC) telle qu'estimée par la méthode Petersen. Peu de variation a été observée entre les estimations individuelles de 1984 à 1993 mais un déclin est observé pour les années 1994 et 1995. Ces estimations représentent approximativement 38% de la valeur estimée pour la population totale de baleine qui se trouvent dans l'aggrégation du Golfe du Maine et approximativement 1.8% de la valeur estimée pour la population totale de l'Océan de l'Atlantique Nord-Ouest. Dans la région de l'île Brier, les taux de présence des Rorquals à Bosse ont été calculés pour des périodes bimensuelles pour les années 1985 à 1989. Les résultats indiquent que les baleines arrivent lentement dans la région durant le mois de Juin, atteignent leur taux de population maximal au mois d'Août, durant la période d'abondance maximale du plankton, et quittent la région entre le mois d'Août et le mois d'Octobre.

Key Words: Humpback Whales, *Megaptera novaeangliae*, photo-identification, population size, seasonal variation, Brier Island, Nova Scotia.

Humpback Whales, *Megaptera novaeangliae*, are generally coastal animals that return to traditional areas for reproduction such that geographically separate breeding groups ("stocks") exist (Baker et al. 1989). These stocks congregate during the winter in temperate and tropical waters. During the summer, the stocks disperse to form feeding aggregations in areas of high productivity at higher latitudes (Baker et al. 1989). Humpback Whales found summering off Brier Island, Nova Scotia, are considered part of the Gulf of Maine feeding aggregation (Clapham and Mayo 1987). A photo-identification study has shown that these whales mix on Silver Bank off the Dominican Republic during winter with Humpback Whales from other major known feeding aggregations of the North West Atlantic stock including Greenland, Newfoundland-Labrador and the Gulf of St-Lawrence (Mattila et al. 1984).

Humpback Whales are presumably attracted to the Brier Island area by a high concentration of local prey such as herring (*Clupea harengus*) and euphasiids (*Meganyctiphanes norvegica*). The strong tidal

streams in the Bay of Fundy coupled with local underwater ledges generate "tidal pump" systems that force plankton-rich cool water to the surface. This water subsequently drifts downstream and sinks in a series of convergence fronts below the warmer surface (Brown 1981). Euphasiid swarms on the order of 200 g/m³ found in these areas presumably attract Humpback Whales directly and also attract them indirectly by supporting concentrations of other prey species (Brown et al. 1979).

Humpback Whales characteristically raise their flukes when they dive. The variation in the pigmentation pattern on the underside of the flukes permits the identification of photographed individuals (Balcomb et al. 1986) and is widely used as a study tool (Katona and Beard 1990).

This paper reports on a study of Humpback Whales off Brier Island, Nova Scotia during the years 1984-1996. Using photo-identification, the average number of whales which frequent the area during a given year was estimated. In addition, seasonal variations in sighting rates were examined for the years 1985-1989.

TABLE 1. Annual population estimates of Humpback Whales off Brier Island, Nova Scotia, using Bailey's modification of the Petersen capture-recapture technique (n_1 = the number of individuals identified from photographs in year 1, n_2 = the number of individuals identified from photographs in year 2, m_2 = the number of individuals identified from photographs in both years and N_1 = the estimated population size).

Year	n_1	n_2	m_2	N_1 (95% CI)
1984	18	50	9	92(43,141)
1985	50	51	29	87(67,107)
1986	51	61	28	107(79,135)
1987	61	63	33	115(89,141)
1988	63	37	25	92(72,112)
1989	37	68	27	91(65,117)
1990	68	58	42	93(79,107)
1991	58	76	44	99(80,118)
1992	76	55	43	97(84,110)
1993	55	56	36	85(69,101)
1994	56	26	22	66(56,76)
1995	26	12	8	38(25,51)
1996	12	-	-	-

Methods

Data were collected from four "Cape Islander" type vessels: the *Kenney and Girls 5* during 1984 to July 1988, the *Cetacean Venture* from August 1988 to 1991, both the *Cetacean Venture* and the *Cetacean Quest* during 1992 to 1995, the *Cetacean Venture*, *Cetacean Quest* and *Captain Grumpy* in 1996. The study area was defined as the waters within 25 km of Brier Island, Nova Scotia (ca 44°15'N 66°23'W) (Figure 1). Few trips were made during 1984-1986 but were attempted daily (weather permitting) during summer months from 1987-1996. Trips lasted, on average, four hours and took place from the beginning of June until the middle of October. These were whale-watching trips with Humpback Whale sightings as their main focus. Consequently, the vessels went to areas where Humpback Whales had been sighted.

At sea, Humpback Whales were sighted visually and then approached. Photographs of flukes and dorsal fins were taken with 35 mm cameras with various lenses.

Developed photographs were sent to the College of the Atlantic (COA; Bar Harbor, Maine) where the curators of the North Atlantic Humpback Whale Catalogue are based. At COA, our photographs were compared with those taken elsewhere in the North Atlantic Ocean. When a photograph did not match any of those already in the catalogue, it was added to the catalogue and assigned a catalogue number.

For making population estimates for pairs of contiguous years we used Bailey's modification of the Petersen capture-recapture technique (Katona and Beard 1990; Seber 1982):

$$N_1 = n_1[n_2+1]/[m_2+1]$$

$$V_1 = [n_1^2[n_2+1][n_2-m_2]]/[([m_2+1]^2[m_2+2])]$$

Where:

N_1 = the estimated population size

n_1 = the number of individuals identified from photographs in year 1

n_2 = the number of individuals identified from photographs in the subsequent year, year 2

m_2 = the number of individuals identified from photographs in both years 1 and 2

V_1 = estimated variance of N_1 .

For this analysis only identifications within the study area were considered. Calves were added to the the catalogue only in their second year because changes in the pigmentation pattern on the underside of flukes may occur during the first year of life (Carlson et al. 1990).

Seasonal fluctuations in the sighting rate of Humpback Whales were expressed as the mean number of whales, not necessarily different individuals, sighted over a period of one hour spent on the water. This information is presented for half-month periods since this interval best indicates the seasonal progression for the information obtained in this study. An individual whale resighted within 30 minutes was not included a second time into the sighting rate. If less than two trips took place during a half-month period, sighting information was omitted from the plots.

Results

During the years 1984 to 1996, a total of 184 individual Humpback Whales were identified from photographs for our study area sent to the College of the Atlantic. The variance weighted mean for the years 1984-1995 was 80 ± 5 (95% CI). The population estimates for each pair of contiguous years were consistent from 1984-1985 to 1993-1994 at about 90 individuals, but then fell to a low of 38(25,51) in 1995-1996 (Table 1).

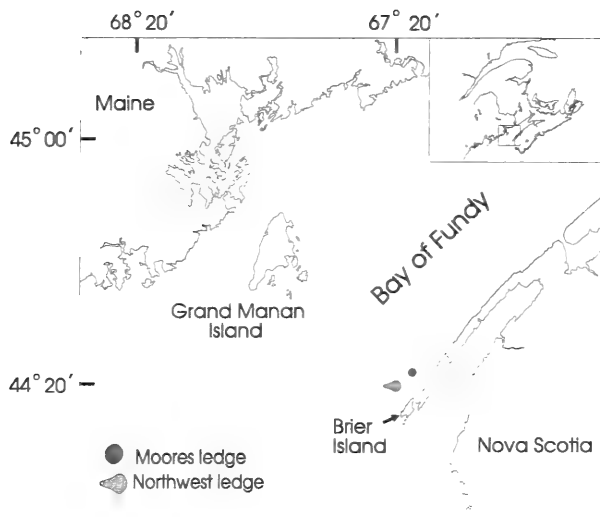


FIGURE 1. The study area is the waters near Brier Island, Nova Scotia. Underwater ledges are indicated by hatched areas.

Sightings rates peaked at somewhat different times in different years (Figure 2). There were no cases of zero sightings when more than two trips were taken during a half-month period. The pooled sighting rates for all five study years indicated low sighting rate values in June (Figure 2F). These steadily increased until the first two weeks of August and then decreased (Figure 2F).

Discussion

Annual population estimates for the Brier Island area represent approximately 38% of the 240 ± 93 (95% CI) total population estimate for the Gulf of Maine feeding aggregation (Katona and Beard 1990). They also represent approximately 1.8% of the 5505 ± 2617 (95% CI) estimated for the total Humpback Whale population in the western North Atlantic Ocean (Katona and Beard 1990). The size of the population visiting the Brier Island area seems quite consistent from 1984 to 1993 but a decline is observed for the last two years of the study. This is likely to have been because the abundance of prey available to the whales in the study area was lower during the final years of the study. Payne et al. (1990) observed that spatial distribution and abundance of Humpback Whales in the Gulf of Maine can be described as a series of ecological responses to human induced changes in the abundance of planktivorous finfish. The same ecological responses are observed in the Brier Island area. However, these responses were probably caused by a slow warming of the sea surface temperatures in the Bay of Fundy, which had an effect on plankton distribution (Carl Haycock, personal communication).

Bailey's modification of the Petersen capture-recapture technique is based on the following assumptions (Hammond 1986):

- (1) Every animal in the population, whether marked or unmarked, has the same probability of being caught in each sample, given that it is alive and in the population when the sample is taken.
- (2) Every marked animal has the same probability of surviving from the i th to the $(i + 1)$ th sample and of being in the population at the time of the $(i + 1)$ th sample, given that it is alive and in the population immediately after the i th sample.
- (3) Marked animals do not lose their marks and all marks are reported on recovery.
- (4) All samples are instantaneous.

Amongst these assumptions, the last three are probably reasonable for this study. However, the first assumption is not. The model does not allow the catchability of an individual to vary from sample to sample (Hammond 1990). Several aspects of the ecology and biology of whales could affect the assumptions of equal catchability in the yearly samples. Some whales may be more likely to travel to the Brier Island area during any year. Whales may show repeated associations or preferred companions resulting in "group bias" (Caughley 1977). Female Humpback Whales with calves apparently show their flukes less often than males (Perkins et al. 1985). Whales may be absent from the sample area on one or more occasions (known as temporary emigration) (Hammond 1990).

In the field, temporary emigration is expressed both by animals being physically absent and by a combination of site specificity within the sample area and a limitation of sampling effort (Hammond 1990). These effects are a result of inherent individual differences in behaviour known as heterogeneity (Hammond 1990). Heterogeneity causes a negative bias in estimating population sizes. Therefore, actual numbers of Humpback Whales visiting the Brier Island area may be somewhat higher than those calculated here.

Humpback Whales arrive off Brier Island slowly in June, become most abundant in August and depart the area between then and October. The sighting rate peak observed in August may be caused by one of two factors or a combination of these. In 1978, Brown et al. (1979) observed the highest number of daytime swarms of *Meganyctiphanes norvegica* off Brier Island during the last half of August. Therefore, the increased concentration of food could explain the increased presence of whales in the area during that period. The results may also reflect a temporal segregation of sexual and maturational classes found on both breeding and feeding grounds (Clapham and Mayo 1987). For example, late arrivals may be mother-calf pairs that tend to spend more time in the warmer waters of the lower latitudes (Dawbin 1966). August may be when all classes are off Brier Island together.

Clapham and Mayo (1987) reported a mother-calf pair of Humpback Whales in the Cape Cod area as

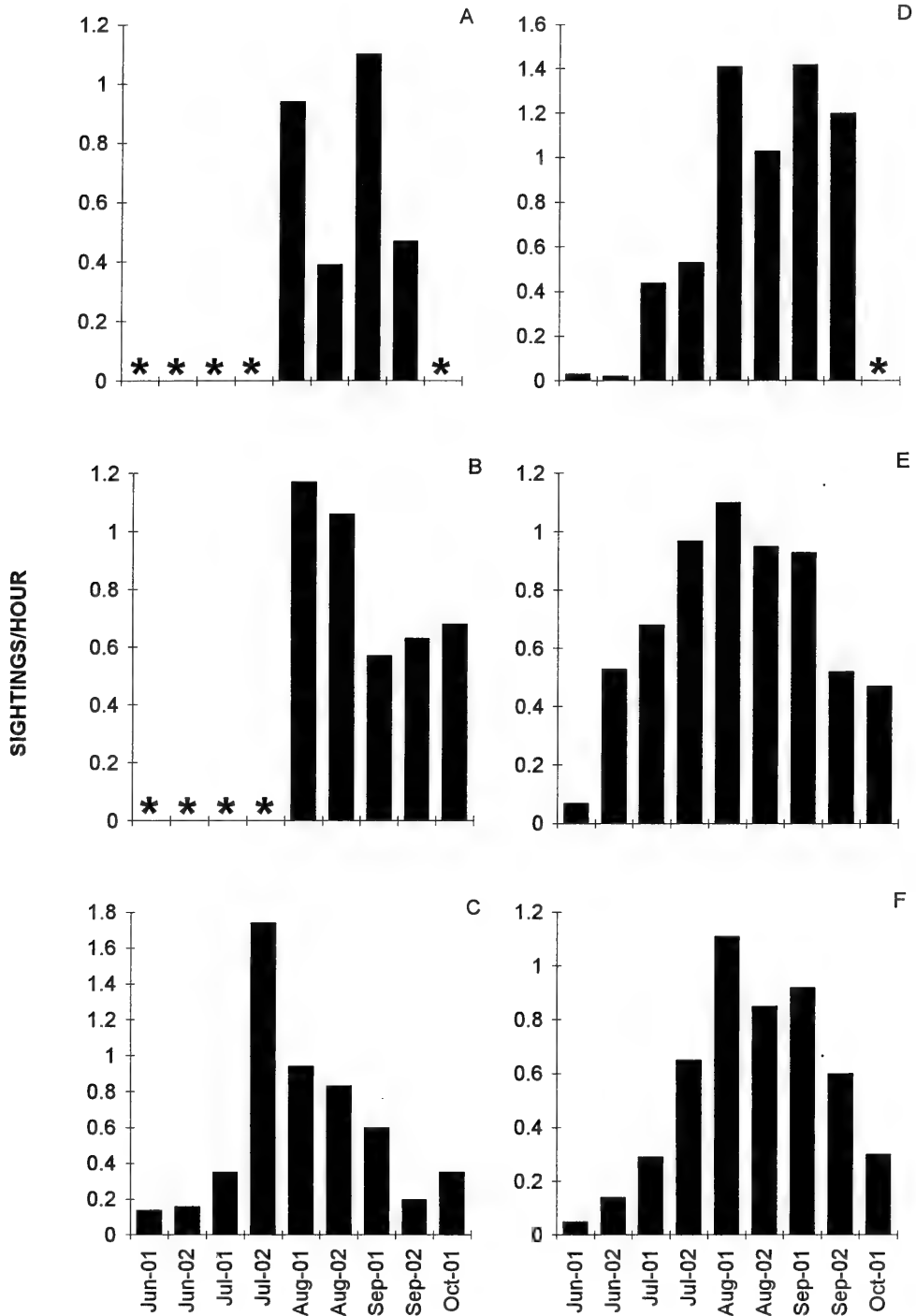


FIGURE 2. Seasonal fluctuations in observed sighting rates for Humpback Whales during the year 1985(A), 1986(B), 1987(C), 1988(D), 1989(E) and pooled results during the years 1985 to 1989(F) for half-month periods (1= first to fifteenth of the month, 2= sixteenth to thirtieth or thirty first of the month). An * indicates than less than two trips were taken for that particular half-month period.

early as April. No such early sightings have been recorded off Brier Island. The waters off Cape Cod are warmer than those in the Bay of Fundy, which could explain early arrivals in the former (Clapham and Mayo 1987). A Humpback Whale was sighted off Brier Island as late as December during 1989.

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Vegetation Succession and Disturbance on a Boreal Forest Floodplain, Susitna River, Alaska

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Vegetation development along the Susitna River floodplain exhibits multiple successional pathways in response to disturbances such as flooding, ice scour, wind, browsing, and logging. These can rejuvenate sites or slow vegetation development through surface erosion, deposition, and stem bending. Youngest vegetation types were dominated by Variegated Horsetail (*Equisetum variegatum*) on silty sites, Feltleaf Willow (*Salix alaxensis*) and Tall Blueberry Willow (*S. novae-angliae*) on medium-textured sites, Balsam Poplar (*Populus balsamifera*) on sandy sites, and Yellow Dryas (*Dryas drummondii*) on cobbly sites. Although Thinleaf Alder (*Alnus tenuifolia*) was sparse in early succession, it grew more rapidly than other species and created a closed overstory with poorly developed understory early in intermediate succession. Browsing disturbances temporarily limited height growth of willows and Balsam Poplar. After Balsam Poplar exceeded the reach of Moose (*Alces alces*), it grew taller than Thinleaf Alder to form Young Poplar Forests. As trees matured and natural thinning occurred, Old Poplar Forests formed with a woody understory including White Spruce (*Picea glauca*). Uprooted trees exposed mineral microsites for germination of Paper Birch (*Betula papyrifera*) seeds. These sites eventually developed into the Paper Birch - White Spruce Forests of late succession with a well-developed shrub understory.

Key Words: Moose, *Alces alces*, vegetation succession, disturbance, floodplain, browsing, riparian, Susitna River, Alaska.

Vegetation succession along floodplains of northern glacial rivers is affected by flooding, ice, wind, and wildlife interactions. The Susitna River drains over 2 million ha in southcentral Alaska near the population center of the state. It provides recreational opportunities as well as habitat for many species of wildlife. Concerns about potential hydroelectric development impacts in the Susitna basin prompted a study to examine present structure of the vegetation, its changes over time, causes of change, and wildlife interactions.

Many other northern rivers have been studied, including the Colville River (Bliss and Cantlon 1957), Chena (Viereck 1970), Tanana (Wolff 1976; Van Cleve et al. 1980; Walker and Chapin 1986; Walker et al. 1986; Viereck et al. 1993, Van Cleve et al. 1996), Stikine (Craighead et al. 1984), Exit Glacier Creek (Helm and Allen 1995) in Alaska and the Mackenzie (Gill 1972), Beatton (Nanson and Beach 1977), and Lillooet (Teversham and Slaymaker 1976) in Canada. The Susitna River differs from many northern river systems in that the (1) youngest stage of vegetation succession has four distinct communities based on substrate textures and (2) a well-developed Paper Birch (*Betula papyrifera*) - White Spruce (*Picea glauca*) Forest is present in later stages of succession. Browsing by Moose (*Alces alces*), Snowshoe Hare (*Lepus americana*), and Beaver (*Castor canadensis*) significantly alters vegetation structure as well as rates or pathways of succession (Bryant and Chapin 1986; Johnston and Naiman 1990; Moen et al. 1990; Naiman et al.

1994). Regeneration of Balsam Poplar (*Populus balsamifera*) on surface-disturbed soils following logging has been documented (Zasada et al. 1981). Prior Alaskan studies have focused on nutrient cycling (Van Cleve et al. 1980; Van Cleve et al. 1986; Van Cleve et al. 1993; Viereck et al. 1993) or biological controls during certain stages of vegetation succession (Bryant and Chapin 1986; Walker and Chapin 1986; Walker et al. 1986). Although effects of windthrow have been documented in southeastern Alaska (Deal et al. 1991; Bormann et al. 1995), ice effects have been largely ignored. Existing vegetation, differences on marked plots 3 and 14 years later, and aerial photographs from 1951 and 1980 were used to document the various successional stages along the Lower Susitna River and propose a conceptual model of effects of various disturbances on the successional pathways.

Site Description

The 500-km-long Susitna River drains the Alaska Range to the north and west, and the Talkeetna Mountains to the east, and flows into Cook Inlet to the south. This study focused on the lower part of the river from Chase (62.5° N 150.1° W) downstream to the mouth of the Deshka River (61.7° N 150.3° W) (Figure 1). Three distinct reaches had different channel structures which affected the amount of fluvial disturbance and the resultant vegetation and substrate structure. The Susitna River above its confluence with the Chulitna River contained armored channels and was subject to larger ice jams during

TABLE 1. Land covered (%) by each vegetation type in the Susitna River floodplain.^a

Class	Alaska Vegetation Classification	Stands	Number of Transects	Lower ^b	Middle	Upper	Total
Barren				15	26	4	14
Early shrub				4	3	8	5
Dryas	Dryas Dwarf Scrub	18	4				
Juvenile Poplar	"Open Low Scrub" ^c	5, 20, 21, 25	15	2	2	8	3
Willow	Open Low Scrub	6, 16, 22	9	1			<1
Horsetail	Mesic Forb Herbaceous	1, 8, 9, 13, 14, 15	18	1	1		1
Intermediate				18	17	6	15
Alder	Closed Tall Shrub Scrub	2, 19, 23, 27	20	17	15	6	14
Young Poplar	Closed Broadleaf Forest	10, 12, 26	18	1	2	0	1
Late				51	47	73	55
Old Poplar	Open Broadleaf Forest	3, 17, 24, 28	24	22	29	24	24
Birch - Spruce	Open Mixed Needleleaf - Broadleaf Forest	4, 11, 29	20	24	17	30	24
Paper Birch				2		19	5
White Spruce				3	1		2
Other				12	6	8	10
Bog				5	5	0	4
Wet sedge-grass				7	1		5
Other forest						6	1

^aData are interpreted from aerial photograph of 24 August 1980, 1:48 000; taken at flow rates of 510 cms Gold Creek; 1840 cms Sunshine; 3370 cms Susitna Station. Percents for subtypes form a separate column to the right of the main types.

^bLower river is from Deshka River to Montana Creek, Middle is from Montana Creek to Chulitna River, and Upper is from Chulitna to Gold Creek.

^cClosest Level III community in Alaska Vegetation Classification (Vioreck et al. 1992) for sampled stages.

breakup compared to the more open reaches with braided and split channels. The section immediately below the Chulitna River had more cobbles than the other two reaches, but the finest materials were in the lowest reach. Reduced gradients and greater width below the confluence resulted in slower water velocities and more sand deposition in the lowest two stretches.

The Susitna River flow is frequently highest in July and August during summer rains when its contributory glaciers are also melting, but high flows also occur during breakup (personal observations). Lowest water levels occur during freezeup, but stalling behind ice may cause river flows almost to summer levels. Additionally, overflow may refreeze and encase some plants in ice.

Methods

Vegetation was stratified into successional stages based on site visits in 1980 and early summer 1981 and on black-and-white aerial photographs of the river in 1951 and 1980 (1:48 000). These stages were identified as Early Shrub (Dryas, Juvenile Poplar, Willow, Horsetail), Intermediate (Alder, Young Poplar), and Late (Old Poplar, Birch - Spruce). Sample sites of relatively homogeneous vegetation were selected in each successional stage in the three reaches of the river and sampled in 1981 (Figure 1). Eleven (1, 5, 6, 8, 9, 13, 14, 16, 21, 22, 25) of the thirteen Early Shrub sites were resampled in 1984, one (20) had been completely or partially eroded between 1981 and 1984 and one (18, Yellow Dryas) was not resampled because it was a minor type. A former Birch - Spruce stand that had been logged was examined in 1981 and a Balsam Poplar - White Spruce Forest was examined in 1984 to understand the transition between Old Poplar Forest and Paper Birch - White Spruce Forest but the site was not sampled quantitatively. Sites were identified according to the Alaska Vegetation Classification System (Viereck et al. 1992), where possible, but that system was not designed for early successional plant communities (Table 1).

Most sites were sampled with four randomly-oriented, non-overlapping 30-m transects in June 1981, and two additional transects were measured in August to obtain adequate precision. End points were marked with 1-m lengths of electric conduit and labelled with metal tags. Phenological development had insignificant effect on plant cover between June and August because leaves had already expanded in June. Some Early Shrub sites were sampled with as few as two transects because of their small size.

Vegetation cover by species in each height category (0.0-0.4 m, 0.4-1 m, 1-2 m, 2-4 m, 4-8 m, 8-16 m, and >16 m) was recorded at points spaced 50 cm along each 30-m transect. These categories were selected to depict the height structure of overstory

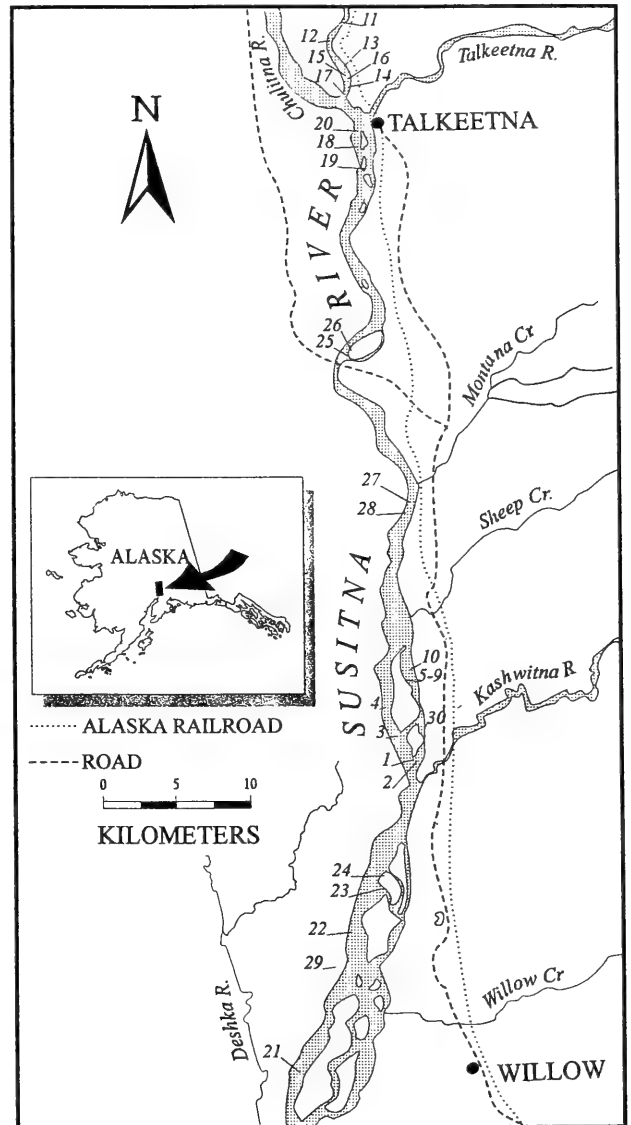


FIGURE 1. Location of study sites along the Susitna River, southcentral Alaska.

and understory and susceptibility to browsing disturbance. Leaf cover for any species at any point occurred within one height category. Hits on taller trees and shrubs were observed through an 8 × sighting scope mounted vertically on a pole placed over the point. The transect length and point spacing had been modified from prior vegetation sampling efficiency studies. Cover by life form categories was determined by counting points for the appropriate species within that life form, thus taking overlapping vegetation into account. Cover by mosses and lichens was minor because of flooding and litter deposition so they are only reported by category.

Ages and heights of dominant woody plants were measured on two randomly selected individuals per species along each transect in 1981. Heights of tall individuals were estimated using a range finder to focus on the tree top. The minimum age of each

TABLE 2. Cover (%) of vascular plants and life form categories along the Susitna River floodplain, summer 1981^a (mean \pm standard error).

	Early Shrub			Intermediate			Late	
	Dryas	Juvenile Balsam Poplar	Willow	Horsetail	Alder	Young Balsam Poplar	Old Balsam Poplar	Paper Birch -White Spruce
Total vegetation	9 \pm 3	20 \pm 3	48 \pm 6	46 \pm 6	87 \pm 3	91 \pm 2	89 \pm 3	93 \pm 2
Trees								
<i>Populus balsamifera</i> , Balsam Poplar	6 \pm 2	14 \pm 2	9 \pm 2	2 \pm 1	13 \pm 3	62 \pm 7	50 \pm 5	52 \pm 4
<i>Betula papyrifera</i> , Paper Birch	6 \pm 2	14 \pm 2	9 \pm 2	2 \pm 1	13 \pm 3	62 \pm 7	49 \pm 5	42 \pm 5
<i>Picea glauca</i> , White Spruce						+	1 \pm 0	12 \pm 3
Tall shrubs								
<i>Alnus tenuifolia</i> , Thimbleleaf Alder		+	1 \pm 1		60 \pm 4	47 \pm 4	43 \pm 3	14 \pm 4
<i>Alnus sinuata</i> , Sitka Alder		+	1 \pm 1		59 \pm 4	40 \pm 4	41 \pm 3	10 \pm 3
Low shrubs								
<i>Dryas drummondii</i> , Yellow Dryas	4 \pm 1	1 \pm 1	12 \pm 3	4 \pm 2	6 \pm 2	6 \pm 1	36 \pm 4	40 \pm 4
<i>Salix alaxensis</i> , Feltleaf Willow	4 \pm 1	1 \pm 1	9 \pm 2	3 \pm 2	5 \pm 2			
<i>Salix novae-angliae</i> , Tall Blueberry Willow			3 \pm 1	+	+	+		+
<i>Salix arbusculoides</i> , Little Tree Willow			+	1 \pm 0				
<i>Salix</i> spp., willow			1 \pm 0	1 \pm 0	+			+
<i>Viburnum edule</i> , High Bushcranberry					+	3 \pm 1	21 \pm 3	19 \pm 4
<i>Rosa acicularis</i> , Prickly Rose					+	3 \pm 1	14 \pm 2	20 \pm 2
<i>Rubus idaeus</i> , American Red Raspberry					1 \pm 0	+	4 \pm 1	3 \pm 1
<i>Ribes triste</i> , American Red Currant					+		3 \pm 1	5 \pm 1
<i>Echinopanax horridum</i> , Devil's Club							1 \pm 1	4 \pm 2
Perennial Forbs								
<i>Equisetum variegatum</i> , Variegated Horsetail	5 \pm 2		26 \pm 6	41 \pm 6	11 \pm 3	9 \pm 2	23 \pm 4	44 \pm 4
<i>Equisetum arvense</i> , Meadow Horsetail	5 \pm 2		25 \pm 6	41 \pm 6	1 \pm 0	+	1 \pm 1	8 \pm 3
<i>Equisetum sylvaticum</i> , Woodland Horsetail	+			+	1 \pm 1	+	3 \pm 1	19 \pm 6
<i>Epilobium latifolium</i> , Dwarf Fireweed	+				+	+	+	2 \pm 1
<i>Epilobium angustifolium</i> , Tall Fireweed					4 \pm 2	1 \pm 1		+
<i>Artemisia tilesii</i> , Tilesy Sage			+		3 \pm 1	+		1 \pm 0
<i>Astragalus</i> or <i>Oxytropis</i>	1 \pm 0		+		+	+		
<i>Hedysarum</i> sp.			+		+			
<i>Cornus canadensis</i> , Bunchberry							+	1 \pm 0
<i>Heracleum lanatum</i> , Cow Parsnip						+	+	
<i>Mertensia paniculata</i> , Tall Bluebell						1 \pm 1	2 \pm 1	2 \pm 1
<i>Pyrola</i> spp., Wintergreen						+	+	
<i>Rubus arcticus</i> , Nagoon Berry						+	+	+
<i>Streptopus amplexifolius</i> , Claspng Twisted-Stalk						+	1 \pm 0	1 \pm 0

Continued

TABLE 2. (Continued).

	Early Shrub			Intermediate			Late	
	Dryas	Juvenile Balsam Poplar	Willow	Horsetail	Alder	Young Balsam Poplar	Old Balsam Poplar	Paper Birch - White Spruce
<i>Sanguisorba stipulata</i> , Sitka Burnet						+	+	+
<i>Trientalis europaea</i> , Twin-Flower					+		+	+
<i>Galium boreale</i> , Northern Bedstraw							1 ± 0	7 ± 3
<i>Dryopteris dilatata</i> , Spinulose Shield-Fern							5 ± 2	4 ± 1
<i>Gymnocarpium dryopteris</i> , Oak-Fern						+	7 ± 3	1 ± 1
<i>Matteuccia struthiopteris</i> , Ostrich-Fern								
Grass-like		1 ± 0	2 ± 1	1 ± 0	38 ± 6	23 ± 5	12 ± 2	18 ± 3
<i>Calamagrostis canadensis</i> , Bluejoint Reedgrass			1 ± 1	+	38 ± 6	23 ± 5	12 ± 2	18 ± 3
Ground layer			2 ± 1		2 ± 2	1 ± 0	1 ± 0	2 ± 1
Lichens			1 ± 1		1 ± 0			
Moss			1 ± 0		1 ± 1	+	+	1 ± 0
Other Categories								
Bare Ground	50	71 ± 5	35 ± 7	47 ± 6	+			
Litter	16	11 ± 4	29 ± 8	8 ± 1	99 ± 1	+	92 ± 6	100 ± 0
Gravel, Cobbles	27	3 ± 1		1 ± 0				
Water				+				

^a Number rounded to closest percent. '+' = <0.5% cover.

TABLE 3. Characteristics of low shrub-sized plants in different successional stages, summer 1981, Susitna River.^a

	Early				Intermediate	
	Dryas	Juvenile Balsam Poplar	Willow	Horsetail	Alder	Young Balsam Poplar
<i>Salix alaxensis</i>						
Height (m)	0.33 ± 0.27	0.51 ± 0.5	0.79 ± 0.10	0.55 ± 0.07	1.55 ± 0.16	
Crown length (cm)	0.22 ± 0.13	0.3 ± 0.0	0.31 ± 0.03	0.16 ± 0.02	0.55 ± 0.08	
Age	5 ± 3	5 ± 1	6 ± 1	3 ± 0	8 ± 1	
Crown dominance ^b	2	2	2	2	6	
n	2	25	18	25	19	
<i>Salix novae-angliae</i>						
Height (m)		0.81 ± 0.0	0.83 ± 0.17	0.37 ± 0.04	1.12 ± 0.12	1.25 ± 0.14
Crown length (cm)		0.6 ± 0.0	0.30 ± 0.04	0.09 ± 0.01	0.51 ± 0.11	0.53 ± 0.07
Age		4	4 ± 0	2 ± 0	8 ± 2	9 ± 2
Crown dominance		2	2	2	6	6
n		1	7	16	4	8
<i>Populus balsamifera</i>						
Height (m)	0.19 ± 0.06	0.32 ± 0.06	0.49 ± 0.10	0.61 ± 0.15	2.48 ± 0.59	
Crown length (cm)	0.19 ± 0.02	0.22 ± 0.03	0.22 ± 0.03	0.32 ± 0.12	1.20 ± 0.37	
Age	5 ± 0	7 ± 1	7 ± 0	5 ± 1	16 ± 3	
Crown dominance	1	2	2	2	6	
n	8	30	18	15	7	
<i>Alnus tenuifolia</i>						
Height (m)			1.67 ± 0.92	0.54 ± 0.09	1.19 ± 0.18	1.39 ± 0.12
Crown length (cm)			0.62 ± 0.29	0.22 ± 0.03	0.43 ± 0.05	0.73 ± 0.09
Age			3 ± 0	3 ± 0	4 ± 1	6 ± 1
Crown dominance			3	2	6	6
n			2	2	7	32
<i>Alnus sinuata</i>						
Height (m)					2.46 ± 0.46	
Basal diameter (cm)					2.23 ± 0.66	
Age					7 ± 1	
Crown dominance					5	
n					4	
<i>Picea glauca</i>						
Height (m)					0.71	
Crown length (cm)					0.34	
Age					10	
Crown dominance					6	
n					1	

^aNumbers are rounded to nearest unit of measurement. n=number of stems sampled.

^bCrown dominance: 1=open grown, 2=dominant, 3=codominant, 4=intermediate, 5=overtopped, 6=subordinate, 7=ground.

measured tree or shrub was determined by counting growth rings on cross sectional cuttings or cores taken as near the ground as possible. Young woody stems were excavated on some sites to determine the total age of stem, part of which had been buried by sediment. Ages analyzed included only the above-ground age. Densities were also recorded by size class: < 0.4 m, 0.4-2 m, 2 m - 4 m tall and <4 cm DBH (diameter-at-breast-height), <4 m tall and >4 cm DBH, and > 4 m tall. Stems >0.4 m tall were considered available browse even though snow could reduce that availability in deep snow years. Moose could reach stems up to 4 m tall or > 4 m tall if DBH

was < 4 cm. These categories are related to the amount of browsing disturbance possible and to the vegetation succession. Crown dominance was also reported for each species: 1 open grown, 2 dominant (received sunlight from above and sides), 3 codominant (received sunlight from above but not the sides), 4 intermediate (barely reaching main canopy), 5 overtopped (below general level of canopy), 6 subordinate (under overtopped), and 7 ground - lowest level. Two soil pits were dug in each site to evaluate depositional profiles.

To estimate the proportion of land area covered by each of the vegetation types at a given stream flow,

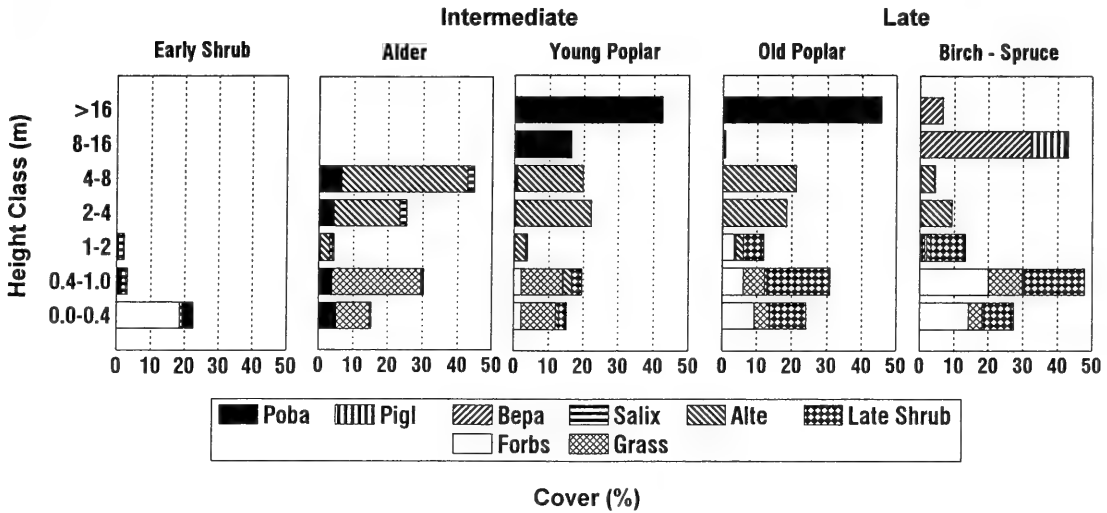


FIGURE 2. Scaled relative cover (%) (relative cover \times total vascular plant cover) by major species or herbaceous life form and height class in each successional stage. Shrubs between 0.4 and 4 m tall are subject to Moose browsing disturbance. Poba = *Populus balsamifera*, Bepa = *Betula papyrifera*, Pigl = *Picea glauca*, Salix = *Salix alaxensis* + *Salix novae-angliae*, Alte = *Alnus tenuifolia*, Late shrub = *Rosa acicularis* + *Viburnum edule* + *Ribes triste*.

transects were plotted approximately every 4 cm (2 km) on aerial photographs (1:48 000 black- and white taken in 1980). Points were systematically plotted approximately every 7 mm (350 m) along each transect from the base of slope on one side of the river to the base of first hill on the other side, which was considered the limit of the floodplain. The points were classified according to successional stage during a helicopter survey in June 1981.

Results

General

Early Shrub sites were most common on the two lower reaches where the floodplain was wide with

split and braided channels. Approximately 20 to 30% of available land in this reach was occupied by Barren or Early Shrub stages (Table 1). Above the Chulitna River confluence, the river was narrower with well-defined channels. Here the mature forests predominated and occupied almost three-fourths of the available land area. Similarly the intermediate stage only occupied 6% of the area compared to >17% in the lower two reaches.

Some Early Shrub sites have remained in early succession from 1951 (aerial photographs) to 1995 although they are periodically flooded. While some Early Shrub sites eroded between 1981 and 1995, others advanced successional. Part of a Birch -

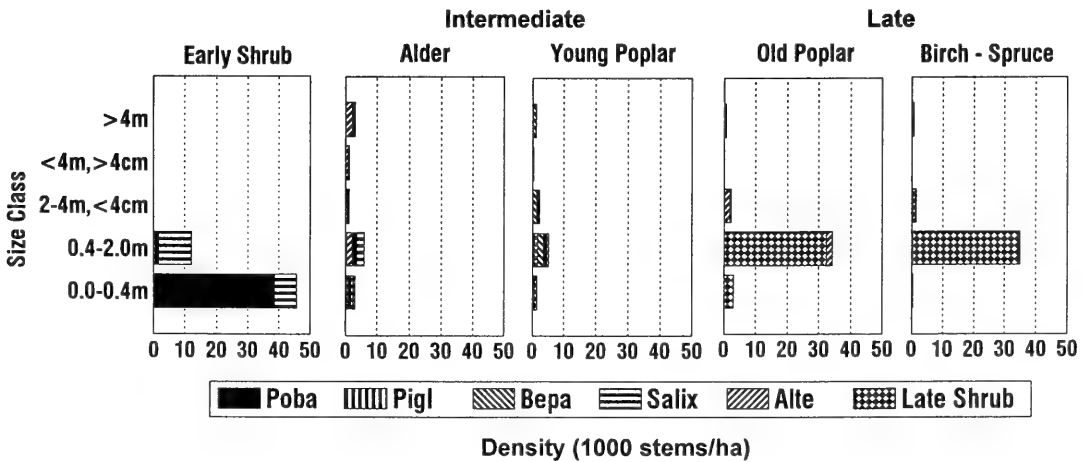


FIGURE 3. Density (stems ha⁻¹) of major woody species by size class in each successional stage. Size classes are by height (first number) and DBH (second number, if present). Stems sized 0.4 to 2.0 m tall and 2 to 4 m with DBH < 4 cm are subject to Moose browsing disturbance. Species codes are explained in Figure 2.

TABLE 4. Characteristics of trees and tall shrubs in different successional stages, summer 1981, Susitna River.^a

	Intermediate		Late	
	Alder	Young Balsam Poplar	Old Balsam Poplar	Paper Birch-White Spruce
<i>Populus balsamifera</i>				
Height (m)	6.2 ± 0.3	14.0 ± 1.1	24.7 ± 0.5	
DBH (cm)	7.2 ± 0.4	24.8 ± 1.9	53.2 ± 2.4	
Age	19 ± 1	44 ± 3	98 ± 6	
Crown dominance	2	2	2	
n	28	36	40	
<i>Alnus tenuifolia</i>				
Height (m)	5.3 ± 0.2	4.9 ± 0.2	5.6 ± 0.3	3.9 ± 0.3
DBH (cm)	7.3 ± 0.4	6.9 ± 0.4	7.9 ± 0.7	3.4 ± 0.5
Age	20 ± 3	22 ± 1	28 ± 2	28 ± 3
Crown dominance	2	4	5	4
n	40	32	36	12
<i>Alnus sinuata</i>				
Height (m)	2.2 ± 0.5	3.5 ± 1.0	2.4	3.4 ± 0.8
DBH (cm)	3.4 ± 2.0	2.6 ± 0.4	2.1	7.3 ± 1.5
Age	17 ± 4	22 ± 3	38	50 ± 12
Crown dominance	4	5	5	5
n	4	3	1	3
<i>Picea glauca</i>				
Height (m)	2.2 ± 0.7	2.6	10.9 ± 1.0	13.8 ± 1.0
DBH (cm)	5.0 ± 0.7	-	21.4 ± 1.7	26.3 ± 1.8
Age	12 ± 2	13	100 ± 8	90 ± 5
Crown dominance	4	6	3	2
n	6	1	16	38
<i>Betula papyrifera</i>				
Height (m)	3.7 ± 0.8	4.6 ± 4.0		12.8 ± 0.6
DBH (cm)	-	-		28.1 ± 1.5
Age	12 ± 2	26 ± 17		70 ± 3
Crown dominance	4	4		2
n	7	2		35

^aNumbers are rounded to nearest measurement unit. n=number of stems sampled.

^bCrown dominance: 1=open grown, 2=dominant, 3=codominant, 4=intermediate, 5=overtopped, 6=subordinate, 7=ground.

Spruce forest along a cut bank was eliminated by flooding and erosion between 1981 and 1984.

Several minor types were also found along the helicopter transect: Bog, Wet - Sedge Grass Meadow, and other forests. The Bog and Wet Sedge Grass Meadow had developed on poorly drained soils rather than on the well-drained sites supporting successional pathways described in this paper.

Early Shrub Stage

Early Shrub communities had the least cover of any successional stage, and most plants were <0.4 m tall (Table 2, Figure 2). Dominant plant species included Yellow Dryas (*Dryas drummondii*), Balsam Poplar, Feltleaf Willow (*Salix alaxensis*), Variegated Horsetail (*Equisetum variegatum*), or combinations of these. Willows were the only species in this stage with mean height > 0.40 m (Table 3). Heights of Balsam Poplar and Feltleaf Willow were suppressed

by browsing and flooding. Age variation in most Early Shrub stands was small, suggesting that recruitment was simultaneous.

The least vegetation cover occurred on the harsh, cobbly Yellow Dryas sites and was not readily detectable on the black-and-white photographs or from the helicopter survey. Overstory development on Yellow Dryas sites was stunted, and Balsam Poplar remained sapling sized for 20 to 40 years on one stand that had been examined but not quantitatively sampled. Balsam Poplar communities occupied dry, nutrient-poor sites with sand content near 90% in many cases. Willow sites had intermediate-textured soils and ground cover. Greatest vegetation cover and finest-textured soils, with silt >60%, among the Early Shrub sites occurred on Horsetail sites, which also included traces of sedges (*Carex* spp.) and cottongrasses (*Eriophorum* spp.).

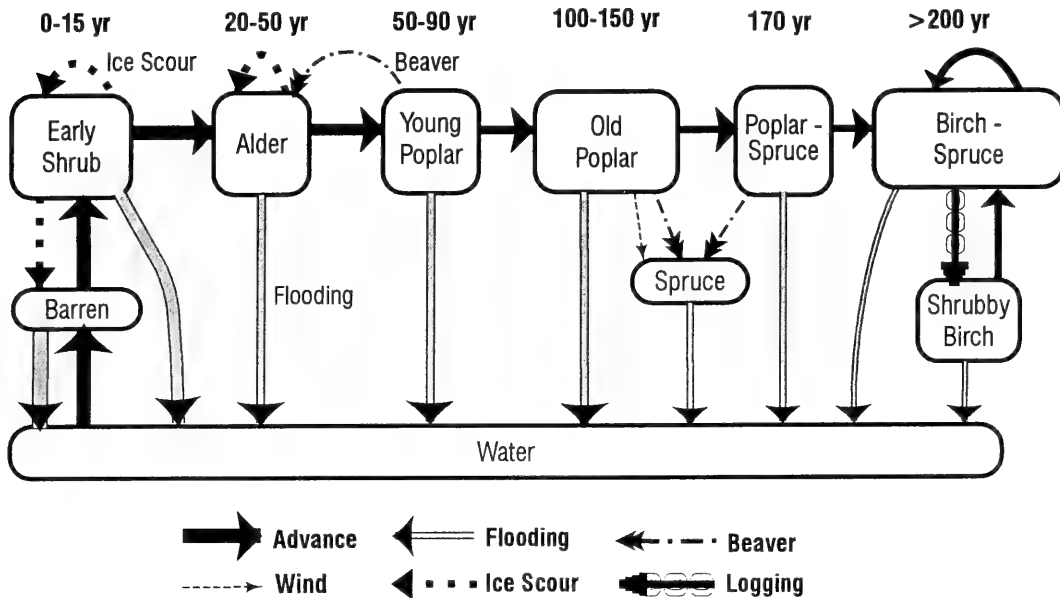


FIGURE 4. Conceptual model of successional pathways along the Susitna River and their controlling factors. Flooding includes erosion and sedimentation. Years above diagram represent generalizations of when types may dominate. Width of arrows represents relative importance of the pathway.

Thinleaf Alder grew more rapidly than other shrubs, 5-year-old alders being approximately 1.5 m tall while same-aged Balsam Poplars averaged approximately 0.5 m in height. Willow stands had the best-developed shrub community within the Early Shrub stage (Tables 2, 3). These shrubs formed the overstory (crown dominance = 2, Table 3).

Many Early Shrub sites changed considerably between 1981 and 1984. One stand (20) was sufficiently eroded that it could not be resampled. Two Juvenile Balsam Poplar stands (21 and 25) had almost identical cover values but stand 21 had more litter in 1984. One horsetail stand (16) had more horsetail and more bare ground in 1984 compared to 1981. Two horsetail stands (8, 9) had more Balsam Poplar in 1984. Willows in another Horsetail stand (13) increased from 1% cover to almost 20% cover. During the same period horsetail cover in a Willow stand (22) increased 22% to 53% while woody cover decreased from 18% to 5%. These different responses were functions of varied disturbance regimes and changes in water levels associated with dissimilar channels.

Intermediate Stage

The intermediate stage of succession accounted for 6 to 18% of vegetated land along the three reaches of the floodplain, and most of this was Closed Tall Scrub Alder (Table 1). These sites were characterized by Thinleaf Alder or Balsam Poplar which had developed into tall shrubs or trees. These would be classified as Open Tall Scrub *Alnus tenuifolia* / *Calamagrostis canadensis* and Closed Broadleaf Forest Balsam Poplar *Populus balsamifera* / *Alnus*

tenuifolia / *Calamagrostis canadensis*, respectively at Level V of Viereck et al. (1992). Low shrub-sized plants (<1.5 m tall) were rare in the understory (crown dominance = 6) beneath a Thinleaf Alder or Balsam Poplar overstory (Figure 3, Tables 3, 4).

Total vegetation cover in Alder stands averaged 87% across all height classes (Table 2). Thinleaf Alder provided 59% cover, whereas Balsam Poplar provided only 13% cover, but was present in all stands. Bluejoint Reedgrass (*Calamagrostis canadensis*) produced a dense understory with 38% cover. Average ages of tall shrub-sized Thinleaf Alder and Balsam Poplar in Alder sites were approximately 20 years (Table 4). Mean Balsam Poplar and Thinleaf Alder heights were 6.2 and 5.3 m, respectively, in the Alder sites, but Thinleaf Alder provided more cover especially in the taller classes (Tables 2, 4, Figure 2). Little browse was available for Moose because of the short stature and low cover values of the other woody species (Figures 2, 3). This was the first stage to have a well-developed litter layer that could contribute to nutrient cycling. Multiple buried organic layers were found where sedimentation buried old litter layers.

Vegetation developed into Young Poplar Forests when Balsam Poplar overtopped Thinleaf Alder (crown dominance shifted from 2 to 4) and dominated the overstory with 62% cover (Figure 2, Tables 3, 4). These Balsam Poplar trees averaged 44 years of age and 14 m in height, which was more than double their height in the Alder stage and twice as tall as Thinleaf Alder in this stage. Thinleaf Alder stems had similar ages in both the Alder and Young Poplar Forests, suggesting that individual Thinleaf Alder

stems may live only 20 years, although parent root systems might live longer. Both Alder and Young Poplar Forests were similar except for the age and species structure of the overstory and increase in Prickly Rose (*Rosa acicularis*) and High Bush-cranberry (*Viburnum edule*) (Table 2, Figure 2). Most Thinleaf Alder cover was limited to the 2 - 4 and 4 - 8 m classes, and Bluejoint still dominated the understory < 1 m tall (Figure 2).

Late Stage

Late stage of succession contained Old Balsam Poplar Forests and Paper Birch - White Spruce Forests which occupied over half of the vegetated land surveyed (Table 1). It also contained transitional Balsam Poplar - White Spruce Forests. Old Poplar and Birch - Spruce stages would be identified as Open Broadleaf Forest Balsam Poplar *Populus balsamifera* / *Alnus tenuifolia* / *Calamagrostis canadensis* - *Rosa acicularis* - *Viburnum edule* and Open Mixed Forest Spruce - Paper Birch *Picea glauca* - *Betula papyrifera* / *Calamagrostis canadensis* - *Rosa acicularis* - *Viburnum edule* types, respectively, at Level V of the Alaskan Vegetation Classification (Vioreck et al. 1992). Old Balsam Poplar Forests characterized 25 to 40% of the vegetated floodplain while mixed stands of Paper Birch and White Spruce occupied 23 to 32% of the area (Table 1).

Although Old Balsam Poplar sites averaged 90% total vegetation cover, the overstory had thinned relative to the Young Poplar Forest (Figure 2). Shrub cover and density, especially of browse species, increased substantially (Figure 2). The oldest Balsam Poplar tree measured in 1984 was approximately 170 years, but many were 110 to 140 years of age. One (stand 3) was an Old Poplar site that had been flooded between 1981 and 1984, and litter was reduced from 100% to 50%. White Spruce was not detected along the sampling transects in 1981, but 9% cover was reported in 1984. In 1981 several minor forbs were found [Tall Bluebell (*Mertensia paniculata*), Pyrola (*Pyrola* spp.), American Red Currant (*Ribes triste*), Northern Bedstraw (*Galium boreale*), ferns], but these were negligible in 1984. The site had about twice as much Prickly Rose, High Bush-cranberry, and Bluejoint Reedgrass in 1984 as it did in 1981. Similarly, another stand (17) went from 67% to 1% litter and many small forbs were no longer present. Prickly Rose and High Bush-cranberry tripled between 1981 and 1984.

Flooding was still an important factor affecting understory species in Old Poplar Forests as evidenced by the preceding observations and numerous buried horizons, indicating that a forest floor was present during the flooding (Vioreck et al. (1993). Changes in vegetation types occurred most often when banks were eroded or plants were physically removed, rather than from these depositional events that temporarily altered understories.

As individual Balsam Poplar trees and understory Thinleaf Alder matured and died, White Spruce trees were released (crown dominance shifted from 3 to 2, Table 4), and Paper Birch became established on soil clinging to the roots of uprooted Balsam Poplar trees. Paper Birch - White Spruce Forests consisted of a mosaic of well-developed treed areas with gaps dominated by shrubs where older trees had died. Herbaceous and low shrub species became more important in the gaps and understory of Birch - Spruce while cover in intermediate layers decreased (Figure 2). Densities of browsable shrubs increased substantially (Figure 3) although many of these stems were in open areas. In one site where Paper Birch had been logged, most stumps had sprouted and associated vegetation had developed the appearance of open patches within other Birch - Spruce stands. The oldest cored Paper Birch in a Birch - Spruce site was almost 170 years although ages of most mature trees were between 100 and 140 years while the oldest measured White Spruce tree was 124 years.

Some abandoned oxbows or otherwise poorly-drained sites developed into wetlands. These were dominated by Thinleaf Alder, Dwarf Arctic Birch (*Betula nana*), Buffaloberry (*Shepherdia canadensis*), Bluejoint Reedgrass, and sphagnum moss (*Sphagnum* spp.).

Discussion

Plant Species Establishment

The first plant species, such as Balsam Poplar and willows, to colonize a site had light, nondormant, wind- or water-dispersed seeds that germinated soon after landing on a moist, suitable substrate (Vioreck 1970; Densmore and Zasada 1983; Walker et al. 1986; Helm and Allen 1995). Species that survived on these new surfaces had to survive flooding and sedimentation. Fall- and winter-dispersed seeds (Thinleaf Alder, Paper Birch, White Spruce) usually lagged summer dispersers by a year before they colonized.

Colonization appeared to be a stochastic event that did not occur each year (Walker et al. 1986). Survivability of new seedlings that germinated along high water lines depended on minimal flooding for the remainder of the summer (Sigafos 1964; Fenner et al. 1985; Bradley and Smith 1986). Helm and Allen (1995) observed that Balsam Poplar seedling survival on a glacial floodplain may depend on dispersal close to summer rains, but early enough so that seedlings could survive flooding. Successful colonization along the Susitna might not occur each year since late summer flows were usually higher than spring flows. Two- to five-year old sites were rare both in 1981 and 1984 which suggested that new sites had not become available or were not colonized during the preceding few years. Bradley and Smith (1986) reported that suitable conditions for

recruitment occurred once every five years on the Milk River, which would be a reasonable estimate for the Susitna River.

Thinleaf Alder colonized where Balsam Poplar, willows, or horsetails were already growing. This delay might have occurred because its seeds were dispersed in the fall rather than during the growing season. Appropriate mycorrhizal fungi may not be present on primary successional sites for Thinleaf Alder to colonize (Helm and Carling 1993; Helm et al. 1996). Partial shade was important for White Spruce seedlings (Safford 1974) while Paper Birch seedlings required light shade for 2 to 3 months (Brinkman 1974), thus reducing the likelihood of successful colonization on barren sand or silt bars. However, Paper Birch and White Spruce established more readily on mineral soils with little or no flooding (Clautice 1974; Youngblood and Zasada 1991). Most White Spruce and Paper Birch seed travel < 100 m (Zasada 1986), making distance from seed source a possible limiting factor.

Paper Birch generally became established after White Spruce, and seedlings occurred only on mineral soil on rootballs of trees uprooted by wind or gravity. This provided mineral soil and elevated the seedling above competition on the forest floor (Beatty and Stone 1986; Jonsson and Dynesius 1993). Old Paper Birch were primarily observed straddling rootballs from uprooted trees that were partially decomposed, indicating that the seedlings we observed on rootballs could indeed mature in those microsites. Gaps and windthrow microsites have been shown to be important for regeneration of other tree species at northern latitudes (Deal et al. 1991; Jonsson and Dynesius 1993).

Mechanisms of Successional Pathway Changes

Figure 4 depicts major successional pathways, relative importance (width of arrows) of each pathway, causes of changes, and approximate "time after stabilization" that various stages occurred. Burial of 5 to 10 years of plant growth with 0.5 m or more of sediment and rotten centers on older trees made aging only approximate. The Water compartment represented surface areas beneath water. Barren represented the first surfaces above water with little plant colonization (<2% cover). At any stage, erosion by flooding could cut banks, remove the substrate and vegetation, and return the location to Water. Older sites were found along cut banks while young sites were more often found on areas of recent deposition rather than along cut banks. Other disturbances usually prevented succession from advancing (arrow pointing to same cell) or regressed the site by removing the overstory.

The several phases within the Early Shrub stage could develop into each other (arrow cycling within that compartment), but substrate differences associated with the various phases likely resulted from

different intensities of flooding and soil deposition (Figure 4). A Willow stand with willows and poplar present in 1981 was dominated by Variegated Horsetail with an understory of new Balsam Poplar seedlings in 1984. In contrast, Feltleaf Willow and Variegated Horsetail both became more abundant and larger between 1981 and 1984 on a hummocky, ice-affected site where the hummocks formed by ice action. In another site Variegated Horsetail, but not Feltleaf Willow, was reduced by flooding some time between July and September 1984.

Ice scour usually bent and scraped willows and juvenile and sapling Balsam Poplar in Early Shrub and Alder stages but did not change the vegetation type (Figure 4). Bent stems sprouted from the horizontal or diagonal stem, substantially increasing the number of browsable stems. Larger woody trunks of Alder communities protected understory plants from ice damage, but in younger sites ice often scraped the substrate, removing both the substrate and plants growing there. These became Barren sites. Ice also transported sediments to some sites.

Browsing by Moose and Arctic Hares slowed vegetation development by reducing heights on many shrubs in earlier stages. This allowed Thinleaf Alder to dominate more rapidly. Beavers were very active on some sites and removed most Balsam Poplar stems in a Young Poplar Forest, reverting it to an Alder site between 1981 and 1984 (Figure 4). Beavers also removed full-sized trees in Old Poplar Forests but did not alter the vegetation type. A hypothetical pathway exists for the formation of White Spruce stands if Beavers removed sufficient poplar from an Old Poplar Forest or Poplar-Spruce Forest. Shade and lack of mineral soil would probably preclude Paper Birch from growing on the site, thus favoring spruce establishment. Although other studies have noted substantial changes in vegetation as a result of tree-cutting by Beaver, the trees were Trembling Aspen (*Populus tremuloides*) (Johnston and Naiman 1990; Moen et al. 1990).

Disturbances could also slow vegetation development indefinitely. Some Juvenile Poplar sites appeared to be on 30-year old surfaces based on comparison of aerial photographs from 1951 and 1981, but above-ground ages were < 10 years. Underground portions of stems extended about 0.5 m below the present soil surface and accounted for 5 - 10 years of additional growth on deeply-sedimented sites. All of our Alder sites had Balsam Poplar as a codominant and would be expected to progress to Young Poplar, rather than remaining in Alder stage indefinitely.

One Old Poplar site had trunks broken 2 to 3 m above the ground, apparently by winter winds since no trees were uprooted from the frozen ground, and most trees fell in the same direction. Some White Spruce regeneration was evident, but the herbaceous

understory was too dense and the soils too organic for hardwood seedlings, especially Paper Birch, to become established. We believe that this site may eventually become a White Spruce site, but could become an herbaceous, low or tall shrub site and remain in this stage indefinitely if other trees do not become established. This is indicated by wind arrow in Figure 4. Logging and firewood cutting in one Birch - Spruce site produced a community similar to the gap portion of the Birch - Spruce Forest although herbaceous competition could sometimes hinder woody regeneration from seed.

Comparisons with Other Northern Rivers

Vegetation succession along the Susitna River was similar to other boreal forest rivers in terms of the early shrub development (Feltleaf Willow, Balsam Poplar) and establishment of Old Poplar Forests, but differed primarily in the effects of substrate on initial community composition and in the importance of Birch - Spruce stage in late succession. Because of the greater presence of deciduous trees, mosses and lichens were only a minor component of the ground layer. Similarities to other northern rivers included the importance of Feltleaf Willow and the rareness of Balsam Poplar - White Spruce sites.

More Feltleaf Willow was found on gravelly alluvium than on sandy or silty materials on the Colville River on the Arctic slope (Bliss and Cantlon 1957) in contrast with the Susitna River. Gill (1972) also found Feltleaf Willow up to 6 m tall on the Mackenzie River delta. Feltleaf Willow almost never reaches these sizes in southcentral Alaska because of intense moose browsing and competition from tree species. These factors generally precluded Feltleaf Willow from reaching even 2 m height along the Susitna River. Observations of heavy browsing slowing growth of palatable species is consistent with observations on the Tanana River in interior Alaska (Wolff 1976; Bryant and Chapin 1986).

Vegetation along the Susitna River differed from other northern rivers in the greater variety of early seral communities resulting from variable river dynamics and substrate textures. The earliest stage described by Viereck (1970) along the Chena River in Interior Alaska was a 15-year-old Feltleaf Willow site. It established on coarser soils than Willow sites in the Susitna River floodplain, and it was much older than most of our Willow. However, Gill (1972) and Teversham and Slaymaker (1976) reported Balsam Poplar species on their coarser sites similar to the Susitna River. The greater variety of substrate textures on the Susitna River resulted from different fluvial dynamics. Sands were frequently deposited by intense summer floods, particularly below the Chulitna confluence, while silts and fine sands were deposited by milder floods and in backwaters behind ice jams (Helm et al. 1985).

Willow was reduced from Alder and later stages of succession by its shorter life span, browsing, and shade intolerance (Walker et al. 1986; Bryant 1987; Viereck et al. 1993). Van Cleve et al. (1980) observed that most willows died under closed canopy, although Feltleaf Willow and Thinleaf Alder survived in a state of reduced vigor. Prickly Rose and High Bushcranberry increased in understories because they were more shade tolerant (Van Cleve et al. 1980; Viereck et al. 1993).

Nanson and Beach (1977) observed that Balsam Poplar transitioned rapidly to White Spruce with no mixed stage in British Columbia. Their White Spruce seedlings were released when Balsam Poplar died on 100- to 150-year-old surfaces, similar to our transitional sites of Poplar - Spruce. White Spruce would normally be expected to follow Balsam Poplar in the successional sequence since it is longer lived and more shade tolerant than Paper Birch (Reed and Harms 1956). However, Paper Birch is able to reproduce on mineral soil in gaps left by fallen trees, and recruitment is sufficient to maintain the Paper Birch - White Spruce stage in the Anchorage - Matanuska Valley adjacent to our study area. This strong deciduous component with associated leaf fall probably limits the development of the moss and lichens in the ground layer. Along the Tanana River moss development did not exceed minor cover until the Balsam Poplar - White Spruce stage when White Spruce became codominant or dominant (Viereck et al. 1993).

Vegetation establishment appeared slower in the Susitna River floodplain compared to the Chena and Tanana Rivers in interior Alaska (Viereck 1970; Viereck et al. 1993). Early Shrub communities could persist in the Susitna River floodplain for 15 years or more while Alder tended to dominate 20 to 50 year old sites. In contrast Closed Alder and Willow stages dominated 5- to 10- year-old sites in the Tanana floodplain, and Young Balsam Poplar dominated 20- to 40-year-old sites (Viereck et al. 1993). Balsam Poplar dominated the canopy in Chena River sites that were approximately 50 years old, then White Spruce became dominant by 120 years (Viereck 1970). However, in the Tanana River floodplain, White Spruce was not dominant until about years 200-300 (Viereck et al. 1993). Our Old Balsam Poplar Forests were over 100 years old, and White Spruce was just becoming important in the understory, which was more similar to the Tanana River than to the Chena River. However, Birch - Spruce stage dominated sites over 200 years old in the Susitna River floodplain and appeared to be self-replacing.

Conclusion

Disturbances caused by flooding, including both sedimentation and erosion, and wildlife herbivory were major factors regulating vegetation succession

along the Susitna River. Vegetation appeared to establish only in certain years, perhaps in response to rainfall and flood regimes. Most disturbances by flooding or ice caused sedimentation of the site and only caused a retrogression to bare ground or water if the substrate itself was eroded beneath the plants. Uprooted trees appeared necessary to produce safe sites with mineral soils and increased sunlight for Paper Birch establishment in forest understories. Small-scale disturbances caused by tree-falls created openings in the canopy and mineral soil for seedling establishment and development of shrub mosaics. Moose restricted the height growth of Balsam Poplar and willows in early stages. Beavers, however, could remove entire trees and force vegetation succession to an earlier stage. Vegetation patterns in the Susitna River floodplain thus resulted from disturbances by flooding, ice, wind, and browsing as well as stochastic events associated with seed dispersal and establishment.

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Moose, *Alces alces*, Habitat Relative to Riparian Succession in the Boreal Forest, Susitna River, Alaska

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We documented Moose, *Alces alces*, habitat characteristics relative to boreal forest succession in the Susitna River floodplain, Alaska. Early Shrub and Old Poplar (*Populus balsamifera*) Forest sites were most important to wintering Moose. Browse availability was the principal factor affecting winter habitat selection by Moose. Feltleaf Willow (*Salix alaxensis*) in Early Shrub was the principal browse species, producing approximately 101 kg/ha of browse. In a year of average snowfall, 76% of available Feltleaf Willow was utilized. Other important species, High Bushcranberry (*Viburnum edule*) and Rose (*Rosa acicularis*) were abundant in Old Poplar Forest and Birch-Spruce (*Betula papyrifera*-*Picea glauca*) Forest, but were unavailable when snow exceeded approximately 110 cm. Non-vegetated sites, dry sloughs and frozen river channels had significantly less ($p < 0.05$) snow accumulation than other sites, making them preferred paths of access during periods of deep snow. Wind speed did not vary significantly ($p < 0.05$) between successional stages older than Early Shrub, and wind did not appear to affect habitat use. Moose exhibited some preference for cover during periods of rest, especially during warm sunny days in late winter. While biologically feasible, enhancement of browse production in the Susitna River floodplain appears logistically impractical and of wrong priority. Habitat enhancement should be focused on upland sites where fire suppression has altered natural ecosystem functions, not in floodplain where the river continues to maintain a constant supply and diversity of successional conditions important to Moose and other wildlife.

Key Words: Moose, *Alces alces*, browse, cover, habitat, snow, vegetation succession, wind, boreal forest, Susitna River, Alaska.

Erosion and redeposition of land by glacial rivers are primary factors in maintaining the productivity and diversity of boreal forest and associated wildlife habitats (Larsen 1980). In regions where fire suppression is reducing the frequency and extent of forest rejuvenation and diversification, the perpetual influences of rivers and streams on forest vegetation and wildlife habitats are of increasing importance. Moose (*Alces alces*), Snowshoe Hares (*Lepus americanus*), Beaver (*Castor canadensis*) and other early successional wildlife are dependent on the availability of early growth hardwoods established following fire, fluvial events or other forest disturbances (Kelsal et al. 1977; Peek et al. 1976; Koehler and Brittell 1990). Not only do early successional wildlife depend on young hardwoods for food, but they can significantly affect successional development of boreal forest (Wolff and Zasada 1979; Bryant 1987; Pastor et al. 1988; Johnson and Naiman 1990; Helm and Collins 1997).

Glacial rivers flow through most major valleys in southcentral Alaska, occurring within important winter ranges of Moose. In the Susitna River valley, Moose prefer floodplain vegetation types in winter (Albert and Shea 1986). Wintering Moose are also attracted to low-lying uplands disturbed by recent fires, homestead or subdivision clearing, and right-of-way construction (Chatelain 1951; Albert and Shea 1986). Floodplains are mainstay habitat for Moose during severe winters,

particularly in areas where lack of recent disturbance in upland forests has led to a decline in browse availability (Simkin 1975; Bishop and Rausch 1975).

Chatelain (1951) ranked the Susitna Valley as the most productive Moose habitat in Alaska. Chatelain observed that high Moose carrying capacity in floodplains of the Susitna River and its tributaries was further augmented by abundant upland browse resulting from wildfires and homestead clearing in the early and mid 1900s. By the early 1970s strict fire suppression and natural succession in old forest burns and homesteads had reduced browse availability causing Moose populations to decline (Bishop and Rausch 1974).

The objectives of this study were to document Moose habitat characteristics related to forest succession in the Susitna River floodplain and the boreal forest generally, and to identify how this riparian system may be best managed for Moose. We considered Moose to be a key indicator species (Hanley 1993), indicating availability of early successional habitat and welfare of associated wildlife.

Methods

We measured characteristics of Moose habitat for a range of successional conditions common to the lower Susitna River floodplain (62° N, 150° W). We made most measurements in a winter of average

snow accumulation, 1992-1993, and in summer 1993. We noted general habitat conditions and differences in Moose distribution from 1981 to 1995.

Vegetation/habitat was represented by Early Shrub stages of early succession; Alder (*Alnus* spp.) and Young Poplar (*Populus balsamifera*) Forest stages of intermediate succession; and Old Poplar Forest and Birch (*Betula papyrifera*)-Spruce (*Picea glauca*) Forest stages of late succession. For more complete descriptions of these successional stages see Helm and Collins (1997).

We used a twig-count method (Shafer 1965) to estimate availability and utilization of browse. We identified browse as twigs occurring at least 0.5 m above the ground, on stems less than 4 cm dbh.

We point sampled horizontal cover in late winter and again in mid summer (Collins in press), by using an 8× monocular to sight the intersection of two lines on a target 1.5 m above the ground, 15 m from the observer. Overlap of the line intersection by vegetation indicated a point of cover. We also point sampled vertical cover in winter and summer, but by using an 8× rifle scope (mounted to a staff and viewed vertically through a 90° mirror reflection). Vegetation overlap of the cross-hair intersection indicated a point of cover.

Snow depth and hardness were measured with a Rammsonde penetrometer (Benson 1962; Coady 1974) at 24 - 30 locations within each vegetation stage, during winter 1992 - 1993 when snow depth fluctuated around the most recent 15-year average (Figure 1). We recorded wind speeds during a relatively strong wind. Successive measurements were made 1.5 m above the ground at 8 m intervals at 90 points arranged in a grid in each site. Each set of 90 recordings was completed simultaneously during a 15-minute period.

Using pellet-group counts (Neff 1968), we measured Moose use of different successional stages in spring, immediately following snow melt. We randomly located fifty belt transects (2 × 60 m) in three representative stands of each successional stage and searched for pellet groups deposited following leaf fall. When transect length exceeded the extent of a vegetation patch, we randomly relocated and completed the remaining portion elsewhere in the same vegetation patch.

Results

Early Shrub vegetation produced approximately 110 kg Moose browse per hectare, making it the most productive successional stage (Table 1). Feltleaf

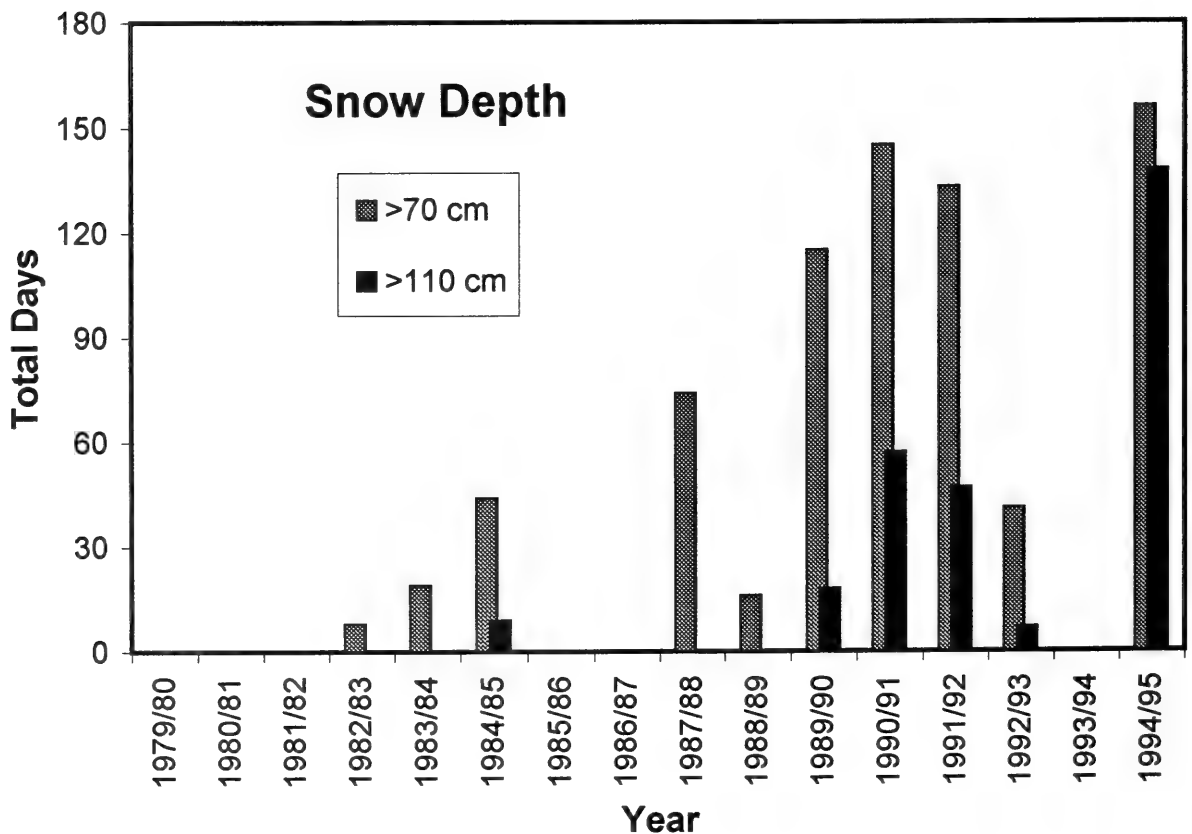


FIGURE 1. Snow depths at Willow, Alaska (White's Crossing), 1979-1995. Figure is based on data recorded by the National Oceanic and Atmospheric Administration. Deepest snow in vicinity of study area occurs at this location.

Table 1. Moose browse availability and utilization in different successional stages of the Susitna River floodplain. Means are followed by standard errors in parenthesis.

Stage	Diameter (mm) at point of browsing	Twig weight (g)	Twigs.stem ⁻¹	Browsed twigs. stem ⁻¹	Stems. hectare ⁻¹	Available browse (kg.ha ⁻¹)	Browse consumed (kg.ha ⁻¹)	% browse utilized
Early shrub								
<i>Populus balsamifera</i>	4.7 (1.2)	1.53 (0.31)	3.80 (3.80)	0.49 (1.25)	1166 (680)	6.78	0.87	12.8
<i>Salix alaxensis</i>	5.4 (1.7)	1.90 (0.60)	6.15 (6.70)	4.61 (8.59)	8633 (2420)	100.88	75.62	75.0
<i>Salix novae-angliae</i>	3.1 (0.9)	0.52 (0.18)	2.85 (1.18)	2.69 (4.73)	1400 (937)	2.07	1.95	94.2
Total						109.73	78.44	71.5
Alder								
<i>Rosa acicularis</i>	3.9 (1.2)	0.64 (0.34)	2.06 (1.20)	0.29 (0.92)	117 (100)	0.15	0.02	13.3
<i>Salix alaxensis</i>	4.1 (0.2)	0.86 (0.37)	7.82 (8.12)	5.08 (3.94)	2684 (2700)	18.05	11.72	64.9
<i>Salix novae-angliae</i>	3.1 (0.9)	0.44 (0.18)	3.02 (2.41)	2.92 (1.59)	83 (66)	0.11	0.11	96.7
<i>Viburnum edule</i>	3.6 (0.8)	0.42 (0.29)	2.67 (1.95)	0.73 (1.40)	467 (247)	0.52	0.14	26.9
Total						18.83	11.99	63.7
Young poplar forest								
<i>Rosa acicularis</i>	3.9 (0.9)	0.92 (0.47)	2.35 (1.53)	1.44 (1.57)	1519 (957)	3.28	2.01	61.3
<i>Salix alaxensis</i>	4.9 (1.6)	1.63 (0.51)	6.27 (5.42)	5.02 (3.88)	352 (287)	3.60	2.88	80.0
<i>Salix novae-angliae</i>	3.1 (0.9)	0.47 (0.25)	3.26 (2.31)	3.15 (2.20)	37 (38)	0.05	0.05	96.6
<i>Viburnum edule</i>	4.1 (0.8)	0.72 (0.51)	2.80 (1.74)	2.36 (1.40)	463 (260)	0.93	0.77	82.8
Total						7.88	5.73	72.7
Old poplar forest								
<i>Rosa acicularis</i>	4.1 (0.9)	1.06 (0.49)	3.15 (2.44)	1.70 (2.25)	10750 (2197)	35.89	19.37	54.0
<i>Viburnum edule</i>	3.9 (0.9)	0.60 (0.43)	3.56 (2.65)	2.58 (2.39)	21833 (2897)	46.64	33.92	72.7
Total						82.53	53.29	64.6
Birch-spruce forest								
<i>Betula papyrifera</i>	3.3 (0.8)	0.44 (0.24)	9.90 (8.63)	2.52 (4.42)	750 (210)	3.27	0.83	25.4
<i>Rosa acicularis</i>	3.8 (0.9)	0.58 (0.31)	2.17 (1.15)	0.58 (1.03)	16933 (1863)	21.31	5.70	26.7
<i>Viburnum edule</i>	4.0 (1.2)	0.57 (0.45)	3.33 (2.52)	0.85 (1.76)	17066 (2610)	32.39	8.27	25.5
Total						56.97	14.80	26.0

TABLE 2. Horizontal¹ and vertical² cover (%) in different stages of riparian forest succession, Susitna River, Alaska. Measurements were made in March and July 1993. Means are followed by coefficients of variation in parentheses.

Stage	Horizontal		Vertical	
	Winter	Summer	Winter	Summer
Early Shrub				
8-yr-old	13.8 (37.7)	35.2 (27.3)	0.3 (10.8)	18.2 (49.2)
14-yr-old	28.2 (11.9)	62.0 (10.2)	8.6 (33.7)	68.0 (10.3)
Alder	24.9 (4.2)	55.5 (5.2)	11.2 (6.8)	65.0 (8.7)
Young Poplar Forest	26.0 (5.3)	46.9 (4.8)	14.8 (5.2)	62.4 (6.8)
Old Poplar Forest	23.0 (6.8)	51.2 (6.1)	23.4 (7.5)	52.1 (9.6)
Birch-Spruce Forest	25.1 (6.2)	48.7 (5.3)	22.2 (5.2)	61.3 (8.3)

¹Horizontal cover = % visual obstruction within 15 m horizontal distance, 1.5 m above ground.

²Vertical cover = % visual obstruction of the sky as observed from 1.5 m above ground.

Willow (*Salix alaxensis*) represented 92% of available browse and 96% of browse consumed in Early Shrub. Our estimates of total browse and Feltleaf Willow availability for Early Shrub were almost identical to the most productive of similar sites measured in interior Alaska (Wolff and Cowling 1981).

Development of an Alder overstory was associated with reduced density and availability of Feltleaf Willow (Table 1). By this point in succession most Feltleaf Willow and Balsam Poplar surviving the combined effects of shading and browsing had grown beyond the reach of Moose, resulting in an 83% decrease in browse availability.

When sites were approximately 50 years age, Balsam Poplar dominated young forest overstories, and the density and availability of Alder and tall browse species had declined (Helm and Collins 1997). Although increases in Rose (*Rosa acicularis*) and High Bushcranberry (*Viburnum edule*) began to offset losses of tall browse species (Table 1), Young Poplar Forest was least productive of Moose browse.

Rose and High Bushcranberry increased when Balsam Poplar overstories opened as a result of tree mortality. This made Old Poplar Forests second only to Early Shrub in terms of browse production and consumption (Table 1).

By the time Birch-Spruce overstories had developed in late succession, density and availability of High Bushcranberry had declined by 78 and 70%, respectively. Rose increased in density by 58% but

decreased in availability by 41% (Table 1). Shrub-sized Paper Birch produced limited browse in late succession.

Horizontal cover in winter, viewed 1.5 m above ground from a distance of 15 m, increased from 0 to 28% within the first 14 years of vegetation succession. It then remained relatively constant through all later successional stages (Table 2). Summer horizontal cover reached 62% in 14-year-old Early Shrub, but declined to approximately 50% in later succession.

Early Shrub provided little vertical cover in winter until approximately 14 years age, when canopies above 1.5 m height began to close (Table 2). Increase in size and density of White Spruce caused Old Poplar Forest and Birch-Spruce Forest to have the greatest winter vertical cover. Summer vertical cover was greatest in 14-year-old Early Shrub and Alder, declining slightly later in succession.

Mean wind speeds measured during winter 1.5 m above ground were greatest for river channels and gravel bars lacking above-snow vegetation (Table 3). Wind speed was significantly reduced in vegetated areas, with wind in Early Shrub being approximately 55% of that in barren areas. Wind speeds in Alder, Young Poplar Forest, Old Poplar Forests and Birch-Spruce Forest were approximately 22% of that in barren areas.

In late February 1993, snow depth in barren locations was significantly ($p < 0.05$) less than at all

TABLE 3. Mean wind speeds ($\text{km}\cdot\text{h}^{-1}$) during a relatively strong wind, 14 March 1993, within different stages of riparian forest succession, Susitna River, Alaska.

Stage	x	CV	minimum	maximum
Non-vegetated	8.8 a ¹	24.9	4	16
Early Shrub (8-yr-old)	4.8 b	57.4	1	10
Alder	1.9 c	47.3	0	4
Young Poplar Forest	1.9 c	48.0	0	4
Old Poplar Forest	2.0 c	44.2	0	4
Birch-Spruce forest	2.0 c	48.6	0	4

¹ Means followed by a common letter are not significantly different ($p < 0.05$).

TABLE 4. Mean depth (cm) and integrated hardness (kg-f cm) of snow within different stages of riparian forest succession, Susitna River, Alaska. Means are followed by coefficients of variation in parentheses. Measurements were made in late March 1993 following a winter of typical snow accumulation.

Stage	Hardness (kg-f cm)	Depth (cm)
Non-vegetated	4.76 (61.3)	48.1 a ¹ (58.8)
Early Shrub (8-year-old)	1.96 (15.3)	83.0 b (4.5)
Alder	1.96 (14.3)	79.5 b (10.3)
Young Poplar Forest	1.95 (12.8)	77.9 b (8.5)
Old Poplar Forest	2.02 (13.4)	77.4 b (10.2)
Birch-Spruce Forest	2.12 (15.1)	75.7 b (11.8)

¹ Means followed by a common letter are not significantly different ($p < 0.05$).

other sites (Table 4). Snow depths in other successional stages did not vary significantly, although snow in Early Shrub tended to be deepest. We observed little variation in integrated snow hardness between vegetated stands, but barren sites were more than twice as hard.

Following winter 1992-1993, Early Shrub and Old Balsam Poplar Forest had the highest densities of pellet groups, 203 and 209 per hectare, respectively (Table 5). Alder had the lowest density of pellet groups, 108 per hectare. Assuming Moose consume an average of 5 kg dry weight per day during winter (Gasaway and Coady 1974) and that they use all areas for the same purposes, browse utilization indicated that Early Shrub was used 48% more than Old Poplar Forest. Pellet group densities were proportionately higher than percentages of browse utilization in Alder, Young Poplar Forest and Birch-Spruce Forest.

tion in Alder, Young Poplar Forest and Birch-Spruce Forest.

Discussion

Habitat

In all years, Feltleaf Willow was the principal browse resource for Moose wintering in the Susitna River floodplain. Not only was it highly preferred, as indicated by rates of utilization, but its availability was less limited by deep snow than were other species. Balsam Poplar saplings were available in all years, but were discriminated against by Moose except during periods of deep snow when other browse resources were less available.

Rose and High Bushcranberry were important browse species, but deep snow prevented their utilization in some winters. Moose utilized these species less in Birch-Spruce than in Old Poplar Forest, because those in the Birch-Spruce stands were shorter and smaller diameter and were bent over and covered by snow earlier than in Old Poplar Forest. Limited use of Rose and High Bushcranberry in Birch-Spruce Forest may also have resulted because those stands occurred primarily in the most stable portions of the floodplain, farthest from recently disturbed Early Shrub where Moose preferred to feed.

Highest percentages of browse utilization occurred in Young Poplar Forests, even though those stands were less productive of browse than any other successional stage. High pellet group density associated with numerous bed depressions indicated Moose preferred Young Poplar Forests and Alder stands for resting (Collins and Urness 1979 and 1981).

Alder and Young Poplar Forest may have been preferred resting sites for Moose because they provided better cover than many Early Shrub stands. Young Poplar Forest and Alder were successional and spatially adjacent to Early Shrub where Moose preferentially browsed. However, requirement for cover did not keep Moose from utilizing preferred Willows within sparsely vegetated stands. Early Shrub isolated on small islands 100's of meters from other vegetation received utilization equivalent to

TABLE 5. Mean number of pellet groups per hectare (p.g. ha⁻¹) within different stages of riparian succession, Susitna River, Alaska. Pellets were counted in early May 1993. Estimates are based on 50 120 m² plots in each successional stage. Moose days per hectare (m-d ha⁻¹) were estimated by: 1) dividing total p.g. by assumed defecation rate of 20 p.g. moose⁻¹ day⁻¹, and 2) by dividing browse utilization (see Table 1) by an assumed forage intake of 5 kg moose⁻¹ day⁻¹.

Stage	p.g. ha ⁻¹	m-d ha ⁻¹ (based on 20 p.g. moose ⁻¹ day ⁻¹)	m-d ha ⁻¹ (based on 5 kg intake)
Non-vegetated	n.d. ¹	n.d.	n.d.
Early Shrub	203 (126)	10.2	15.7
Alder	108 (148)	5.4	2.4
Young poplar forest	161 (137)	8.1	1.1
Old poplar forest	209 (133)	10.5	10.7
Birch-spruce forest	160 (165)	8.0	3.0

¹No data were obtained for non-vegetated sites because they included extensive snow and ice covered river channels and sloughs which were washed clean of pellet groups before snow had melted and pellet groups could be counted.

Early Shrub within a few meters of dense cover. The only other apparent preference of Moose for cover occurred in late winter on warm, sunny days.

In March and April, Moose frequently lay in the shade of mature White Spruce during sunny days, suggesting warmer temperatures and more direct sunlight caused them to seek shade to reduce heat stress (Schwab and Pitt 1991). Renecker and Hudson (1986) observed that Moose were more likely to show signs of heat stress than cold stress in winter. They observed increased metabolic rates of Moose when ambient temperatures exceeded -5.1°C , and observed Moose panting at 2.2°C . Demarchi and Bunnell (1995) similarly observed that cow Moose used denser forest during periods of heat stress in summer. Forage was not available beneath spruce and, therefore, we do not believe food attracted Moose to spruce as it sometimes does to upland spruce (LeResche and Davis 1973).

Moen (1973) concluded that reduction of wind velocity is one of the most significant benefits of cover to animals in winter, usually even more important than its effect on radiant energy flux. Nevertheless, we and Modafferi (personal communication) have not observed Moose increasing their use of denser cover in the Susitna floodplain during periods of wind. One-minute-wind speeds (National Oceanic and Atmospheric Administration, Climatological Data, Alaska, 1979-1995) exceeding 28.8 km h^{-1} , the limit to thermoneutrality for Moose calves at -20°C (Renecker et al. 1978), did not occur in March and April when Moose used Spruce cover.

Snow on barren gravel bars and ice-covered river channels was wind compacted and twice as hard as in vegetated sites, but did not support Moose. Except for winters 1989-1990, 1990-1991, 1991-1992 and 1994-1995 snow in these sites did not exceed the 70 cm depth Coady (1974) concluded represents a slight impediment to Moose. Consequently, braided river channels represented a network of corridors, providing Moose good access to all parts of the floodplain.

Besides elevating energetic costs to Moose, snow deeper than 70 cm (Figure 1) reduced browse availability. Rose and High Bushcranberry represented 22% and 29%, respectively, of all browse available in early winter, but they were buried when snow depth reached 70-110 cm. Snow greater than 110 cm caused Moose to stop browsing in forests by mid November in winter 1994-1995 and by late December in winters 1989-1990, 1990-1991, and 1991-1992 (NOAA).

Our estimates of Moose densities based on pellet group densities were subjective, since we did not determine defecation rates. We computed Moose densities, using a rate of 20 pellet groups per day (Andersen et al. 1992), because we assumed the quality and availability of forage in fall and early winter would have elevated food consumption and

defecation rates above those determined in late winter by Franzmann and Arneson (1975), producing a season average closer to 20.

We became concerned about loss of pellet groups prior to counting, because Moose regularly used ice covered river channels and dry sloughs for access to feeding sites. We observed that spring flooding washed pellet groups away before snowmelt allowed pellet groups to be counted. Collins and Urness (1979) reported that Elk (*Cervus elaphus nelsoni*) defecated 11 to 18 times more frequently when traveling from one location to another, causing approximately 40% of all defecations to occur within 3.5 to 5.6% of the day as the animals were walking between feeding or resting sites. We concluded pellet groups could not be used to estimate overall Moose density in the floodplain but that they were useful in conjunction with other data for describing Moose distribution.

Browse utilization, tracks, beds and fecal deposition indicated only rare, localized summer use of the lower Susitna River floodplain by Moose. There were no indications of Moose in most areas in summer, an exception being use of several islands north of Talkeetna in late May and June. This agrees with Modafferi (1988) who observed a tendency for radio-collared cow Moose north of Talkeetna to leave the floodplain as snow receded but then to return for the period late May through June.

We believe that Moose are currently utilizing the lower Susitna River floodplain near winter capacity. During a year of average snowfall, Moose utilized preferred browse species at approximately 75%, a level Wolff and Zasada (1979) suggested represents carrying capacity for similar vegetation. Browse not utilized was apparently of poorer quality and/or less efficiently ingested. Although abundant reserves of less preferred browse species existed, snow depths exceeding 70-110 cm triggered several events that combined to decrease food availability and reduce Moose productivity and survival.

Deep snow eliminated availability of Rose, High Bushcranberry and short individuals of other browse species, confined Moose to the most accessible sites, and accentuated negative energy balance for Moose by causing them to expend greater energy for movement. Griese (*in press*) observed a 35% decline in the Susitna Valley Moose population following the deep-snow winter 1989-1990. Since that time, a continuing series of deep-snow winters has resulted in the population remaining at or below the 1990 level. Griese (*in press*) reported that Susitna Valley Moose have experienced significant winter die-off at least once each decade starting in the 1950s.

Management implications

Erosion and redeposition of substrates within a braided river system like the lower Susitna River is a dynamic process controlled almost entirely by dis-

charge variations and sediment loads (Leopold 1964). Conditions necessary for vegetation succession to proceed are established as sedimentation elevates sites, reducing flooding frequency. Shifts of river channels quickly reverse succession, rejuvenating or eliminating browse stands (Helm and Collins 1997).

Unless flow of the Susitna River is interrupted by hydroelectric development, there is no need or reasonable opportunity to enhance browse productivity. While total area of floodplain covered by each successional stage may remain relatively constant over time, and while successional timeframes are generally predictable, life expectancies of specific sites are unpredictable. Eleven of 20 early successional sites we monitored were either temporarily denuded or completely eroded and redeposited down stream during the period 1981-1995, effectively rejuvenating them without human intervention. By contrast, browse production in upland sites can be efficiently and predictably enhanced by crushing, cutting, or prescribed burning (Oldemeyer and Regelin 1987; Collins 1996).

Browse production within Balsam Poplar Forest and Birch-Spruce Forest can be stimulated by a combination of overstory removal and scarification (Zasada et al. 1981; Collins 1996), costs being subsidized by timber sales. However, costs and accessibility make it difficult to justify overstory removal in floodplain solely to enhance browse production. Felling of Balsam Poplar and Birch must be followed by timely scarification to obtain hardwood density meeting minimal reforestation standards (Collins 1996). This requires use of heavy equipment during that time of year when it is not possible to construct winter roads or ice bridges to cleared sites. Browse regeneration failed in floodplain stands winter logged as much as 30 years ago, because the sites were not scarified, and preexistent Bluejoint Reedgrass (*Calamagrostis canadensis*) and Alder (*Alnus* spp.) increased to exclude other species (Mitchell and Evans 1966; Collins 1996). Tree harvest eliminated opportunity for natural scarification through uprooting by wind and gravity (Jonsson and Dynesius 1993; Helm and Collins 1997). Similarly, we observed regeneration failure in Young Poplar Forest where most Balsam Poplars were felled by Beavers.

The rapidity with which early seral vegetation in floodplains grows out of reach of Moose and/or the frequency with which it is rejuvenated by fluvial forces make it impractical to assess the welfare of Moose and their habitat by traditional methods of monitoring condition and trend (Stoddart et al. 1975). However, general assessment of browse within the floodplain indicates Moose are near ecological carrying capacity, being periodically limited by snow-induced shortages of food (Caughley and Sinclair 1994). Ecological carrying capacity of the

Susitna Valley as a whole is primarily limited by fire suppression in lands adjacent to the floodplain.

Moose are limited by frequency of natural disturbances supporting establishment of early successional vegetation. Therefore, effective management must recognize the collective importance of all naturally occurring disturbances (erosion, forest diseases, windfall and fire) in maintenance of primary productivity within the boreal forest (Attiwill 1994). Managers should first attempt to enhance Moose habitat by eliminating or altering management practices which disrupt or prevent natural forces from maintaining diverse and productive habitat. Direct efforts to enhance habitat are not only more costly, but often, as on the Susitna River floodplain, misplaced.

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Detection and Distribution of the Apple Leaf Midge, *Dasineura mali*, in Nova Scotia

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The Apple Leaf Midge (*Dasineura mali* (Kieffer)) (Diptera: Cecidomyiidae), a foliar pest of apple trees, originated in Europe and was first found in Canada in 1964, when the midge was detected in New Brunswick. Adult midges oviposit on developing apple leaves; the feeding activity of hatched larvae prevents these leaves from unrolling properly, resulting in reduced photosynthesis. Midge infestations on mature trees are not usually problematic. On nursery stock or young trees, however, midge infestations can cause stunting and disrupt tree training. Using data from monitoring records for the period 1990 to 1994, we trace the establishment and spread of the Apple Leaf Midge in Nova Scotia. Results from a 1993 survey of the severity of midge infestations in apple orchards are also presented. Both surveys demonstrate the speed with which the midge spread from the area of initial detection throughout the apple-growing region of Nova Scotia.

Key Words: Apple Leaf Midge, *Dasineura mali*, apple orchards, Nova Scotia.

The Apple Leaf Midge, *Dasineura mali* (Kieffer) (Diptera: Cecidomyiidae), a foliar pest of apple trees, originated in Europe and accompanied the spread of apple from this region to other parts of the globe. In the USA, *D. mali* was first detected in 1928 in Massachusetts; by 1933, the midge had infested an area of approximately 1000 square miles, which included parts of Massachusetts and New Hampshire (Whitcomb 1934). By 1936, orchards in Maine and New York state were attacked, possibly because of wind dispersal of adult midges (Whitcomb 1937). In New Zealand, the midge was initially found in 1950 at Auckland, Palmerston North, and Tauranga; in Auckland it had spread from the original infestation site to neighbouring orchard areas by 1952 (Morrison 1953). In Canada, *D. mali* was first detected in 1964 in Charlotte County, New Brunswick. From there it spread to infect orchards throughout the Saint John River Valley from Woodstock to the Gagetown-Queenstown area by 1978 (MacPhee and Finnamore 1978). The midge is presently found in all apple growing regions of New Brunswick (M. Mazerolle, personal communication). In 1993, larvae found in apple leaf samples collected near Clearbrook, British Columbia were tentatively identified as *D. mali*; formal identification awaits the collection of adult specimens in good condition (H. Philip, personal communication). Here we report on the establishment and spread of *D. mali* in Nova Scotia.

In Nova Scotia, *D. mali* was first discovered in an orchard in Aylesford in 1990, where its presence was detected by the distinctive damage caused by larval feeding. Adult leaf midges deposit eggs on

the margins of growing leaves; when the eggs hatch, the feeding activity of the larvae prevents the leaf from unrolling properly, resulting in the formation of a tight roll (a gall), with the edges of the leaves rolled toward, and parallel to, the midvein. Leaves attacked in this manner do not function properly, and eventually become brittle and discoloured; affected leaves may drop prematurely. Because *D. mali* only attacks growing shoots, it is not of major concern in mature trees, which can usually sustain this type of damage; in nursery stock or young trees, however, this pest can cause stunting and disrupt tree training (Whitcomb 1934). There are usually two to three generations of the Apple Leaf Midge in Nova Scotia.

Methods

Distribution of the Apple Leaf Midge in Nova Scotia's Annapolis Valley for the period 1990-1994 was determined using presence / absence data. The majority of this data was taken from the records of Agricultural Pest Monitoring (APM), a private company which offers custom pest monitoring programs to fruit growers in the Annapolis Valley. Agricultural Pest Monitoring surveys approximately 150 orchard blocks per year; the presence of Apple Leaf Midge was recorded for each orchard in which it was encountered. Distribution data was also obtained during the Intensive Integrated Pest Management Project (IPM), a technology-transfer project funded by the Agri-Food Development Agreement; during this project, eleven orchards were monitored weekly throughout the growing season for a period of five years.

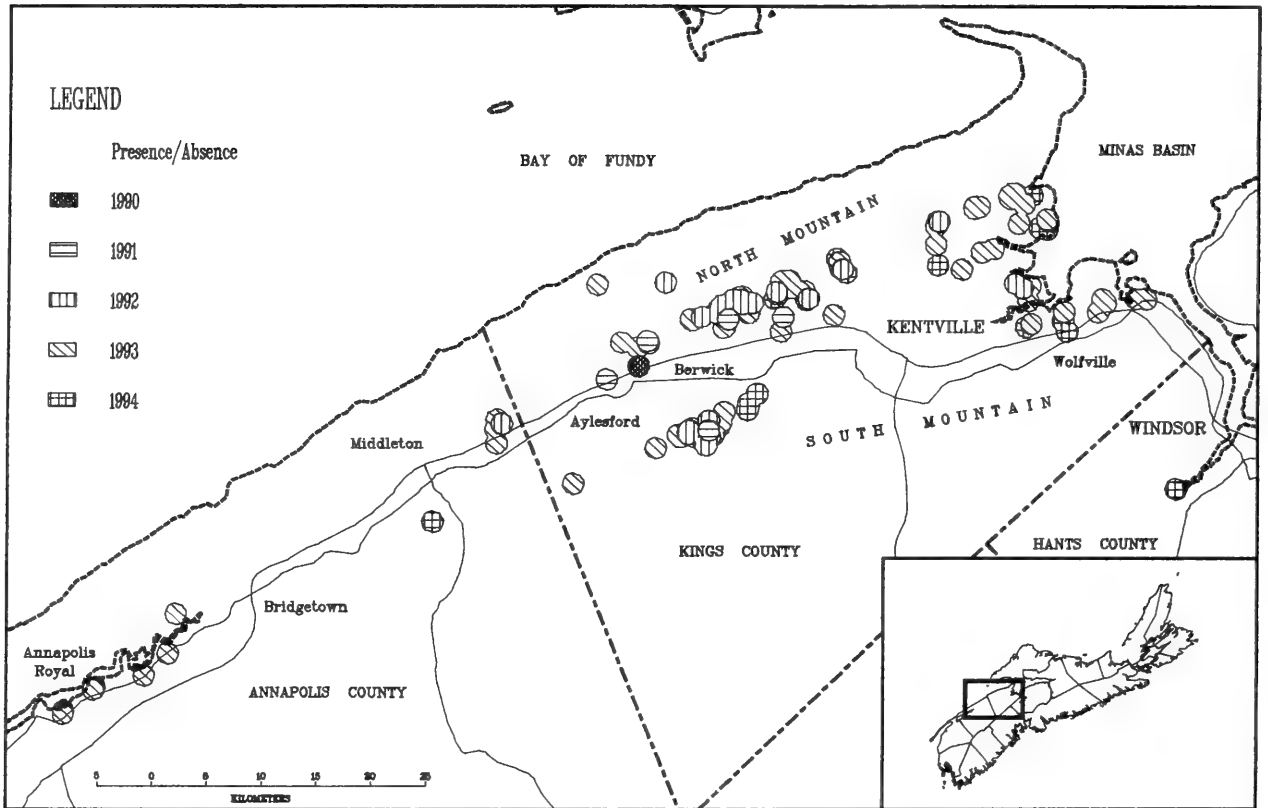


FIGURE 1. Distribution of Apple Leaf Midge infestations in the Annapolis Valley of Nova Scotia for the period 1990-1994. Each circle represents one orchard. In cases where the midge was found in the same orchard in multiple years, the year of first infestation is shown. Inset shows the location of study area within the province.

Presence / absence data was also recorded during a survey of the severity of Apple Leaf Midge infestations in the Annapolis Valley. This survey was done between 21 September and 3 November 1993, and included 57 orchards, some of which were the same orchards monitored by APM or during the IPM project. Orchards were surveyed in autumn because galls formed by the last generation of the midge are usually more numerous than those from earlier generations, making detection of the pest in an orchard easier. The object of the severity survey was to determine where in the Annapolis Valley the Apple Leaf Midge was most prevalent. Orchards from the eastern (Windsor area) to the western end (Annapolis area) of the Valley were surveyed, as well as orchards on the valley floor, and on the slopes of the North and South Mountain. Severity of midge infestation in each orchard was rated according to the following scale: 0 - no midge galls found, 1 - at least one gall found, 2 - a few galls throughout the orchard, 3 - a few galls on many trees, 4 - several galls on all trees, or many galls on a few trees, and 5 - galls on 50% or more of the new growth.

Locations of orchards surveyed for Apple Leaf Midge presence or infestation severity were plotted on 1:50 000 topographic maps. For each orchard, the universal transverse mercator grid (UTM) coordinate

corresponding approximately to the centre of the orchard was recorded. These coordinates were used to generate maps of midge distribution and severity ratings in Nova Scotia.

The distribution map (Figure 1) was constructed using a process known as buffering, in which a boundary of a fixed size is drawn around a geographic point, forming a series of large dots (Roberts et al. 1993). In mapping the distribution of the leaf midge, a buffer of 1000 m was drawn around the point coordinate used to designate each orchard. Where infested orchards occur in close proximity, the dots for each orchard blend together, forming belts where leaf midge were found. In those cases where the midge was found in the same orchard in multiple years, only the year in which it was first detected is mapped. In Nova Scotia, little success has been achieved in eradicating the Apple Leaf Midge from infested orchards. Therefore, it is reasonable to assume that when an orchard becomes infested by this pest, it generally remains infested.

The map of severity ratings (Figure 2) was constructed by assigning a symbol reflecting the severity of the infestation (the larger the symbol, the worse the infestation) to the point representing each orchard. A different symbol was used to designate orchards where no midge population was found.

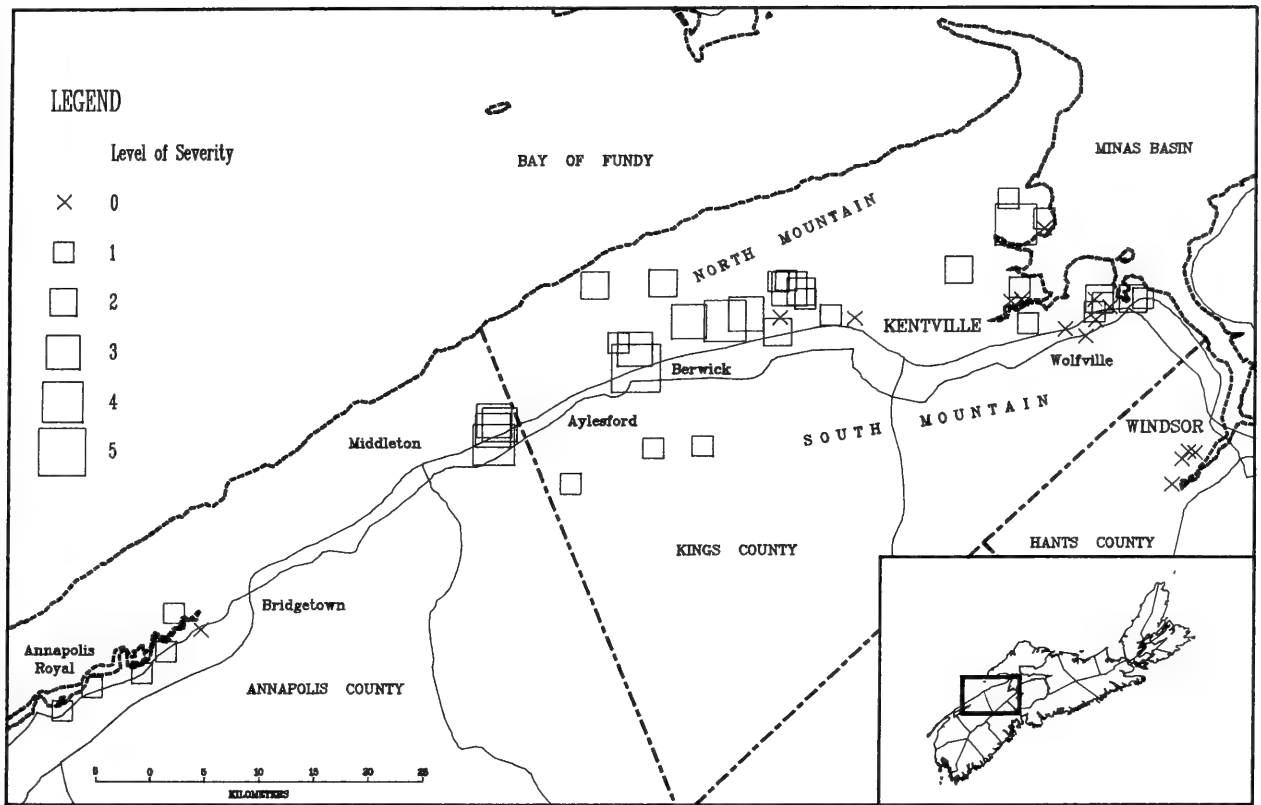


FIGURE 2. Severity of midge infestations in individual orchards in the Annapolis Valley of Nova Scotia in 1993. The size of the symbol for each orchard reflects the severity of the infestation, not the size of the orchard. Severity levels were rated according to a six number scale, with 0 being the lowest severity, and 5 the highest. Inset shows the location of study area within the province.

Each symbol is centred about the point denoting the orchard's coordinate; the size of the symbol does not reflect the geographic extent of the infestation in that area, but merely reflects the severity rating assigned to that orchard.

Results and Discussion

Apple orchards in the Annapolis Valley are concentrated in Kings County, which contains approximately 90% of the Valley's production by area (Embree et al. 1984). The Apple Leaf Midge, initially discovered near Aylesford in 1990, spread quickly throughout Kings County, infesting an increasingly large number of orchards (Figure 3). The midge reached orchards near Kentville (to the east) and Kingston (just over the Kings/Annapolis County border to the west) by 1992 (Figure 1). By 1993, the midge was detected at the far western end of the Valley, around Annapolis Royal, while it first appeared at the far eastern end, near Windsor, in 1994. Both these regions are somewhat isolated from the main apple producing areas.

Results from the 1993 severity survey in general reflect the history of leaf midge distribution in Nova Scotia (Figure 2). The most severe infestations were concentrated around the Aylesford area, with less

acute cases at the ends of the Valley, which the midge had invaded more recently. Even isolated orchards on the slopes of the North and South Mountain had moderate infestations.

Severity ratings of leaf midge infestations should be interpreted with some caution, as the severity depends on several factors, including apple tree variety (Whitcomb 1942), and the amount of new tissue growth available (Todd 1959). *D. mali* adults only oviposit on new growth; when little new growth is available, fewer leaves are infested. Those which are attacked, however, have large numbers of eggs (Whitcomb 1941). The amount of new growth is influenced, in turn, by climatic conditions, time of the season, rootstock, tree variety, and orchard management practices such as pruning and fertilization regimes. We surveyed midge infestations during the fall, when no tree growth was occurring, but the impact of the midge during the past season was evident. We did not estimate the amount of new growth which had been produced by trees in individual orchards.

Both the presence / absence data and the severity survey suggest that the Aylesford area served as the initial invasion point of the Apple Leaf Midge into the Annapolis Valley. Once in the Valley, this pest

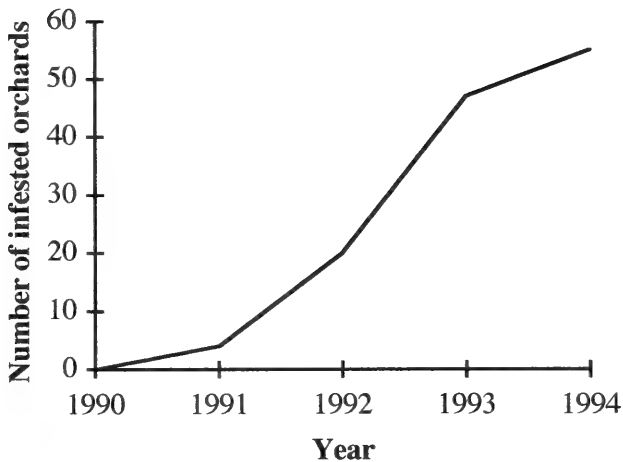


FIGURE 3. Number of orchards sampled by Agriculture Pest Monitoring company which were infested by Apple Leaf Midge. Approximately 150 orchards were sampled annually.

spread quickly throughout the apple-growing region. This rapid dispersal through a newly invaded area parallels experiences in the USA and New Zealand (Whitcomb 1934; Morrison 1953). Infested plant material has been the suggested route of invasion in both the northeastern United States, where material from France was implicated (Felt 1932), and New Zealand, where the appearance of the midge was linked to importation of material from Holland (Morrison 1953). No specific case of human introduction has been suggested for the appearance of the leaf midge in New Brunswick. There has been some suggestion that the infestation in British Columbia may have originated from root stock imported from Holland, though this has not been confirmed (H. Philip, personal communication). Movement of the midge into Nova Scotia (possibly from New Brunswick) may have resulted from wind dispersal or the movement of material or equipment (such as apple bins) into Nova Scotia. The midge would have had to travel approximately 135 km (straight-line distance) over the open water of the Bay of Fundy from infested areas in New Brunswick to reach the site of first detection in Nova Scotia. Moreover, because Nova Scotia is an isthmus, and virtually no apples are grown within 90 km or more of the Nova Scotia - New Brunswick border, it seems unlikely that the dispersal of the midge to Nova Scotia is a natural event. The most probable scenario is that the midge was introduced to the province via equipment that was moved from New Brunswick to Nova Scotia, or infested plant material from other areas where the midge is found.

In the USA, Whitcomb (1937) found that the Apple Leaf Midge had spread from its original infestation area in northeastern Massachusetts and south-eastern New Hampshire in 1933, to southern Maine

(a distance of approximately 36 km) and Rochester, New York (a distance of approximately 540 km) by 1936. Whitcomb (1937) suggested that the spread of the midge into Maine may have resulted from wind dispersal of the adults; he did not make a similar suggestion for the appearance of the midge in New York. In British Columbia, the midge spread from the original 1993 infestation site near Clearbrook, to orchards in the Yarrow area by 1995, a distance of about 25 km (H. Philip, personal communication).

The leaf midge, while not usually damaging to mature trees, does pose a threat to nursery stock and young plantings. Research in midge control in Canada has centred on finding pesticides which would offer good control, and the use of biocontrol agents. Between 1981 and 1985, 730 adults of *Inostemma contariniae* Széleányi (Hymenoptera: Platygasteridae) and 7472 adults of *Platygaster marchali* Kieffer (Hymenoptera: Platygasteridae) (from Austria and Italy) were released in New Brunswick (Agriculture and Agri-Food Canada 1995). Adult females of most species in this family of wasps deposit their eggs within the midge embryo encased in its own egg; when the parasitoid eggs hatch, the wasp larvae feed on the larva of the midge, eventually killing it. The present status of these species in New Brunswick is unknown.

In 1993, several hundred adults of *Platygaster demades* (Walker) (Hymenoptera: Platygasteridae) from Holland were released in an orchard near Berwick, Nova Scotia to combat the leaf midge (Hardman 1993). The parasite survived the Canadian winter, and *P. demades* larvae were found infesting leaf midge larvae in the fall of 1994 and 1995 (Hardman, personal communication). The spread of the parasite is expected to be slow, but hopefully it will offer some degree of natural control over the leaf midge in the future.

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Songbird Nest Placement in Vermont Christmas Tree Plantations

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We studied arboreal nest site selection in three Vermont Christmas tree plantations as a way to simplify analysis of variables that affect nest placement. Nests of House Finch (*Carpodacus mexicanus*) and Chipping Sparrow (*Spizella passerina*) were most common (16 and 8 nests, respectively, of a total of forty), followed by American Robin (*Turdus migratorius*) (6 nests). Accounting for differences in availability of spruce and fir trees for nesting, five of the six bird species that nested in the plantations preferred White Spruce over Balsam-Fraser Fir. Overhead shading of nests in spruce, our measure of nest concealment, was significantly higher than in fir; shading from the side was similar. Almost all bird species exhibited tree-height and nest-height preferences but height of nest placement tended to increase significantly with tree height. Concealment of nests from overhead predators, or protection from inclement weather, appeared to be the primary factors in nest-site selection for most species that nested in these plantations.

Key Words: House Finch, *Carpodacus mexicanus*, Chipping Sparrow, *Spizella passerina*, American Robin, *Turdus migratorius*, nest site selection, nesting substrate, edge-species, interior-species, Vermont.

Determining which cues are used by birds to select nest sites is difficult because many factors influence suitability of a potential site. Variables which may influence nest placement (reviewed in Martin and Roper 1988; Holway 1991; Martin 1993; Filliater et al. 1994) include availability of food, competition, substrate, natal imprinting, bird age and experience, vegetation structure, cover and concealment, surrounding land use, nest microclimate, relationship to edge, and vulnerability to nest predation. These potentially interacting variables impart a uniqueness to each nest location that greatly complicates efforts to determine specific characteristics of desired nest locations, or how these characteristics vary among bird species. We designed a study that greatly reduced the number of covariates in nest-site selection (e.g., structural and compositional complexity of the forest) by studying nest placement in Christmas tree plantations. The plantations that we selected for study enabled us to compare nesting preferences directly by substrate height, substrate location (edge vs interior), and substrate type (spruce or fir). We also evaluated the extent to which nest placement was related to shading of nests by foliage.

Methods

Study Sites

Three Christmas tree plantations in central Vermont were selected for our study of nest-site selection. One plantation each was located in three of the region's main physiographic provinces (Champlain Lowlands, Green Mountains, and Vermont Piedmont; Johnson 1980). The climate

varies somewhat by elevation and physiographic province but the region is generally characterized as humid continental, with warm summers and long, cold winters. Weather early in the nesting season (April and May) is often cold and unpredictable, and diurnal temperatures may vary by 20° C.

Plantations ranged in area from 29 to 59 ha, with totals of 877 to 1764 planted trees. All three plantations were established in old fields, and the meadow buffer which immediately surrounded each plantation (6 to 18 m wide) was mowed two to three times each year. Two plantations were surrounded by mature hardwood forest (> 50 years since the last major harvest), composed largely of Sugar Maple (*Acer saccharum*), White Ash (*Fraxinus americana*), and other northern hardwoods (Braun 1950). The third plantation was surrounded by hayfields, cornfields, and apple orchards.

All three plantations were planted in blocks of White Spruce (*Picea glauca*) and Balsam/Fraser Fir (*Abies balsamea/fraseri*; Robinson and Thor 1969), in spacings of 1.8 m between trees. Vegetation between trees was mowed two or three times each summer, reaching a maximum height of 15–25 cm. Trees were trimmed annually in July or August to maintain desired shape and foliage density. Heights of trees ranged from 1.0 m to 3.0 m (Table 1).

Nest Placement

All trees in each plantation were carefully surveyed in early April 1994 for arboreal open cup nests built during the 1993 breeding season. This enabled us to make a number of measurements with-

TABLE 1. Summary of potential nest substrates by species, height, and location relative to edge in three Vermont Christmas tree plantations, 1994.

	fir		spruce		fir & spruce combined	
	#	%	#	%	#	%
Location of trees						
Interior	1710	68.1	757	63.7	2467	66.6
Edge	803	31.9	432	36.3	1235	33.4
Total	2513	-	1189	-	3702	-
Height of trees (m)						
(HC ₁) 1.0-1.5	837	33.3	368	30.9	1205	32.5
(HC ₂) 2.5-2.0	1124	44.7	252	21.2	1376	37.2
(HC ₃) 2.0-2.5	538	21.4	550	46.1	1088	29.4
(HC ₄) 2.5-3.0	14	0.6	21	1.8	35	0.9

out compromising nest success (Gotmark 1992). We are extremely confident that all nests constructed during the 1993 breeding season were located and included in our survey. Nests built before 1993 were very easily recognized and were not included in any analysis.

Located nests were identified to bird species (Nickell 1965; Harrison 1975; Harrison 1978) and nests with problematic identifications were returned to the lab for more careful inspection and identification. We were unable to identify finch nests to species so we revisited the plantations in May 1995 and 1996 on non-windy, non-rainy mornings to determine which finch species were nesting in the plantations. We found only House Finches (*Carpodacus mexicanus*) during those surveys and therefore assumed that all located finch nests were built by House Finches. During these visits we also noted which bird species flushed from which trees.

Several characteristics related to nest location were recorded for each nest. Each nest tree was identified to species and tree height class (Table 1), and nest height and position on the tree (relative to trunk and lateral branches) were also recorded. Trees growing in perimeter rows of each plantation were classified as "edge trees" as were trees growing along the edge of clearings within the plantation (i.e., surrounded by fewer than six adjacent trees). All other plantation trees were classified as "interior trees." Both tree species, and all four height classes, were represented equally at the edge.

Nest Shading

To evaluate the extent to which shading by foliage might contribute to nest site selection, we measured shading at each nest (April 1994) using a Sunfleck Ceptometer. This instrument is a hand-held wand with multiple light sensors that measures irradiance in wavelengths corresponding to photosynthetically active radiation. We limited measurements with the Ceptometer to the last 10 cm of the wand, the approx-

imate diameter of most nests that we encountered. Overhead light was quantified at each nest location by placing the wand 3cm above the nest cup with the light sensors oriented skyward. Side-lighting was quantified in similar fashion after rotating the wand 90° and 270°. Corresponding measurements were taken in full light so that percent of relative light transmission could be calculated (e.g., overhead nest lighting/overhead open lighting × 100). The light transmission values were then converted to percent shading for ease of discussion (100% - light transmission % = % of light shaded by foliage).

Statistical Analyses

Differences in nest placement (by species of bird, species of tree, height of tree, height of nest, shading, location of nest relative to forest edge) were evaluated using two-way analysis of variance with interactions (Sokal and Rohlf 1981) and hierarchical log-linear chi-square analysis (Bishop et al. 1975; Haberman 1978; Norusis 1993), a statistically more conservative approach than repeated chi-square analyses. Comparisons of bird species were limited to the three species with the most nests: House Finch, American Robin (*Turdus migratorius*), and Chipping Sparrow (*Spizella passerina*).

Results

Despite a careful and thorough search, only 40 nests, representing at least six bird species, were located in the 3702 trees sampled (1.08% of all trees sampled had a nest). No fallen nests were found on the ground and no tree had more than one nest. All nests of all species were built against tree trunks rather than on mid-sections of branches. Thirty-four nests were identified to species, two were identified only as sparrow nests, and four were not identified.

Overall, nests of House Finch and Chipping Sparrow were most common (16 and 8 nests, respectively), followed by American Robin and Song Sparrow (*Melospiza melodia*) (6 and 2, respectively).

Gray Catbird (*Dumetella carolinensis*) and White-throated Sparrow (*Zonotrichia albicollis*) had one nest each. The plantations differed significantly ($p < 0.05$) in density of nests of different bird species. Nests of Robin were disproportionately common in the plantation surrounded by agriculture (0.23% of the trees had a Robin nest compared to 0.10% of the trees in the plantations surrounded by forest). Nests of House Finch, in contrast, were more common in plantations surrounded by forest (0.67% of the trees had a House Finch nest, compared with 0.23% in the plantation surrounded by agriculture). These apparent trends, as well as those below, were also evident when we revisited the plantations during the 1995 and 1996 breeding seasons and noted which birds flushed from which trees in which plantations.

Notwithstanding the small number of nests found in plantation trees, a number of highly significant trends were revealed. A significant ($p < 0.001$) and disproportionately greater number of nests were found in spruce than in fir (2.11% of spruce trees had a nest but only 0.54% of the firs) and this resulted in different bird assemblages in spruce and fir trees ($p < 0.05$). Excepting White-throated Sparrow (only one nest sampled), all bird species placed more nests in spruce than in fir ($p < 0.001$; Figure 1). House Finch exhibited the strongest preference for nesting substrate (nine-fold more nests in spruce on a per tree basis than in fir) followed by Robin (four fold more nests in spruce than in fir). Chipping Sparrow was the least specific in preference for nesting substrate.

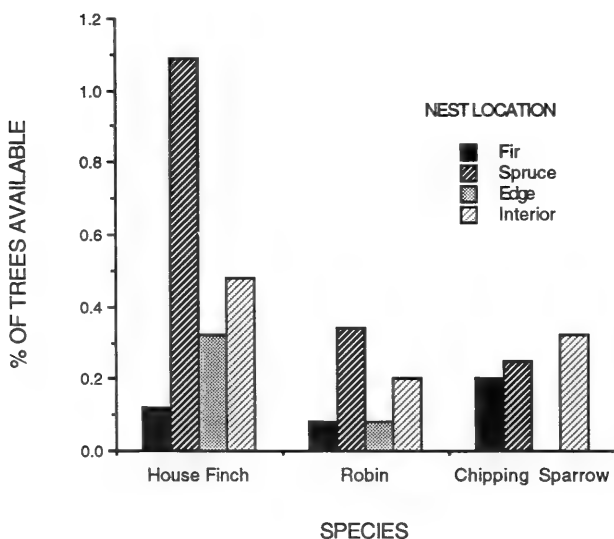


FIGURE 1. Nest-site selection by songbirds in Christmas tree plantations of spruce and fir trees in central Vermont, 1994. “Edge” nest locations were along the plantation perimeter; “Interior” nest trees were surrounded by other plantation trees. Column values = number of trees with nests for a nest location type/total number of trees sampled for the same nest location type $\times 100$.

Bird assemblages in interior and edge trees differed significantly ($p < 0.05$), with interior trees disproportionately selected ($p < 0.05$) by all birds for which nests could be identified (1.32 % of all interior trees had a nest, 0.63 % of all edge trees had a nest). In relative terms, House Finch exhibited the weakest preference for interior trees (1.3 \times more nests in interior trees than in edge trees).

The preferred tree height for nesting varied somewhat by species of bird and also by substrate ($p < 0.05$), but trees 2.0 – 2.5 m in height (HC3) had significantly more nests than expected and trees 1.0 – 1.5 m in height had fewer than expected ($p < 0.001$; Figure 2a, 2b). Trees in HC3 were pre-

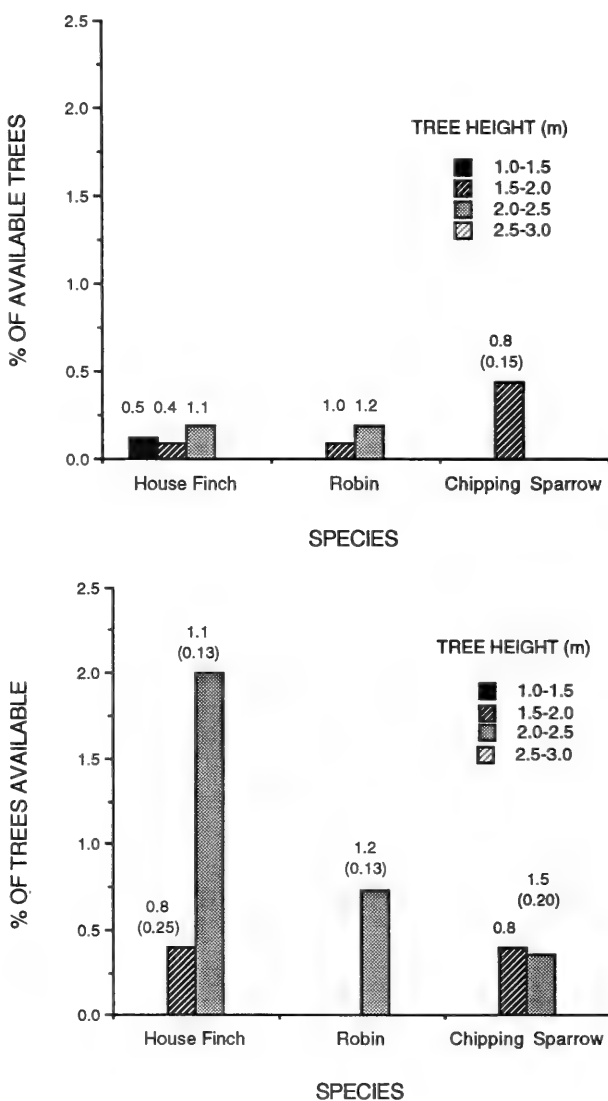


FIGURE 2. Nest-site selection by tree height in Christmas tree plantings of fir (a) and spruce (b) in central Vermont, 1994. Column values = number of nest trees in a height class/total number of trees sampled for the same height class $\times 100$. Values over columns indicate average above-ground height of nests (+/- standard errors of the mean). Values lacking standard errors had but a single observation.

ferred, sometimes exclusively, by four of the five identified species which nested in spruces (Figure 2b) and by two of the five species (House Finch and Robin) which nested in firs (Figure 2a). Chipping Sparrows exclusively used 1.5 – 2.0 m tall firs (HC₂) and HC₂ and HC₃ spruce trees (Figure 2a, 2b). Of the four bird species that nested in both fir and spruce, three species (House Finch, Robin, Chipping Sparrow) exhibited the same height class preference in both tree species.

Nest height differed by bird species ($p < 0.05$), and taller trees had significantly higher nests ($p < 0.01$). Height of nests was independent of substrate, however. For example, House Finches that nested in HC₃ trees placed their nests 1.1 m above-ground, regardless of tree species (Figure 2a, 2b). Similarly, Chipping Sparrows that nested in HC₂ trees placed their nests 0.8 m above-ground, irrespective of tree species. Robins built the highest nests (average height = 1.2 m).

There was more overhead shading than side shading of nests, and bird species differed somewhat in the extent to which their nests were shaded (Figure 3). The average overhead shading of nests ranged from 92.1% (Chipping Sparrow) to 95.2% (House Finch) (Figure 3); average shading from the side ranged from 82.8% (Robin) to 93.1% (House Finch). The highest and lowest overhead shading for a single nest was 98.4% (House Finch) and 86.8% (Chipping Sparrow). The highest and lowest side-shading for a

single nest was 98.3% (House Finch) and 68.8% (Robin). Overhead shading was significantly higher in spruces than in firs ($p < 0.005$), but side-shading in the two tree nesting substrates was not significantly different. Nests of House Finch were most shaded overall, but differences among birds were not significant ($p > 0.05$).

Discussion

Location and predation of nests may explain > 50% of the variation in clutch size and annual fecundity of common North American Passeriformes, including the species which nested on our sites (Martin 1995). Almost certainly nest location, nest concealment, and nest predation are interrelated for some species (Martin and Roper 1988). Shading of nests, our evaluation of nest concealment, varied somewhat by species of nesting bird (Figure 3), a pattern that has been noted elsewhere using other measures of concealment (Holway 1991). Directionality of nest concealment (overhead vs. from the side) also varied by species of bird and we suspect that this reflects differential responses to predator avoidance.

That all located nests in our plantations were built next to tree trunks rather than on open branches may suggest that support of nests or protection from wind were important factors in nest placement (Collias and Collias 1984). This seems especially plausible since many plantation trees had thin branches with little forking for nest support. We believe that concealment from predators was a more important factor, however. First, nests varied greatly in mass, size, shape, and construction (Harrison 1975; Harrison 1978), and equal structural support of nests of the different species was clearly not needed. Second, high winds rarely reached interior trees where most nests were placed because of the sheltering effect of surrounding trees. Third, almost 30% of all trees surveyed for nests (height classes HC₃ and HC₄) had a number of stout, forked branches that could have supported nests much larger than any of those we found in our study, yet not one nest of any type was placed on any of these thousands of potential mid-branch sites.

Density of nests in our plantations was three-fold higher than that in a Minnesota Christmas tree plantation having Scotch pines (*Pinus sylvestris*) of similar height and density (Buech 1982). Nesting birds on our sites selected certain tree heights and nest heights preferentially but placement was not related to availability of sites. Height of nesting substrate has been shown to affect nesting success (Yahner 1983), perhaps through its influence on height of nest placement (Kern et al. 1993). In our study, nest height generally increased with tree height (see also Chapman 1932; Preston and Norris 1947), and most nests were placed in taller trees. We suspect that this was related

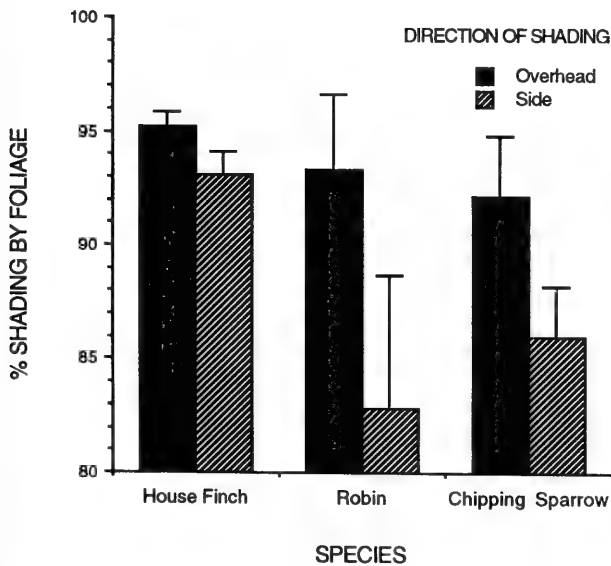


Figure 3. Relationship between foliage shading and nest site selection in Christmas tree plantations of spruce and fir trees in central Vermont, 1994. Column values represent average shading of the nest [1 - (transmission to nest/transmission in open) × 100] with standard errors of the mean. "Overhead" refers to foliage shading directly above the nest, "Side" refers to lateral shading.

to avoidance of ground predators. Nest predation is the primary source of egg and nestling mortality for most birds (Martin 1992a, 1992b) and predation can alter the height at which subsequent nests are placed (Marzluff 1988). Our nest shading data revealed that higher nest placement in taller trees did not compromise overhead nest concealment, and may have improved nest concealment from below.

The degree of preference for substrate and nest height varied among bird species (Figure 2). Nest heights of Chipping Sparrows in HC₂ firs, for example, ranged from 0.3 to 1.1 m above-ground. These variable placements, which tended to be somewhat lower than nest heights for this species reported elsewhere (Chapman 1932; Walkinshaw 1944; Messersmith 1963), may be explained by some combination of differential natal nest imprinting (Marzluff 1988), experience (Marzluff 1988), time of nest building (Walkinshaw 1944), or different availabilities of tree heights. Nest placement of older Chipping Sparrows also may be influenced by loss of previous nests to predation (Reynolds and Knapton 1988), which may be related to incomplete concealment of nests (Buech 1982).

Robins on our sites placed their nests lower, and in shorter substrates, than has generally been reported elsewhere (Howell 1942; Preston 1946; Yahner 1983), where availabilities of nesting substrates were more varied. This also was the case with House Finches (Evenden 1957). Robins and House Finches did exhibit a preference for taller trees in the plantations (Figure 2), but nests were placed in shorter trees as well. This lack of specificity in nest placement, which has been shown elsewhere to increase rates of nest predation (Best and Stauffer 1980), may be beneficial in habitats such as plantations that have very low structural and compositional diversity. Consistent and predictable nest placement in homogeneous habitats would likely promote increased nest predation because predators can more easily develop a search image that reduces search effort and increases search efficiency.

Many bird species have been shown to exhibit preferences for nesting substrate (Martin 1993) and this was the case in our study. Spruce was strongly preferred over fir as a nesting substrate and this preference probably was more related to nest concealment or protection from inclement weather than to availability of food. Food was equally available to birds nesting in spruce and fir (both tree species were similarly dispersed in the plantations), but shading of nests in the two tree species was very different. Nests in spruces had almost twice as much overhead shading as those in firs but about equal shading from the side. Placement of nests in spruce rather than in fir confers advantages of better protection from rainfall and snow, and better concealment from overhead predators such as hawks.

Almost all of the nests on our sites were placed within the interior of plantations rather than along the edge, suggesting that birds differentiate between these habitat locations. Spring weather in Vermont during nesting is often cold, and this would be expected to favor nesting on south-facing edges of trees and plantations where sunlight is more direct. Such nest placement did not occur on our sites, however. Disproportionate placement of nests in interior trees may have been a response to nest parasitism by Brown-headed Cowbirds (*Molothrus ater*) (Buech 1982), but cowbirds were sighted (during our May surveys) only along the edge of the plantation surrounded by agriculture.

Our study of nest placement in Vermont Christmas tree plantations indicates that several factors strongly influence nest placement by House Finches, Chipping Sparrows, and American Robins. Whereas Chipping Sparrows placed similar numbers of nests in spruce and fir, House Finches and American Robins were significantly more inclined to nest in spruce than in fir. Shading of nests was much higher in spruce than in fir, suggesting that nest concealment may be especially important for House Finches and American Robins. Preferred tree height for nesting varied by species, with House Finch and American Robin selecting taller (2.0 – 2.5 m) trees to place their nests. Chipping Sparrows, in contrast, favored shorter trees (1.5 – 2.0 m). All nests of all species were built against tree trunks rather than on mid-sections of branches, and nests were disproportionately placed in interior rather than edge trees. We strongly suspect that preferences for tree species, and location of nests within the tree and within the plantation, were related to concealment of nests from nest predators, and protection from inclement weather.

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Reproductive Success of the Common Loon, *Gavia immer*, on a Small Oligotrophic Lake in Eastern Canada

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Wolfe Lake, Fundy National Park, is marginal Common Loon (*Gavia immer*) habitat owing to its small size (22 ha) and its low primary productivity. A pair of Common Loons has nested on Wolfe Lake every year since 1989. The production from this pair has been 1.4 fledged young per year. The growth of the chicks is near linear for the first six weeks.

Key Words: Common Loon, *Gavia immer*, reproduction, Wolfe Lake, Bay of Fundy, New Brunswick.

Fundy National Park, New Brunswick was established in 1948 to protect 207 km² of the Maritime Acadian Forest. Despite this protection, Common Loons (*Gavia immer*) did not utilize the freshwater lakes of the park for breeding until 1989 when the first confirmed nesting took place on Wolfe Lake. This small (22 ha) oligotrophic lake is located 14.5 km (65° 08' W, 45° 39' N) from the Bay of Fundy at an elevation of 305 m.

There has been no active management of the aquatic resources of the lake since stocking of Brook Trout (*Salvelinus fontinalis*) ceased in 1980. A gradual reduction in recreational use of the lake followed. By 1989 the decline in camping activity was nearly 60% (Clay and Clay 1994*).

After the loons became resident, a monitoring program was implemented to develop our understanding of their behavior and general ecology. The objective was to identify factors that influenced the reproductive success of the newly resident loons and to compare their reproductive success with that from other North American studies.

Study Area and Methods

Three lakes in Fundy National Park meet the minimum size requirements of Common Loons, about 10 ha (or 20 ac) (Barr 1973; Masse 1991*) but only Wolfe Lake was used by a pair of Common Loons as a nesting area. Loons were reported occasionally on Bennett Lake and Tracey Lake, but none became resident. Wolfe Lake, created by an earth dam on the upper reach of the East Branch of the Point Wolfe River, is at the lower size limit of preferred nesting areas but it does have two small islands with a combined area of <0.1 ha. The lake has little surface inflow, is shallow with wide shoals and an average depth of 3.8 m and maximum depth of 8.5 m (Kerekes et al. 1975*).

Water quality data were collected during 1993 and 1994 to ascertain the productivity of the lake.

Analyses were conducted by the Environment Canada Water Quality Laboratory, Moncton, New Brunswick.

Bird sighting data prior to the study period (1989–1996) were gleaned from the Fundy National Park Bird Sighting Cards (BSC) which were maintained from 1948 to 1980 with some intermittent reports after 1980. Observations recorded during this monitoring program were opportunistic except during those periods considered significant. These key periods included the arrival and departure, nest establishment, egg laying and chick hatching. Nomenclature of the development follows that used by the Canadian Lakes Loon Survey, Long Point Observatory.

Results

Common Loons were first reported on Wolfe Lake in 1965 when three were reported on the BSC. Intermittent sightings of one to two Common Loons were made through the 1970s but the first indication of possible breeding was an unverified report of two loon chicks in 1983. There were no additional recorded sightings until 1989, after which there have been annual sightings.

Low productivity was shown by water clarity readings with a secchi disk that were greater than the maximum depth. The pH of the lake averaged 6.4, nitrogen 0.2 ppm, phosphorus 0.005 ppm, potassium 0.3 ppm and dissolved organic carbon 1.2 ppm. Calculations of fish yield from empirical models gave a range of 0.25 to 1.55 kg/ha fish production for Wolfe Lake.

The loons arrived as the ice broke up, often with 50% of the lake still covered in ice (Table 1). Within the first week several other loons arrived and remained for a couple of days. Other piscivorous birds also arrived at this time and were chased by the loons (Clay and Clay 1994*).

Courtship display as defined by Crowley and Link (1987), was observed at different times and the

*See Documents Cited section after Acknowledgments.

TABLE 1. Nesting activities of Common Loons on Wolfe Lake in Fundy National Park.

Year	1989	1990	1991	1992	1993	1993	1994	1995	1996
Date Arrival at Wolfe Lake (=50% ice out)				10 May	nest 1 29 April	nest 2 29 April	28 April	28 April	30 April
Date eggs laid			11 June 10 July	19-27 June 19 July	late May	2-3 July 01 August	15 June 13 July	5-9 June 02 July	25-30 June 22 July
Date Eggs Hatched		06 July	2 2 2	2 1 0	0 2 0 0	2 1 1	2 2 2	2 2 2	2 1 1
Clutch size	2	1? 1 1							
Number of Chicks Hatched	2								
Number of LY fledged	2								
Date Parent left Wolfe Lake *	2			27 July	n/a	05 November 13 November	05 October 05 October	05 October 12 October	19 October 13 November
Date LY left Wolfe Lake					n/a	1 egg missing reason unknown			1 egg broken (embryo inside)
Reason for failure				1 chick dead 1 egg with membrane intact, probably predators	nest flooded 2 eggs lost mid-June				

*One adult leaves in early to mid-September, about a month before the remaining adult and chick, this is the estimated date of departure of the second adult.

activity took place over about a one week period, the commencement of which varied from year to year. A late cold spring as in 1992 and 1996 delayed the courtship and nesting by about two weeks. Eggs were usually laid before the middle of June except for 1992 and 1996 when eggs were laid in the last week of June.

Clutch survival varied over the eight years. Hatching dates for surviving chicks ranged between 2 July and 1 August with mean date of 12 July. All clutches hatching after the middle of July had some mortality (Table 1).

The last sighting date on the lake varied according to chick hatching date. In most cases one parent left the lake in early September, while the other adult remained with the young feeding it until early to mid-October (Table 1). In 1994 and 1995 the large young took practice flights at the end of September and they were last seen 4 October 1994 and 12 October 1995. In 1993, the lone chick from the second nesting hatched in August and the adult stayed with it until November. The large young was seen feeding alone for the first two weeks of November and it left the lake on 13 November 1993. In contrast, when the offspring died in 1992, the adults left Wolfe Lake at the end of July.

The loons were banded in 1995 and 1996 in cooperation with staff of the Canadian Wildlife Service. The weight of the adult male was found to be 5.250 kg and the female was 4.925 kg. One chick in 1995 was 3.550 kg at six weeks and another chick in 1996 was 2.025 kg at four weeks.

Discussion

Wolfe lake offers only marginal habitat for Common Loons, being small and unproductive (oligotrophic), with limited seasonal surface inflow. The water is low in nutrients and dissolved solids (Kerekes and Schwinghamer 1978*; Clay and Clay 1994*). Barr (1996) estimated that 423 kg of food is required to support a pair and two chicks for 5.5 months. He calculated that a chick required 53 kg of fish to fledge. Adult loons eat approximately 10% of their body weight (Barr 1996) in fish and aquatic organisms per day. The average weight of the adult loons on Wolfe Lake was 5.1 kg (5.250 kg male and 4.925 kg female), thus one adult Common Loon would require 510 g of food per day or 76.50 kg for a season May through September. Wolfe Lake Common Loons would require 12 kg/ha of fish to support two adults and two chicks.

Total fish yield¹ of Wolfe Lake was estimated to be 34.1 kg (range 32.02 to 35.25 kg) or 1.55 kg/ha, by Clay and Clay (1994*) using the Ryder et al.

¹In this model, fish yield refers to only what fish could be harvested from a water body.

TABLE 2. Common Loon chick survival estimates from various North American studies compared to those of Wolfe Lake, Fundy National Park.

Authority	Chick Survival from Eggs	Number of Fledged Young per Nesting Pair	Young Fledged
This study	65 %	1.4	92 %
Benjamin and Kerekes 1993		0.5	
Vogel 1993 (Nova Scotia)		0.7	
Vogel 1993 (New Brunswick)		0.6	
Robinson et al. 1988		1.1 ²	
Titus and van Druff 1981		0.5	
Trivelpiece 1979		0.8	
Meyer 1994		0.9	78 %

²This value was calculated from Robinson et al. (1988) by assuming 75% of the nests were successful and then estimating chick production from all nests (see text).

(1974) morphoedaphic index. In comparison, Bennett Lake, with a significant surface inflow, had a total estimated fish yield of 72.2 kg (range 71.41 to 72.88 kg) or 2.33 kg/ha. Using three other models, which incorporated total phosphorus (Hanson and Leggett 1982), total fish yields for a three year mean ranged from 0.25 to 1.15 kg/ha for Wolfe Lake.

Whatever the absolute values of fish yield chosen, the estimated range of 0.25 to 1.55 kg/ha fish production for Wolfe Lake is at the low end of the range of 19 oligotrophic lakes of Kelso and Johnson (1991) and it was only 10% of the loons' food requirements. Loons are known to feed on a wide range of aquatic organisms (Alvo 1986; Parker 1988) and more food would be available than these simplified estimates of fish production indicate. The loons must supplement their nutrient requirements with amphibian and other foods and they probably fished in nearby lakes. Single adult flights to and from the lake were noted, especially departures at dawn and returning after dusk (Clay and Clay 1994*).

Chick survival was 65% on average for the past eight years with 11 young surviving from a potential of 17 eggs. Under normal circumstances chick mortality is rare after three weeks of age (Parker 1988). Of 12 loon chicks that hatched over the last eight years, only one died in the first few days after hatching. Reproductive success which is defined as the number of fledged young per breeding pair per year was 1.4, with 92% of the young fledged (Table 2). Over a five-year period at Grafton Lake, Kejimikujik National Park, Nova Scotia the average reproductive success was 0.5 (Benjamin and Kerekes 1993*). The Canadian Lakes Loon Survey reported the average for New Brunswick and Nova Scotia as 0.64 and 0.74 respectively (Vogel 1993*).

By comparison loon reproductive success in the USA showed similar variability. In Michigan 70-80% of loon nests produced at least one chick (Robinson et al. 1988) with an average brood size of 1.5 chicks per successful nest (Table 2). Titus and van Druff (1981) considered it normal for the average Common Loon pair to produce a single offspring every other year (0.5 fledged/pair/year). Common Loons in New York have been found to fledge 0.8 young / pair/ year (Trivelpiece et al. 1979). In Wisconsin reproductive success was 0.94 young/nesting pair with 78% of chicks fledged (Meyer 1994).

The reasons for nest failure or chick loss varied. In 1990 it is believed that only one egg was laid, as a limited number of shell fragments, sufficient for one egg, were found in the nest. In 1992 no chicks survived, probably owing to parental abandonment caused by human interference both from fishers on the shore and canoe traffic. Human disturbance can vary from interference by individuals (intentional or unintentional) to heavy metal poisoning or entanglement in fishing gear (Clay and Clay 1996*) One chick was found dead near the nest, presumably abandoned and the other egg with its small end broken still had the membrane inside suggesting predation. In 1993, visitor boating and fishing activity near the larger island coincided with loon nesting activity. The loons abandoned their first choice of nest site and moved to the smaller island. Both eggs from this first nest on the small island were washed away. The loons returned to the larger island and re-nested. One of the two eggs disappeared.

Nesting loons are more severely affected by slow-moving boats, especially canoes and fishing boats that hug the shoreline, than they are by motor boats (McIntyre 1975). Although loons have been found to habituate to human disturbance they still leave their nests, albeit for shorter periods, leaving the young exposed to natural predators (Christenson 1981). Fishing activity and canoe traffic on Wolfe Lake from the opening of the fishing season on Victoria Day in May until the closure of the season 15 September affected the movement, nesting behavior and the fishing activity of the loons. During intrusion near their nest sites, incubating loons slipped off their nest, swam underwater and emerged at a distance. This left the nest open to predation, especially by ravens, similar to the observations of McIntyre (1986).

Unexpected water level fluctuations have contributed to nest failure. The water level of Wolfe Lake is relatively stable, however, in recent years increasingly large fluctuations occurred in spring and summer for several reasons. Aquifers and springs have dried up in periods of drought. This reduced inflow coupled with a "leaky" dam has caused the water level to drop as much as 45 cm. Heavy rainfall has on occasions caused a rapid fill of the lake. In 1993, the wooden

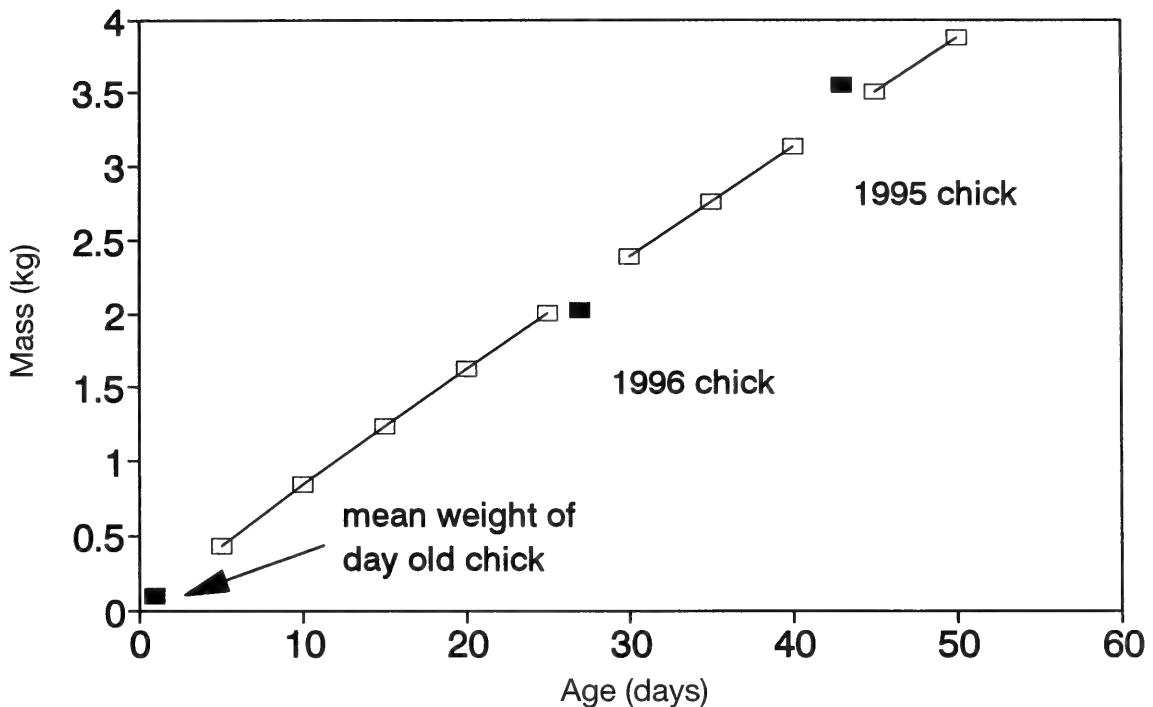


FIGURE 1 Growth of juvenile Common Loons (*Gavia immer*), Wolfe Lake, New Brunswick estimated from banding of approximately 4- and 6-week-old chicks and from the mean weight of day old chicks from Barr (1996).

gate structures of the dam developed a small breach that caused a sudden water level drop of about 20 cm during the loon nesting season. The resident beaver repaired the breach in the dam after nesting had taken place. Water levels rose quickly and, together with a strong wind, washed the eggs from the nest.

In the past it has been unknown whether the same pair of loons returned to Wolfe Lake each year. A study in Isle Royale National Park, Minnesota (Evers 1995) found that the monogamous relationships previously assumed for loons may be questionable. He observed that one-fifth of banded Common Loons switched partners or sneaked onto other territories (Fair 1994). The loons at Wolfe Lake were captured and tagged in 1995 and recapturing in 1996 confirmed that the same pair returned to the lake.

From the known weights-at-age and assuming a starting chick weight of 90 to 100 g (Barr 1996), the growth of chicks on Wolfe Lake indicated a near linear relationship between weeks 1 and 6. Barr (1996) found loon chicks became relatively independent and attained near adult size and shape by 11 weeks. Weights of our tagged chicks showed that juvenile growth was rapid (Figure 1). This agrees with that recorded by Barr for hand-fed loons, but appeared advanced by about two weeks.

The loons of Wolfe Lake are new arrivals to the area. If the fish population remains stable there appears to be sufficient fish and other aquatic organisms in Wolfe lake and other nearby lakes to provide two adult loons and two young with their nutrient

requirements. The biggest problem is human interference, with more educational programs and better communication between the guardians of the park and the public there is hope that these loons will continue to return to Wolfe Lake.

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The Effect of Egg Coloration on Predation of Artificial Ground Nests

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Effects of egg coloration on predation of artificial ground nests in upland habitat adjacent to a cattail marsh were explored by deploying nests containing either a brown or a white chicken egg. Predation rates were similar on the two nest types after 13 days of exposure. Nest concealment (vegetation height, overhead concealment, vegetation density) did not differ between surviving and destroyed nests. Our results suggest that coloration of eggs did not affect the outcome of our predation experiment using artificial ground nests.

Key Words: artificial nest, egg coloration, nest concealment, predation.

Predation is a major cause of nesting failure in many bird species (Ricklefs 1969) and generally accounts for high nest losses in waterfowl (Johnson et al. 1989). To examine the role of predation in waterfowl nest success, many authors used artificial nests. Coloration of eggs used in studies of artificial ground nests has varied considerably. Either white (Esler and Grand 1993), brown (Jobin 1991), dyed (Sugden 1987) or painted (Picozzi 1975) domestic fowl eggs have been used, as well as pheasant eggs (Jones and Hungerford 1972).

Most birds are visual predators that hunt in daylight, whereas mammals hunt generally at night and rely mostly on scent to find their prey (Storaas 1988). Experiments with eggs of different coloration that were presented simultaneously to corvids did not demonstrate a significant advantage of cryptic coloration (Montevecchi 1976; Salonen and Penttinen 1988). However, Verbeek (1990) showed that a Northwestern Crow (*Corvus caurinus*) egg with a different coloration than the others in the clutch was subjected to more intense avian predation pressure. Examination of avian predation on Black-headed Gull (*Larus ridibundus*) nests showed that egg coloration could play a significant role in nest survival (Tinbergen et al. 1962). Nest and egg concealment should, therefore, be taken into consideration when predation studies are conducted in areas where avian predators are numerous (Clark and Nudds 1991). The objective of our study was to compare predation rates on artificial ground nests containing either a brown or a white chicken egg. We also evaluated the effect of concealment on nest predation.

Study Area

We conducted this study in upland habitats adjacent to the Des Laiches marsh, a cattail (*Typha latifolia*) marsh adjoining the Ottawa river between Gatineau and Angers, Quebec (45° 30' N, 75° 30' W).

Upland habitats consisted of scrubland dominated by willows (*Salix petiolaris*), Meadow-sweet (*Spiraea alba*), Reed-canary Grass (*Phalaris arundinacea*) and sedges (*Carex* spp.), and hayfields dominated by *Phleum pratense*, *Lotus corniculatus* and *Vicia cracca*. Several hedgerows consisting of Wild Cherry (*Prunus* spp.), hawthorn (*Crataegus* spp.), ash (*Fraxinus americana*) and elm (*Ulmus rubra*) trees were present between fields. Waterfowl nesting in the area were Blue-winged Teal (*Anas discors*), Mallard (*Anas platyrhynchos*), and Wood Duck (*Aix sponsa*), but no systematic search for nests of these species was conducted. The main predators in this area were American Crow (*Corvus brachyrhynchos*), Raccoon (*Procyon lotor*), Striped Skunk (*Mephitis mephitis*), Mink (*Mustela vison*), and Red Fox (*Vulpes vulpes*) (Jobin 1991).

Methods

Artificial ground nests were constructed by pressing dead vegetation together to form a shallow cup (external diameter: 30 cm, internal diameter: 12 cm, depth: 8 cm). One large, fresh chicken egg, either brown or white, was placed in each nest. We established eight nests, 20 m apart, along each of six transects beginning at the edge of marsh vegetation and running perpendicular to the marsh in upland habitats. Transects were > 50 m apart and nests were either located in scrubland or in hedgerows. Nests with a brown egg and nests with a white egg were alternated along each transect and the color of the egg in the first nest of each transect was also alternated between adjacent transects. Special care was taken not to disturb vegetation around the nests. We established 48 nests, 24 containing a brown egg and 24 containing a white egg. Actual manipulation of the nests occurred only when setting them up. No nest markers were used; natural landmarks allowed us to find nests in subsequent visits.

Four nest-concealment variables were measured when the nests were established, always by the same observer. Height of live and dead vegetation above each nest was measured to the nearest 5 cm. Vegetation density around nests (within 5 m) was categorized as light, medium or heavy (see Bowman and Harris 1980), relative index 1, 2 or 3, respectively. Overhead concealment was defined as percentage of the nest visible from 1 m above the nest (see Dwernychuk and Boag 1972). This variable was rated on a scale of 0 to 4: 0 = completely visible; 1 = 1-10% of the nest concealed; 2 = 11-50% concealed; 3 = 51-90% concealed; 4 = 91-100% concealed. Nests were deployed 7 June 1990, inspected the following day and then visited four times at three-day intervals. We inferred that predation had occurred when an egg was found destroyed or moved away but still near its nest. Nest-concealment variables were compared between nests with brown eggs versus nests with white eggs using Chi-square test and the non-parametric Mann-Whitney test. Because of small sample sizes, Fisher's exact test was used to compare predation patterns between the two types of nest. Logistic regression was also performed to identify factors predicting nest success. Variables measured at each nest and included in the analyses were egg color, height of live and dead vegetation, vegetation density, overhead concealment, and distance from marsh edge. Statistical analyses were performed on JMP 3.0 and Fish 1.001 (categorical statistics) statistical softwares for Macintosh computers. Statistical significance was set at 0.05.

Results

Height of live and dead vegetation, vegetation density and overhead concealment at the onset of the experiment did not differ between nests with brown eggs and nests with white eggs (live vegetation: $U = 329.0$, $P = 0.3973$; dead vegetation: $U = 309.0$, $P = 0.5564$; overhead concealment: $\chi^2 = 3.78$, $df = 3$, $P = 0.2865$; vegetation density: $\chi^2 = 0.93$, $df = 2$, $P = 0.6286$). Predation rates were similar between nests with brown eggs and nests with white eggs

throughout the study (Table 1). Two nests with brown eggs and one nest with a white egg were depredated during the first 24 hours of exposure. Predation rates were generally high during the next three days of exposure when 58% of all eggs were depredated. By the end of the experiment (day 13), the two nest types had suffered similar losses (87.5%).

Logistic regression analysis revealed that neither egg color, nor any concealment variable were good predictor of nest success ($P > 0.60$ for all variables; nests with brown eggs and nests with white eggs combined; data from successful and destroyed nests after four days of exposure). The only variable that entered the model was distance of the nest from the marsh edge ($P = 0.02$). Nests located farther from the marsh were destroyed more rapidly than those deployed near the marsh. Note that this relative security would, however, be temporary because most nests were nevertheless destroyed after 13 days of exposure.

Discussion

We expected that nests containing white eggs would suffer higher predation rates than nests with brown eggs because white eggs are more visible from a distance. However, our results demonstrated that this was not the case. Salonen and Penttinen (1988) exposed artificial nests containing white and dyed brown hen eggs to predators, mainly birds (corvids), of Great Crested Grebe (*Podiceps cristatus*) nests and found no difference in predation rates on the two types of nest. Janzen (1978) found no evidence for differential predation rates between ground nests containing white, brown, and dyed blue chicken eggs in a deciduous forest in Costa Rica. He concluded that camouflage based on egg color would be irrelevant if predation occurred mainly at night. Although egg coloration should theoretically play a significant role in reducing chances of nest predation, those two studies and our results failed to demonstrate differential predation rates between nests containing conspicuous versus cryptic eggs.

TABLE 1. Number of depredated nests, initially containing one brown or one white chicken egg, at three day intervals near Des Laîches marsh, Quebec, June 1990.

Days of exposure	Number of depredated nests			
	Brown (n = 24)		White (n = 24)	
	n	%	n	%
1	2	8.3	1	4.2
4	16	66.7	15	62.5
7	18	75.0	17	70.8
10	20	83.3	20	83.3
13	21	87.5	21	87.5

Note: Results from Fisher's exact test reveal no significant difference ($P = 1.00$) between predation rates on nests with brown eggs and nests with white eggs for all five comparisons.

If mammals dominated the predator community in our study area, one would not expect nests containing brown and white eggs to be destroyed at different rates. During our study, several nests were destroyed by mammals, mainly Raccoon and Striped Skunk (B. Jobin, unpublished data). Crows were also seen regularly in the study area and were responsible for several nest predation events. Crows would refrain from landing in areas with dense vegetation and poor visibility (Picman 1988; Sullivan and Dinsmore 1990). Sugden and Beyersbergen (1987) showed that survival of artificial nests was maximum at a vegetation height of 70 cm. In our study, mean vegetation height was greater than 100 cm, which could have reduced nest visibility to flying crows. In addition, although Sullivan and Dinsmore (1990) concluded that increases in cover height above 50 cm did not substantially reduce predation, 74% of nests under such cover height were not destroyed. Sugden (1987) showed that vegetative cover which provided less than 30% concealment was sufficient to reduce depredation from crows on his artificial nests. He concluded that "...when the outline of the eggs was broken by plant cover, crows experienced more difficulty in detecting them". This suggests that eggs clearly visible from above are more readily found and that even a minimum level of overhead concealment would reduce chances of being detected. In our experiment, both brown and white eggs disappeared rapidly during the first four days of exposure but predation rates recorded after day 7 were lower and were mostly attributed to mammalian predation (B. Jobin, unpublished data). Eggs placed in the nests destroyed in the first stages of the experiment must have presented fairly unbroken outlines, hence these eggs disappeared rapidly. The remaining eggs were, therefore, relatively protected against predators and most particularly against avian predators.

Predation experiments using artificial nests have been conducted for many years, and comparison of results between these experiments is a common practice. The possible bias brought about by the use of visually different eggs has however seldom been addressed. Our data did not demonstrate differential predation rates between nests containing brown eggs and nests with white eggs. Note that artificial nests were deployed at about 16 nests/ha which largely overestimated actual breeding bird density in the study area. Sugden and Beyersbergen (1986) showed that predation on artificial ground nests increased markedly when nest density exceeded 2 nests/ha. Density-dependant effect in nest predation experiments was also demonstrated in several other studies whereas others failed to demonstrate such effect (see Clark and Nudds 1991). It is possible that any advantage of egg coloration or nest concealment could have been overwhelmed by such high

nest density, especially in the first four days of exposure when two-thirds of all nests were destroyed. However, low predation rates recorded after day 4 suggests that any density-dependant effect, if present, was rapidly invalidated. Nevertheless, similar nest losses occurring on the two types of nests before and after day 4 suggest that, in our study area where avian and mammalian predators were present, egg coloration did not affect the outcome of our predation experiment using artificial ground nests.

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Effects of Hunting and Loss of Escape Cover on Movements and Activity of Female White-tailed Deer, *Odocoileus virginianus*

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We monitored radio-collared female White-tailed Deer (*Odocoileus virginianus*) at Sand Lake National Wildlife Refuge, South Dakota, before and during hunting seasons in 1992 and 1993 to assess the effect of hunting on deer movements and activity. Unexpected flooding throughout the refuge in 1993 also allowed us to evaluate the effects of loss of escape cover (i.e., robust emergent wetland vegetation) on deer movements and activity. Although >70% of diurnal locations occurred in escape cover in 1992, use of escape cover was <28% in 1993 as a result of unexpected flooding that rendered most escape cover unavailable to deer. In 1992, hunted deer remained in areas similar to those used before the hunting season and responded to presence and activity of hunters by moving farther into escape cover. In 1993, deer moved to adjacent private lands when availability of escape cover decreased on the refuge. Deer located on private lands increased movements during the hunting season. In 1992, deer exhibited diurnal activity patterns before and during hunting seasons; crepuscular activity patterns were observed before and during hunting seasons in 1993. Differences in activity patterns before hunting seasons in 1992 and 1993 indicated that availability of escape cover was the major factor influencing deer activity patterns.

Key Words: White-tailed Deer, *Odocoileus virginianus*, activity, escape cover, hunting, movements, South Dakota.

White-tailed Deer populations can be maintained at high (Larson et al. 1978) or low (Swenson 1982) densities when intensively managed. Availability, quality, and juxtaposition of forage and cover, as well as hunter density and human-deer encounter rate before harvest are important aspects related to the vulnerability of deer to hunting. Swenson (1982) suggested using percent cover as an index to vulnerability of deer to hunting; however, deer movements and use of cover during hunting have been highly variable (Marshall and Whittington 1968; Root et al. 1988). Studies with refuges (i.e., non-hunted areas) in proximity to hunted areas have indicated either deer responded to hunting by moving into refuges (Zagata and Haugen 1973; Kammermeyer and Marchinton 1976) or refuges received no additional use during hunting (Pilcher and Wampler 1982; Root et al. 1988). Similarly, Marshall and Whittington (1968) concluded that deer movement increased as hunting increased, while Kufeld et al. (1988) observed that deer modified habitat use without increasing movements.

White-tailed Deer are usually crepuscular (Montgomery 1963; Kammermeyer and Marchinton 1976; Eberhardt et al. 1984). However, deer may modify activity patterns in response to weather (Beier and McCullough 1990) and moonlight (Kammermeyer 1975). White-tailed Deer also may modify activity in response to hunting or loss of escape cover; however, such a response has not previously been documented.

Our objectives were to evaluate the effect of hunting and loss of escape cover on movements and activity of female White-tailed Deer. Escape cover was defined as the tall, dense and rank emergent wetland vegetation that was located within the refuge we studied. Inundation of escape cover that occurred throughout the refuge in 1993 provided an opportunity to study the effects of flooding on movements and activity of female White-tailed Deer. Our null hypothesis was that deer movements and activity would not differ before and during hunting seasons and that loss of escape cover would not influence deer movements and activity. Our study is unique in the nature and severity of flooding that occurred.

Study Area and Methods

Sand Lake National Wildlife Refuge (SLNWR) is 8693 ha in size and lies within the James River Lowland in Brown County, South Dakota. Water control structures that were constructed in the late 1930s to control water levels have created two large marsh and open water areas that comprise 45% of SLNWR. Tall, dense and rank stands of emergent wetland vegetation (i.e., cattail [*Typha* spp.] and Common Reed [*Phragmites australis*]) that we defined as escape cover were readily available to deer in fall 1992. However, escape cover on SLNWR was flooded in 1993 due to heavy summer rains. Inundated conditions that persisted into fall 1993 rendered escape cover unavailable to deer during 1993 SLNWR hunting seasons.

Vegetation communities other than escape cover on SLNWR include uplands (34%), which are largely Brome-dominated (*Bromus inermis*) grasslands intermixed with native species such as Big Bluestem (*Andropogon gerardii*), Little Bluestem (*A. scoparius*), and Indiangrass (*Sorghastrum nutans*). Harvested crops (9%) include corn (*Zea* spp.), Alfalfa (*Medicago sativa*), and small grains (e.g., Wheat [*Triticum aestivum*]). The remaining area consists of open water (11%) and shelterbelt plantings of trees (1%) such as Cottonwood (*Populus deltoides*), Green Ash (*Fraxinus pennsylvanica*), and Russian Olive (*Elaeagnus angustifolia*).

Privately-owned land adjacent to SLNWR is intensively farmed. Agricultural crops constitute 72% of land use. Crops grown on privately-owned lands are similar to those planted on SLNWR. Permanent pasture (17%) and idled areas (12%) (i.e., Conservation Reserve Program fields and wetlands) comprise the remaining land area.

Hunting seasons in 1992 and 1993 were similar in length and timing on SLNWR. Two-deer permits were issued to 135 new hunters during the two, 6-day and two, 7-day rifle seasons that were conducted consecutively (18 November - 13 December 1992; 17 November - 12 December 1993). Deer were hunted on private lands in a 213 km² area surrounding SLNWR. Rifle hunting on private lands was one, 9-day season in which 900 hunters were issued either one- or two-deer permits. The hunting season on private lands was from 28 November to 6 December 1992 and 27 November to 5 December in 1993.

We digitized ground-truthed upland vegetation communities from 1:8000 scale black-and-white aerial photographs into a PC ARC/INFO (Environmental Systems Research Institute, Incorporated, [ESRI], Redlands, California, USA) geographic information system (GIS). Maximum acceptable root mean square error (i.e., mapping error) was 0.03 (ESRI 1991). We obtained wetland vegetation communities and open water areas as a digital coverage (United States Department of the Interior, Bureau of Reclamation, Bismarck, North Dakota, USA), which was combined with upland vegetation communities in the GIS. Robust emergent wetland vegetation communities that we defined as escape cover were coded separately from open water areas and other vegetation communities that did not contain robust emergent wetland vegetation.

We captured deer in modified Clover traps (Clover 1956) and radio-collared them (Telonics, Incorporated, Mesa, Arizona, USA) during the summers of 1992 and 1993 and the winter of 1993 (Naugle et al. 1995). We received signals with a Telonics model TR-2 receiver (Telonics, Incorporated, Mesa, Arizona, USA) and estimated azimuths with a vehicle-mounted null antenna system fitted with an integrated azimuth locating device (Hallberg

et al. 1974; Balkenbush and Hallett 1988). We estimated accuracy of our telemetry system at a distance of 866 m by placing a transmitter at locations unknown to the observer. We recorded 10 independent azimuths for each of three observers. The standard deviation of the error angle was 0.7.

We monitored 12 radio-collared females 16 October to 13 December (430 locations) in 1992 and 17 radio-collared females 1 October to 12 December (817 locations) in 1993. Number of females monitored in 1992 was reduced to 8 (2 yearlings, 6 adults) because of harvest ($n = 1$) and movement to non-hunted areas ($n = 2$). We excluded from analyses one female that only used SLNWR nocturnally. In 1993, our sample was reduced to 13 adult females due to harvest ($n = 4$).

We also monitored 5 radio-collared males 16 October to 13 December (224 locations) in 1992 and 10 radio-collared males 1 October to 12 December (458 locations) in 1993. In 1992, number of males monitored was reduced to 4 (3 yearlings, 1 adult) because of harvest ($n = 1$). In 1993, our sample was reduced to 3 males (2 yearlings, 1 adult) due to harvest ($n = 7$).

We estimated deer locations by triangulation from 2 to 5 known receiver locations (e.g., road intersections) with Program XYLOG (Dodge and Steiner 1986). We did not use deer locations in analyses that required >20 minutes to collect. Mean 95% confidence ellipse was 0.001 ha for 1992 locations ($n = 406$) and 0.0004 ha for 1993 ($n = 764$). Mean distance to signal source was 1034 m in 1992 and 727 m in 1993.

We determined independence between locations by intensively monitoring three deer for 48 hours in fall 1992. We tested cumulative distances between locations for each deer in a 48-hour intensive monitoring period for autocorrelation to determine time of independence (Swihart and Slade 1985). We obtained independence and representation of locations over the 24-hour period by locating each deer every 20 hours (i.e., monitoring period). We located deer in the same order each monitoring period and lagged the start time of each monitoring period until monitoring had begun with each hour of the day.

We selected diurnal locations (0730 - 1700 hr before hunting, 0800 - 1700 h during hunting) to evaluate effects of hunting on deer. We combined diurnal locations with vegetation communities to compare deer locations before hunting to locations during hunting with Multiresponse Permutation Procedures (MRPP) (Mielke et al. 1981) contained within Program BLOSSOM (Slauson et al. 1991).

We calculated individual 95 percent home ranges before and during hunting each fall with an adaptive kernel method (Worton 1989) contained within Program CALHOME (United States Department of Agriculture, Forest Service, Pacific Southwest Research Station and California Department of Fish

TABLE 1. Average 95% home range size, average distance to nearest edge for locations in escape cover, and average distance between successive locations using diurnal locations of radio-collared female White-tailed Deer before and during hunting at Sand Lake National Wildlife Refuge, South Dakota, fall 1992-1993.

n	Home range size (ha)				\bar{x} distance between locations (m)				\bar{x} distance to edge (m)			
	Before Hunt		Hunt		Before Hunt		Hunt		Before Hunt		Hunt	
	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE	\bar{x}	SE
1992	283 ^a	34.9	639	94.1	806 ^c	39.9	1027	51.9	264 ^e	39.7	514	104.8
1993	257 ^b	55.0	756	793.9	691 ^d	66.9	1173	217.5	101 ^f	35.7	148	52.4

^aValues differ within 1992 ($t = 2.986$, 7 df, $P = 0.020$).

^bValues differ within 1993 ($t = 2.594$, 12 df, $P = 0.023$).

^cValues differed within 1992 ($t = 3.589$, 7 df, $P = 0.009$).

^dValues differed within 1993 ($t = 2.126$, 12 df, $P = 0.055$).

^eValues differed within 1992 ($t = 2.514$, 7 df, $P = 0.040$).

^fValues did not differ within 1993 ($t = 1.695$, 12 df, $P = 0.116$).

and Game, California, USA). We used average distance moved between successive locations before and during hunting, calculated using CALHOME, as an index to deer movement. We used 23 (SE = 0.63) locations before hunting and 30 (SE = 0.18) locations during hunting per deer to calculate home ranges and indexes to distances moved in 1992; we used 44 (SE = 0.32) locations before hunting and 19 (SE = 2.05) locations during hunting per deer in 1993. We estimated distance to nearest edge of cover by summing distances of locations in escape cover to the nearest edge of escape cover and dividing by number of locations in escape cover per deer. We used independent t-tests to detect differences in home range size, distance moved, and distance to the nearest edge of escape cover within years.

Radio-collars were equipped with mercury-tip switches, which allowed us to determine whether deer were active (Beier and McCullough 1988; Lariviere et al. 1994). We adjusted activity for daylight savings and changes in sunrise/sunset (Montgomery 1963). We partitioned activity data for the diel period by computing percent of time active during 3-hour intervals (e.g., 0001-0300) (Beier and McCullough 1990). We used Pearson correlations to evaluate relationships between percent of time that females and males were active within and between years. We also used Pearson correlations to evaluate relationships between percent of time that females were active before and during hunting.

Results

We detected differences ($P < 0.05$) in central tendency and dispersion of the cumulative distribution of points between groups of locations (i.e., locations of females before and during hunting) in 75% ($n = 8$) and 85% ($n = 13$) of female home ranges in 1992 and 1993, respectively. Female home ranges were larger during than before hunting in 1992 and 1993 ($P < 0.05$) (Table 1). Our index to distances that females moved also was larger during than before hunting in 1992 and 1993 ($P < 0.05$). Distance to edge of locations in escape cover increased ($P < 0.05$) during hunting 1992 (Table 1). Diurnal use of escape cover by females was 72% before and 85% during hunting in 1992. In 1993, diurnal use of escape cover by females was 11% before and 27% during hunting. In 1992, diurnal use of SLNWR by females was 94% before and during hunting. In 1993, diurnal use of SLNWR by females was 26% before and 35% during hunting. Number of diurnal female relocations outside of escape cover increased 55% in 1993. Diurnal female use of areas outside escape cover in 1992 was 15% while 80% of deer located outside escape cover were active. Low sample sizes for radio-collared males precluded evaluating locations that occurred before and during hunting.

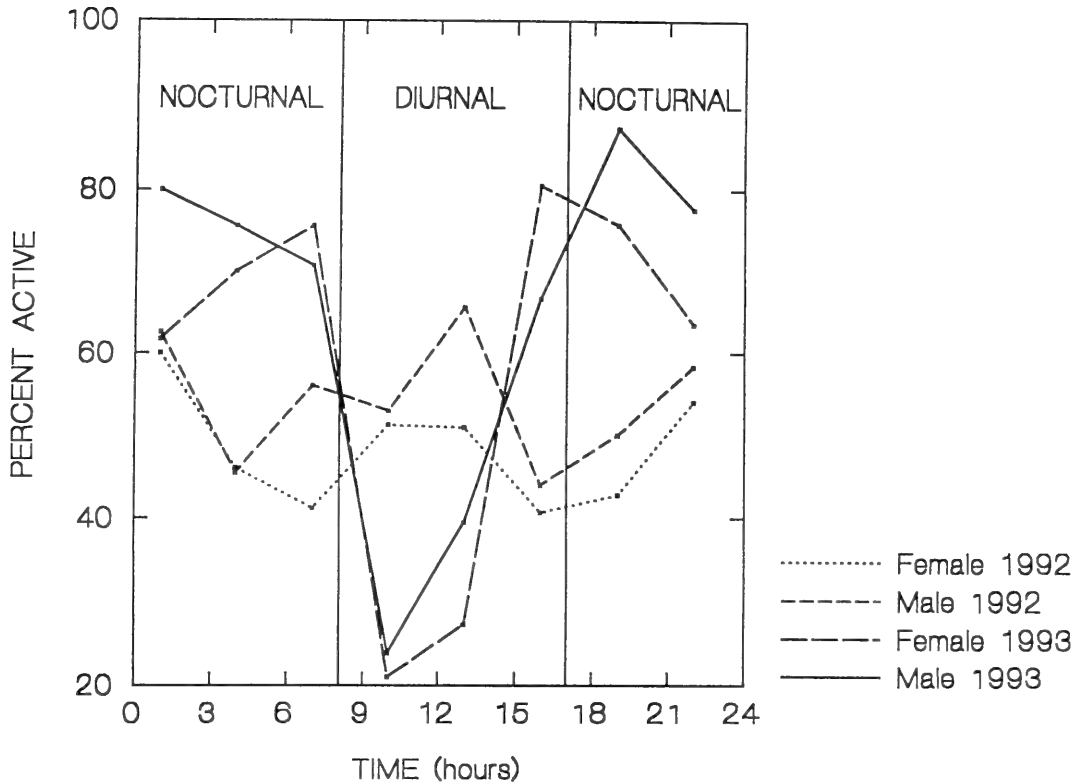


FIGURE 1. Activity (% active) of female and male White-tailed Deer during fall 1992 and 1993 at Sand Lake National Wildlife Refuge, South Dakota.

We obtained activity for 98% ($n = 421$) of female locations in 1992 and 91% ($n = 743$) in 1993. We also obtained activity for 86% ($n = 193$) of male locations in 1992 and 92% ($n = 421$) in 1993. Activity of females and males in 1992 was positively correlated ($r^2 = 0.471$, $n = 8$, $P = 0.060$) (Figure 1). Activity of females and males in 1993 also was positively correlated ($r^2 = 0.782$, $n = 8$, $P = 0.004$) (Figure 1). Activity was not correlated for females (1992 vs. 1993) ($r^2 = 0.241$, $n = 8$, $P = 0.217$) or males (1992 vs. 1993) ($r^2 = 0.045$, $n = 8$, $P = 0.614$) (Figure 1). Activity of females before and during hunting in 1993 was positively correlated ($r^2 = 0.879$, $n = 8$, $P = 0.001$) (Figure 2). Activity of females before hunting in 1992 and during hunting in 1993 was negatively correlated ($r^2 = 0.801$, $n = 8$, $P = 0.003$) (Figure 2). Activity of females before hunting in 1992 and 1993 also was negatively correlated ($r^2 = 0.685$, $n = 8$, $P = 0.011$) (Figure 2).

Discussion

Although deer may move to refuges when hunted despite abundant cover within hunted areas (Kammermeyer and Marchinton 1976), deer movements during the hunting season on SLNWR were similar to those reported by Kufeld et al. (1988) and Root et al. (1988); hunted deer remained within areas similar to those used before the hunting season. Deer use of escape cover on SLNWR was high before and

during hunting in 1992. Deer used SLNWR almost exclusively when water within the James River was at normal levels. Similar use of escape cover (80-90% of diurnal locations) has been reported for White-tailed Deer in Tamarack (*Larix laricina*) swamps of south-central Wisconsin (Larson et al. 1978).

Deer home ranges and movements increased during hunting in 1992 as deer responded to presence and activity of hunters by moving farther into escape cover. Decreased deer use of escape cover on SLNWR from 1992 to 1993 indicated that availability of escape cover was reduced by unusually high water levels in 1993. Deer movement onto private lands was reflected in the increased number of diurnal deer relocations in areas other than escape cover from 1992 to 1993. However, deer adapted differently to hunting in 1993 than 1992 even though home ranges and movements increased similarly during hunting seasons in both years.

Despite the shorter hunting season on private lands, most deer movement that caused increases in home ranges and movements occurred during this period. Habitats on private lands may provide deer with immediate concealment similar to escape cover on SLNWR; however, habitats on private lands that provide such concealment were generally smaller in size than larger expanses of escape cover found on SLNWR. Habitats such as treebelts only constituted 1-2% of private land use, but deer use indicated that tree-

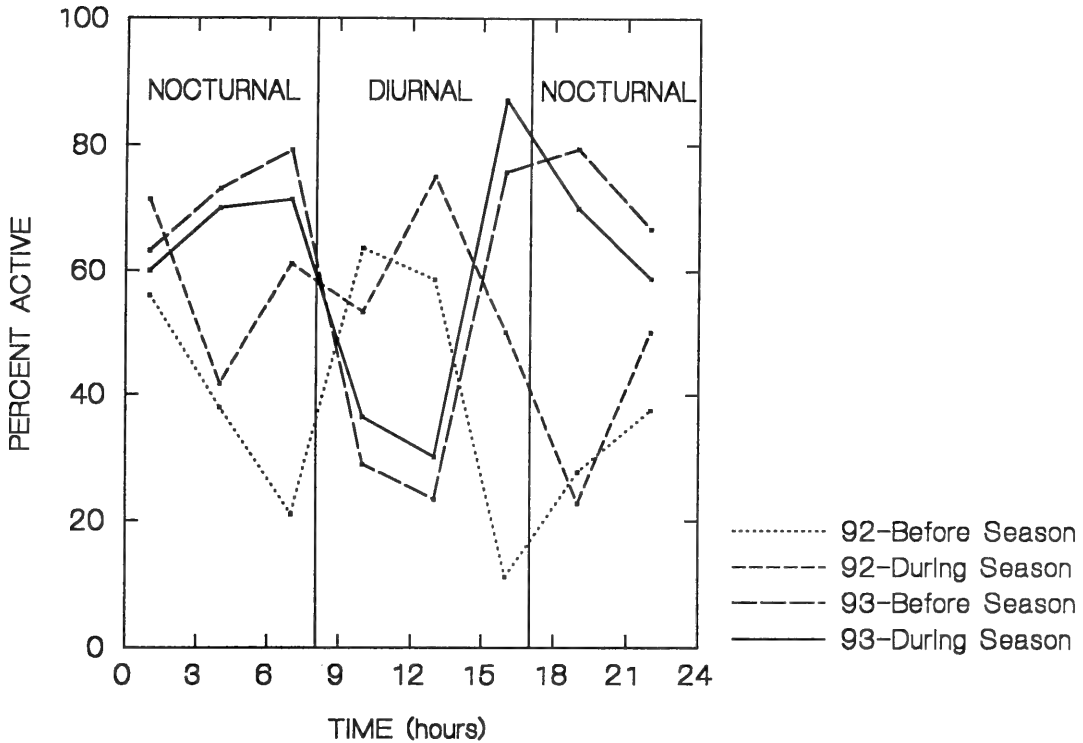


FIGURE 2. Activity (% active) of female White-tailed Deer before and during hunting seasons at Sand Lake National Wildlife Refuge, South Dakota, 1992 - 1993.

belts were an important habitat during hunting (Naugle 1994). Nevertheless, such small and linear habitats do not constitute high quality escape cover. As a result, deer located on private lands in 1993 increased movements during hunting. In east-central South Dakota, Sparrowe and Springer (1970) also reported increased movements of hunted deer in habitats similar to those on private lands adjacent to SLNWR.

Activity of females in 1992 differed from that reported for deer in forested-agricultural (Montgomery 1963; Kammermeyer and Marchinton 1976) and sagebrush- (*Artemisia* spp.) steppe habitats (Eberhardt et al. 1984). In 1992, females were most active on SLNWR at mid-day before and during hunting (Figure 2). High diurnal activity also has been reported for an un hunted Columbian White-tailed Deer (*O. v. leucurus*) population in Washington (Suring and Vohs 1979).

Kammermeyer and Marchinton (1976) suggested that deer fed nocturnally in open agricultural fields because they were more secure in exposed habitats at night. Although diurnal deer use of habitats outside of escape cover 1992 was low, most deer located outside of escape cover were active. Deer may have experienced a similar "psychological security" diurnally while in close proximity to escape cover in 1992. Suring and Vohs (1979) also reported that presence of dense cover in the vicinity of forage attracted deer.

Although diurnal activity was high throughout fall in 1992, deer were more active during hunting than

before hunting. Major changes in activity between periods in 1992 occurred during crepuscular hours. Deer increased crepuscular activity during hunting while maintaining high diurnal activity. Increased activity during hunting may be related to hunting or other factors such as search strategies of females during rut (Holzenbein and Schwede 1989). However, rutting activities probably were not responsible for variation in activity patterns before and during hunting in 1992 because similar responses were not evident before and during hunting in 1993.

Activity of females during high water levels in 1993 followed crepuscular patterns (Figure 2) similar to those reported for deer in other habitats (Montgomery 1963; Kammermeyer and Marchinton 1976; Eberhardt et al. 1984). Crepuscular activity patterns of females before and during hunting in 1993 (Figure 2), which were positively correlated, indicated that female activity was not affected by hunting. Changes in female activity that may have occurred during hunting would not have been detected due to the short hunting season on private lands.

Breeding season occurred coincident with hunting on SLNWR and surrounding private lands. However, activity patterns of females and males that were positively correlated within fall 1992 and 1993 and activity patterns of males and females that were not correlated (i.e.; fall 1992 and 1993; Figure 1) indicated that the shift from a diurnal activity pattern in 1992 to a crepuscular activity pattern in 1993 was not

attributable to rut. Relyea and Demarais (1994) also noted similar variation in intersexual activity patterns during rut for Mule Deer (*Odocoileus hemionus crooki*) despite differences in activity from prerut to postrut. Consequently, activity patterns before hunting in 1992 and 1993 (Figure 2) that were inversely related indicated that availability of escape cover was the major factor influencing deer activity patterns.

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A New Surgical Technique for Implanting Radio Transmitters in Beavers, *Castor canadensis*

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A surgical method of intraperitoneal implantation of radio transmitters using a ventral-lateral muscle-split technique is described. Forty-two transmitters were implanted in beavers weighing 6.4 to 20.5 kg ($\bar{x} = 11.4 \pm 3.9$ kg). Recaptured implanted animals showed good growth with no post-operative complications at 3 to 36 months. Transmitter life span was 46 to 718 days ($\bar{x} = 213.1 \pm 155.6$ days) excluding animals which left the study area in the first 30 days. This method is suitable for all ages of Beavers, and is easily performed in the field.

Key Words: Beaver, *Castor canadensis*, radio transmitters, radio-telemetry, surgical implantation.

Beavers are aquatic, nocturnal mammals and, in many parts of their range, confined to lodges and under-ice movement during winter. Radio-telemetry is an ideal method for the study of their movements. Guynn et al. (1987) discussed some of the difficulties associated with external transmitters. Externally mounted transmitters have been used on Beavers, but with only limited success and they are restricted to adult individuals. Tail collars (Busher 1975; Courcelles and Nault 1983; and Wheatley 1989) and neck collars (Lancia 1979) may cause abrasions or more serious injury to the animal and may only stay attached for a short period of time (Busher 1975; Wheatley 1989). For longer term data gathering, implanted transmitters are required. Davis (1984) and Davis et al. (1984) reported on a method of implanting intraperitoneal transmitters in Beavers using a dorsal incision. They also attempted two subcutaneous implants with poor success.

For my study of Beaver movements in the taiga of southeastern Manitoba (Wheatley 1989, 1994, 1997a, 1997b, 1997c) I required a method of implanting transmitters that incurred a low risk for the Beavers and was feasible under field conditions. This paper describes the method developed, using a ventro-lateral incision, the post-operative history of the Beavers and performance of the transmitters.

Methods

Beavers were captured in Hancock live traps and held in a darkened building at Taiga Biological Station (TBS) for 1.5 to 12 hours before surgery. All surgery was carried out at TBS. The surgical approach was developed in consultation with a surgeon (Dr. B. Wheatley, F.R.C.S. Ed.) and a veterinarian (Dr. L. Webster, D.V.M., Pembina Veterinary Hospital, Winnipeg, Manitoba) and was based on the standard "gridiron" muscle split human appendecto-

my approach (Farquharson 1962). Prior to beginning the project, initial dissection of Beaver cadavers showed that for a successful muscle split, the incision needed to be closer to the costal margin than in human subjects. All work was approved by the University of Manitoba Animal Care Committee and animals were cared for in accordance with guidelines of the Canadian Council on Animal Care (1980).

The implantable transmitters (Austec Electronics, Edmonton, Alberta) consisted of the transmitter and a C-cell lithium battery encased in beeswax and then in biologically inert Elvax (Mini-mitter Co., Sunriver, Oregon). The finished cylindrical package measured about 6 cm x 4 cm and weighed about 80 g. Each package was sterilised in 70% alcohol for 2 hours and rinsed in sterile water immediately before insertion.

I anaesthetized Beavers with simultaneous intramuscular injections of ketamine hydrochloride and acepromazine maleate (Lancia et al. 1978). Dosage was 20 mg ketamine hydrochloride per kg body weight and a standard dose of 2.5 mg acepromazine maleate for all Beavers under 18 kg. Beavers larger than 18 kg were given 4 mg of acepromazine maleate. Booster doses of 50 to 80 mg ketamine hydrochloride were given intramuscularly as necessary to maintain anaesthesia. I also injected 40 mg of lidocaine, a local anaesthetic subcutaneously along the incision line.

I performed the surgery in a log laboratory building, log and mosquito screen "gazebo" or in an 2.4 x 3 m wall tent in the field. Following anaesthesia, the Beaver was placed on the operating table and the front and hind legs were constrained to prevent involuntary movement. The eyes were protected with an antibiotic ointment (Rogar-mycine, Rogar/STB Inc., London, Ontario), and a wet paper towel was wrapped around the Beaver's tail to pre-

vent overheating (Lancia et al. 1978). All personnel wore sterile surgical gloves and masks during the operation. Instruments were sterilized between operations by boiling for 30 minutes, then heating in an oven at 120°C for at least 1 hour.

I clipped the fur from an area 3 cm wide and 8 cm long on the ventral surface immediately caudal to the right costal margin and perpendicular to the midline. I left about 4 mm of fur to help prevent the Beaver from catching the stitches during grooming (Dr. L. Webster, personal communication). The underfur of the Beaver prevents the Beaver's skin from getting wet (Djoshkin and Sofonow 1972) and leaving a small amount of fur helps keep the incision dry during healing. I washed the area with a 30:1 solution of Savlon and then rinsed with 70% ethanol. Excess moisture was blotted up. A plastic incise drape (Steri-drape, 3M Medical-Surgical Division, St. Paul, Minnesota) was placed over the Beaver, providing a sterile field. I cut a hole in the plastic over the site for the incision.

I made the incision using a # 22 scalpel blade after separating the fur in a line to expose the skin. The incision started 1.5 to 2 cm lateral to the midline and 3 to 4 cm caudal to the costal margin. It extended about 8 cm away from the midline, angling slightly towards the costal margin.

The connective tissue between the skin and the external oblique muscle was cleared using fine scissors, separating the two layers and exposing the muscle layer. The external oblique muscle was opened using a muscle-split technique. A small, blunt haemostat was placed against the muscle and was opened with gentle downward pressure, along the line of the muscle fibres. This was repeated as necessary until the internal oblique muscle could be viewed through the split in the external oblique. The external oblique muscle was separated from the internal oblique muscle and the internal oblique was then split by blunt dissection in the same manner as the external oblique. The internal oblique and transversus abdominis muscles were separated and the transversus abdominis muscle was split in the same manner as the other muscle layers. In all Beavers, the peritoneum was attached to the inner wall of the transversus abdominis muscle. It was therefore opened at the same time as the transversus abdominis was split.

Once the opening in the transversus abdominis muscle and the peritoneum was large enough, I clipped haemostats on the peritoneum at each end of the incision to facilitate control and to prevent further splitting while inserting the sterilized transmitter through the incision. The transmitter was gently pushed towards the midline and a 1 million IU dose of Penicillin G Sodium (Crystapen, Glaxo) was poured into the peritoneal cavity.

I sewed up the transversus abdominis muscle and

peritoneum as one layer with a continuous 3 '0' plain or chromic gut suture. The internal oblique and external oblique muscles were sewn up as separate layers in turn in a similar manner. I sutured the skin with 15 to 20 interrupted stitches using 3 '0' silk sutures. Derapen (Ayerst Laboratories, Montreal, Quebec), a penicillin antibiotic, was given intramuscularly at a dose of 0.22 ml per kg body weight (66 000 IU per kg). To facilitate visual identification of individuals, I also attached uniquely numbered and coloured ear tags (Monel Number 3) to both ears (Miller 1964).

The Beaver was returned to the live trap. For most of the 48 hours after surgery, it was kept in a cool dark building to allow for post-operative and post-anaesthetic recovery and because in many cases the location of the home lodge was not known. Beavers frequently swam long distances (up to 5 km) immediately after release. After 24 hours, the Beaver, in the trap, was placed partly in the water for 4 to 5 hours and Trembling Aspen (*Populus tremuloides*) branches were supplied. The incision site was inspected before the animal's release at the capture site.

Results

Transmitters were implanted in 42 Beavers weighing 6.4 to 20.5 kg with a mean weight of 11.4 ± 3.9 kg (Table 1). Beavers became alert and active between 2 and 5 hours post-operatively, but then became sluggish at 6 to 8 hours and remained sluggish until 30 to 36 hours post-op. By 48 hours after surgery they were again alert and active.

With this technique, the range of transmitters was found to be from 0.1 km (transmitter and receiver in dense alder bog) to 2 km (receiver on high ridge). Range was about 1 km on the lake and about 4 km from the air.

Ten Beavers disappeared from the study area within 1 month (Table 1). The 30 remaining Beavers (two received two transmitters during the study) were active 3 months to 4 years after surgery. I recaptured four implanted Beavers a total of seven times in the 3- to 36-month period after surgery. All the Beavers had a palpable scar, but no other sign of the incision site. Beaver 1848 increased in weight from 13.2 kg to 15.9 kg over the first 3 months after implantation and to 17.7 kg 35 months after implantation. She bore her first kits 2 years after implantation. Beaver 1846 increased in weight from 9.5 kg to 11.4 kg in 11 months. This Beaver may have had a low weight on recapture because the capture was shortly after breakup, when winter weight loss may be evident (Aleksiuk and Cowan 1969a, 1969b). Beaver 294 (later retagged 1510) increased in weight from 11.4 kg to 20.45 kg over a 36-month period. Beaver 1611 (later retagged 1516) was an adult at the time of implantation and recapture 12 months

TABLE 1. Age class, sex and weight of Beavers implanted with radio-transmitters in this study, and lifespan and fate or status of transmitters. The term "signal disappeared" refers to animals where there was no visual confirmation of the animal still being present after loss of the signal. "Transmitter failed" refers to animals which were observed visually after loss of the signal.

Beaver #	Age Class	Sex	Weight (kg)	Date Implanted	Last signal	Fate / Status
1846	Yearling	Male	9.5	08-06-87	18-11-87	transmitter failed, 164 days, recaptured 08-05-88, 11.4 kg
1834	Yearling	Female	10.0	12-06-87	30-05-89	signal disappeared, 718 days
1848	2-year-old	Female	13.2	03-07-87	24-10-88	transmitter failed, 479 days, recaptured 28-09-87, 15.9 kg, 23-10-88, 17.2 kg, 28-05-89, 17.3 kg lactating, 13-05-90, 17.7 kg lactating
B280	Yearling	Female	9.1	06-07-87	23-07-87	signal disappeared, 17 days*
B286	Yearling	Female	10.5	12-05-88	14-10-89	signal disappeared, 519 days
B434	2-year-old	Male	11.8	25-08-88	29-08-88	signal disappeared, 4 days, located 30-03-89 during aerial survey, 36 km from capture site, 218 days
B294	2-year-old	Male	11.4	26-09-88	09-03-89	transmitter failed, 164 days, new transmitter, 25-09-91, see 1510
B481	2-year-old	Male	13.2	22-05-89	03-12-89	signal disappeared, 196 days
B420	Yearling	Male	9.6	24-05-89	17-06-89	signal disappeared, 24 days*, trapped 48 km away on different watershed, 10-91
B292	2-year-old	Female	13.2	25-05-89	02-06-89	signal disappeared, 8 days*
B109	Yearling	Male	6.4	26-05-89	21-08-89	signal disappeared, 87 days
B181	Adult	Male	17.7	27-05-89	31-08-89	transmitter failed, 96 days, observed visually
B290	2-year-old	Female	11.8	30-05-89	15-07-89	signal disappeared, 46 days
B491	Adult	Male	16.8	09-06-89	27-10-89	transmitter failed, 140 days, animal seen 06-90
B433	Yearling	Male	10.5	10-06-89	14-08-89	signal disappeared, 65 days
B403	2-year-old	Female	15.0	11-06-89	27-10-89	signal disappeared, 138 days
1631	Yearling	Male	10.5	04-05-90	12-05-90	signal disappeared, 8 days*, last seen heading south
1603	Yearling	Female	6.8	05-05-90	15-05-91	signal disappeared, 10 days*
1646	Yearling	Female	6.8	05-05-90	11-05-90	deceased, see text, transmitter functioning
1680	2-year-old	Female	13.2	11-05-90	27-05-90	signal disappeared, 16 days*
1686	2-year-old	Female	12.3	12-05-90	09-09-90	signal disappeared, 120 days
1649	Yearling	Male	8.2	14-05-90	14-04-91	transmitter failed, 334 days, trapped at different lodge, 17-11-91, 16.4 kg, see text
1641	Yearling	Male	8.6	17-05-90	17-09-90	signal disappeared, 123 days
1617	Adult	Male	17.7	17-05-90	01-11-90	signal disappeared, 168 days
1682	2-year-old	Female	12.3	18-05-90	14-08-90	signal disappeared, 88 days
1611	Adult	Male	20.5	28-05-90	11-05-91	transmitter failed, 348 days, new transmitter, 18-05-91, see 1516
1684	Yearling	Male	10.5	29-05-90	12-05-91	signal disappeared, 348 days
1623	Yearling	Female	10.9	30-05-90	17-07-90	transmitter failed, 48 days, visual observations
1697	Yearling	Male	10.0	09-06-90	18-06-90	signal disappeared, 9 days*
1516	Adult	Male	18.6	18-05-91	-	transmitter continuing, 05-92

Continued

TABLE 1. (Continued)

Beaver #	Age Class	Sex	Weight (kg)	Date Implanted	Last signal	Fate / Status
1526	Yearling	Female	8.6	23-05-91	08-09-91	signal disappeared, 108 days
1532	Yearling	Female	9.5	24-05-91	01-06-91	signal disappeared, 8 days*, heading north
1534	Yearling	Male	6.8	25-05-91	08-09-91	signal disappeared, 106 days
1524	Yearling	Male	6.8	26-05-91	03-07-91	signal disappeared, 38 days
1502	Yearling	Female	9.5	29-05-91	18-03-92	beaver killed by Otters, functioning transmitter found on land, buried in snow (apparently by Red Fox), 294 days, temperature -18°C
1528	Yearling	Male	9.5	02-06-91	23-04-92	signal disappeared, 333 days
1539	Yearling	Female	11.4	17-09-91	20-09-91	signal disappeared, 3 days*, heading west
1520	Kit	Female	6.8	23-09-91	-	transmitter continuing, 05-92
1522	Kit	Male	6.8	24-09-91	-	transmitter continuing, 05-92
1518	Kit	Male	6.8	24-09-91	-	transmitter continuing, 05-92
1510	Adult	Male	20.5	25-09-91	28-04-92	transmitter failed, 217 days, observed visually
1508	Adult	Female	17.7	25-09-91	23-04-92	transmitter continuing, 05-92

* Signals which disappeared within 30 days were assumed to have dispersed.

later. He had lost a small amount of weight, going from 20.45 kg to 18.6 kg. Again this may be the result of winter weight loss because the capture was only shortly after breakup.

Beaver 1649 was trapped in a Conibear trap by the local trapper 18 months after implantation. This animal had increased in weight from 8.2 kg to 17.3 kg. The transmitter was encased in many layers of connective tissue and had a large multi-branching vascular bundle leading to it and wrapped around it. A small scar was visible on the peritoneum and internal wall of the transversus abdominis and on the inner side of the skin.

All 10 Beavers that left the study area during the first 30 days after surgery were yearling or 2-year-old animals (Table 1). Two are known to have dispersed: B434s signal was located 36 km away from the capture site during an aerial survey; and B420 was trapped in Ontario 48 km away, two years later. Three other Beavers (1631, 1532 and 1539) were last seen heading away from the study area.

Excluding the nine non-relocated dispersers, but including the relocated disperser, transmitter life varied from 46 to 718 days and averaged 213.1 days (± 155.6 days) (Table 1). These values should be viewed as minimum lifespan of the transmitters because some of these Beavers may also have dispersed and therefore the transmitters did not necessarily cease to function at the shorter periods. Five transmitters were still active at the conclusion of the study, including one in an adult female (1508) who

had successfully produced kits while carrying the active transmitter.

One Beaver ceased to move six days after release. The body was located three days later. Weight loss (including dehydration after death) was 2.3 kg from the original weight of 6.9 kg (10 days earlier). An autopsy showed all internal organs to be healthy except for the first 30 cm of the small intestine which appeared gangrenous. The transmitter was found lying between the liver and duodenum.

Beaver 1502 was apparently killed by Otters in March 1992. The transmitter, completely devoid of blood or tissue, was found on land, about 20 m from shore, buried in snow, apparently by a Red Fox. There were a few small teeth marks in the wax of the transmitter casing, but despite the -18°C temperatures, the transmitter continued to function 294 days after implantation.

Discussion

Implanted transmitters can be used in almost any size animal because they provide no hindrance to growth and there is no potential for snagging on vegetation. The greatest risk to the animal is infection due to surgery, but this can be reduced by sterile technique and antibiotics. I found no evidence of infection in any of the recaptured Beavers. Guynn et al. (1987) reported one death due to adhesion to the large intestine with resultant blockage of the lumen in Davis's (1984) study. Guynn et al. (1987) reported that after six weeks, intraperitoneally implanted

transmitters appeared to be encapsulated in fibrous tissue, and my finding in the Beaver trapped by the local trapper would agree with this. Once encapsulated, there appears to be little effect on the animal (Guynn et al. 1987), as also evidenced by pregnancy in implanted animals which I recaptured.

As in this study, Davis et al. (1984) found little problem with intraperitoneal implants. Their method used a dorsal incision rather than ventral. This could be more dangerous to the animal. From my observations of Beaver over a 6-year period, I have found that their natural repertoire of movements during grooming and feeding tends to stretch the dorsal muscles and skin more than the ventral muscles and skin. In addition, the kidneys and blood vessels on the dorsal wall of the abdomen may present a greater chance for complications with a dorsal incision. In the ventral-lateral method I describe, no large blood vessels or organs are in the vicinity and this reduces the risk of complications, especially when surgery is performed in the field. With this technique there is also natural closure of the layers because of the muscle split and because the layers of muscle fibres are at right angles to each other.

Kenward (1987) reported that a mid-ventral, or linea alba, incision is the usual means of access to the peritoneal cavity. This method has been used in physiological studies of Beaver (Dyck 1991). While this procedure may contribute to a faster operation, because there are fewer layers, other problems may arise. Connective tissue (the linea alba) is virtually avascular and therefore slower to heal than muscle and provides for a much weaker incision after suturing than the muscle-split technique (Farquharson 1962). The alternating directions of the split muscle layers with the ventral-lateral incision provide a much better seal than the linea alba incision. In addition, the transmitter may sit directly over a mid-ventral incision (Kenward 1987) and thereby affect healing, whereas with the off-centre incision, this is less likely. More abrasion of the incision site is also likely with a mid-ventral incision because it is on the lowest part of the abdomen, and is more likely to catch on the ground and vegetation than the off-centre incision.

The method I describe is also relatively blood-free. Since only the skin is cut, there is very little bleeding and it is possible to see most blood vessels associated with the muscle layers and avoid them. This is very important in the field setting where such items as cauterizing equipment are not readily available.

Recent developments in animal surgery suggest some possible improvements to the anaesthetic and analgesic regime used in this study. Greene et al. (1991) describe a method of anaesthesia using ketamine initially with subsequent tracheal intubation and halothane gas in oxygen administration. However, gas anaesthesia is not practical in the field setting. Jalanka et al. (1990) describe a combination drug regimen of Medetomidine and Ketamine, which

may be effective for Beavers although no doses are given for Beavers. The sluggishness noted in the post-operative period may result from lack of pain control (Dr. N. Caulkett, DVM, Department of Veterinary Anesthesiology, Radiology and Surgery, University of Saskatchewan, personal communication). The area of pain control and pain assessment in animals has presented many problems (Flecknell 1994). Recent studies in this area have suggested administration of buprenorphine or bupivacaine to relieve post-operative pain (Liles and Flecknell 1993). The addition of some form of post-operative anaesthesia to the surgical method described in this paper would be advised.

In summary, the surgical technique described herein provides a safe, relatively straightforward method of implantation of radio-transmitters in Beavers. Since this technique avoids major organs and blood vessels and can be performed rapidly, it is well suited for use in field settings. The addition of analgesic agents post-operatively is advised.

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The Condition and Trend of Aspen, *Populus tremuloides*, in Kootenay and Yoho National Parks: Implications for Ecological Integrity

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Kay, Charles E. 1997. The condition and trend of aspen, *Populus tremuloides*, in Kootenay and Yoho National Parks: Implications for ecological integrity. *Canadian Field-Naturalist* 111(4): 607–616.

Aspen (*Populus tremuloides*) communities were measured in and near Yoho and Kootenay National Parks to determine condition and trend. Most aspen stands were heavily invaded by conifers as they had not burned in 60 years or more due to modern fire suppression and the elimination of aboriginal burning. Aspen is also declining due to repeated ungulate browsing, primarily by Elk (*Cervus elaphus*). Even where disturbed by logging and burning outside the parks, many aspen stands failed to produce new stems greater than 2 m tall because all the suckers were repeatedly browsed. Only where ungulate numbers were low was aspen able to successfully regenerate. Aspen, though, is not “seral,” as that term is commonly used because the species seldom grows from seed due to its demanding seed bed requirements. This, coupled with high biodiversity, makes aspen an excellent indicator of ecological integrity as mandated by Parks Canada statute.

Key Words: Aspen, *Populus tremuloides*, Kootenay National Park, Yoho National Park, ecological integrity, Elk, *Cervus elaphus*.

Aspen (*Populus tremuloides*) is an excellent indicator of ecological integrity because the species seldom grows from seed due to its demanding seed bed requirements (Perala 1990). In fact, there are no known instances of aspen clones having established from seed anywhere in the southern Canadian Rockies or in the Intermountain Western U.S. during the period of recorded history (Kay 1993). It is thought that environmental conditions have not been conducive to seedling growth and clonal establishment since shortly after the glaciers retreated 10 000 or more years ago (McDonough 1979, 1985; Perala 1990; Jelinski and Cheliak 1992; Mitton and Grant 1996). This means that the aspen clones found throughout the southern Canadian Rockies today have likely maintained their presence on those sites for thousands of years via vegetative regeneration. Thus, aspen may be among the oldest living organisms on Earth (Mitton and Grant 1996). In fact, Peterson et al. (1995*:14–17) classified aspen as old-growth ancient forest.

Aspen seedlings are more common in the northern Canadian Rockies (Peterson and Peterson 1992, 1995) and there may be “windows of opportunity” that allow seedling establishment at infrequent, 200 to 400 year or longer, intervals (Jelinski and Cheliak 1992: 728), but successful sexual reproduction of aspen is still exceedingly rare (Mitton and Grant 1996). Aspen trees invariably occur as clones in which all the individual trees (ramets) are genetically identical, having grown from a common root sys-

tem by vegetative shoots (Shepperd and Smith 1993). If aspen clones are lost due to forest succession or other factors, there are no known means of reestablishment (Kay et al. 1994). As a relatively short-lived tree (< 150 years), long-lived aspen clones are often dependent on periodic disturbance such as fire to stimulate vegetative regeneration via root suckering, and to reduce conifer competition (Bartos and Mueggler 1979, 1981; Bartos et al. 1991, 1994; Shepperd 1993; Shepperd and Smith 1993). In the absence of fire or other disturbance, most aspen clones in the southern Canadian Rockies will eventually be replaced by more shade-tolerant species. Thus, the condition and trend of aspen provides information not only on an area’s fire history, but also addresses the question of whether past fire suppression practices have had a significant impact on park resources (Walker and Irons 1993). While 70 or more years of active fire suppression may not have had a detectable effect on coniferous species (Masters 1990), fire exclusion may have had a greater impact on aspen communities (DeByle et al. 1987; Bunnell 1995).

In addition, aspen provides highly palatable forage for Elk (*Cervus elaphus*) and other ungulates in the Canadian Rockies (Nelson and Leege 1982; Poll et al. 1984; Timmermann 1991). Aspen is, however, sensitive to repeated browsing. High-density Elk populations commonly strip bark from mature aspen and severely browse aspen suckers, thus preventing stand regeneration which may eventually lead to the

*See Documents Cited section following Acknowledgments.

loss of aspen clones (Krebill 1972; Olmsted 1977, 1979; Weinstein 1979; DeByle 1985; Kay 1990; Shepperd and Fairweather 1994). Unlike herbaceous plants, the long-term grazing and fire histories of aspen communities can also be judged from historical and repeat photographs (Kay and Wagner 1994).

Moreover, aspen communities support an array of other species and may have the highest biodiversity of any forest type in the Canadian Rockies (DeByle and Winokur 1985; Peterson and Peterson 1992, 1995*; Stelfox 1995). Bird communities, for instance, vary with the size, age, and location of aspen clones, as well as with grazing intensity and history (Young 1973, 1977; Flack 1976; Winternitz 1980; Daily et al. 1993; Johns 1993; Westworth and Telfer 1993; Pojar 1995; Stelfox 1995). If aspen is lost, many birds and small mammals will decline; some precipitously (Ehrlich and Daily 1993).

In Yoho National Park (established 1886) and Kootenay (established 1920), aspen is common on lower-elevation montane slopes with southerly or westerly aspects (Kuchar 1978*; Achuff et al. 1984) — areas that are also rated as prime winter habitat for Elk and other ungulates (Poll et al. 1984; Van Egmond 1990). To the east in Banff National Park, high ungulate populations are believed to be having a negative effect on that park's aspen communities (Cowan 1944*, 1947, 1950; Flook 1964, 1970; Kay and White 1995). In U.S. national parks, such as Yellowstone and Rocky Mountain, Elk have had a major impact on aspen, often eliminating the species from many areas (Olmstead 1977, 1979; Kay 1985, 1990; Hess 1993; Kay and Wagner 1996). Aspen, however, has not previously been studied in Kootenay or Yoho. Moreover, none of the montane areas in either park have burned in more than 60 years due to active fire suppression programs (Kay and White 1995), which raises the prospect that Yoho and Kootenay's aspen communities may be declining due to advancing forest succession. To address these and other questions, I measured and surveyed aspen in and near Kootenay and Yoho National Parks.

Methods

I conducted a systematic survey of aspen communities in Kootenay and Yoho National Parks during September 1994 and September 1995. Both parks are situated immediately west of the continental divide in British Columbia between 50° 30' – 51° 40' N and 116° 10' – 117° 15' W. Due to both park's thick coniferous forests, steep terrain, and limited budget it was not possible to undertake a random survey of aspen stands. Instead, sampling was confined to established trails, old fire-roads, and along park highways. Each trail or road was first driven or walked and all aspen stands plotted on 1:50 000 topographic maps. Then a representative number of stands was selected for detailed measurement.

At each aspen community that was sampled during this study, a 2 x 30 m belt transect was placed perpendicular to the slope in the stand's center. To facilitate data recording, I subdivided each 30 m transect into 3 m segments and then recorded the number of live aspen stems by size classes within each 3 m segment. The following size classes were used: (1) stems less than 2 m tall, (2) stems greater than 2 m tall but less than 5 cm diameter at breast height (DBH), (3) stems between 6 and 10 cm DBH, (4) stems between 11 and 20 cm DBH, and (5) stems greater than 21 cm DBH. Ages of aspen within each size class were determined by counting annual rings. The ages of large aspen were obtained with the aid of an increment bore while smaller stems were cross-sectioned, usually those less than 5 cm DBH. Stems less than 2 m tall were not aged.

Within each stand, the following information was also recorded: (1) elevation as determined from topographic maps; (2) Universal Transverse Mercator (UTM) grid coordinates, again estimated from topographic maps; (3) aspect; (4) estimated slope in percent; (5) estimated stand size in meters; (6) bark damage — percent of stems that exhibited old black-scar, ungulate bark damage and the percent of stems with new or recent bark damage — wounds that had not yet healed over with black-colored bark, usually less than two years old (Krebill 1972); (7) an estimate of the mean percent of each stem that had been damaged by ungulate bark stripping; (8) if the stand had newly regenerated stems greater than 2 m tall but less than 5 cm DBH, an estimate of the percent that showed evidence of ungulate highlining — where the ungulates browse off all the lower branches as high as the animals can reach, usually 2 m; and (9) the percent of stems less than 2 m tall that exhibited ungulate browsing.

Items 6 to 9 provided an estimation of past ungulate use. Only Elk or Moose (*Alces alces*) strip-off and eat the bark of aspen, and bark damage usually occurs during winter when other foods are in short supply (Krebill 1972). Neither Mule (*Odocoileus hemionus*) nor White-tailed deer (*O. virginianus*) strip aspen bark, but both species of deer, as well as Elk and Moose browse aspen. Since at least 1940, however, Elk have dominated the ungulate communities in Kootenay and Yoho, especially during winter (Poll et al. 1984; Van Egmond 1990). In areas with high Elk populations, bark stripping can be so severe that the lower 2 m of aspen trunks are black instead of their normal white coloration (Kay 1990; Kay and Wagner 1994).

In addition, at each stand the number and species of conifers was recorded on the 2 x 30 m belt transect that was used to count aspen stems. Conifers were recorded by the same five size classes that were used for aspen. Total percent conifer canopy cover in each stand was also estimated according to guidelines

established by Mueggler (1988). Finally, understory species canopy cover was estimated for each stand but those data are not reported here (see Kay 1996*).

This was part of a larger project to assess long-term ecosystem states and processes in the southern Canadian Rockies (Kay et al. 1994; Kay and White 1995), but here I only report the results of my aspen research in and around Yoho and Kootenay. Aspen outside Yoho and Kootenay was included because other studies have found a marked inside-outside park difference in aspen community dynamics due to differences in ungulate use. Inside Yellowstone National Park, for instance, the area occupied by aspen has declined approximately 95% since park establishment in 1872 and even burned aspen stands have failed to successfully regenerate due to repeated ungulate browsing (Romme et al. 1995; Kay and Wagner 1996). Outside that park, however, where hunting limits Elk numbers, aspen stands have successfully regenerated without fire or other disturbance and display characteristics of climax communities (Kay 1985, 1990). The same is true in Colorado's Rocky Mountain National Park (Hess 1993). By measuring aspen stands in the same drainage with similar histories of disturbance, but with different histories of ungulate use, it is possible to determine if climatic change, fire suppression, or grazing is primarily responsible for any observed differences in community structure (Kay 1990). Kuchar (1978*), Achuff et al. (1984), Poll et al. (1984), Van Egmond (1990), and Tymstra (1991) provided information on vegetation, wildlife, and climatic conditions in Kootenay and Yoho.

Results

A total of 269 aspen stands were measured in or near Kootenay ($n = 168$) and Yoho ($n = 101$) National Parks. Most aspen stands were heavily invaded by conifers, primarily White Spruce (*Picea glauca*), Lodgepole Pine (*Pinus contorta*), or Douglas Fir (*Pseudotsuga menziesii*); mean conifer canopy cover = 38% (SEM = 2.6%). Ungulates have also had a significant impact on these aspen communities. Only where ungulate use was low had aspen stands been able to successfully regenerate — defined as producing new stems more than 2 m tall. In Kootenay National Park, aspen successfully regenerated in the Columbia Valley where there are few Elk, but not in the Kootenay Valley where most of the park's Elk winter. While in Yoho National Park, except for a handful of stands, no aspen communities successfully regenerated.

Even clear-cut stands were not able to successfully regenerate in the Cross River drainage south of Kootenay National Park. Although logging and associated soil disturbance increased sucker densities 60 fold (mean = 291 stems/ha unlogged vs. 17 337 stems/ha logged), aspen height growth was limited

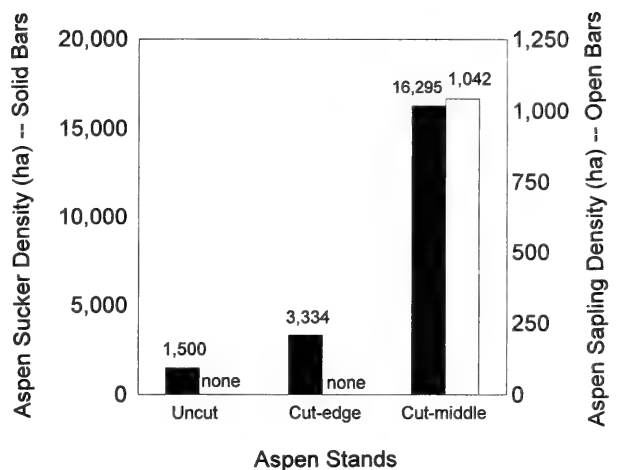


FIGURE 1. The impact of cutting and ungulate browsing on aspen regeneration west of Yoho National Park. Uncut stands had low sucker densities and no successful aspen regeneration. Fourteen years after they were treated, aspen stands within the edge of the cut-block had slightly elevated sucker densities but successful aspen regeneration was absent. In the center of the cut-block, however, where ungulate browsing was less (Brunt 1990: 88), aspen sucker densities were significantly higher and some stems had recently grown beyond the reach of ungulates. Aspen suckers = the number of aspen stems less than 2 m tall. Aspen saplings = the number of aspen stems more than 2 m tall but less than 5 cm DBH.

by ungulate browsing. A few stems, though, escaped browsing, and in only eight years, those plants attained 3 to 4 m in height, which suggests that both the site and the climate can support excellent aspen growth (Bartos et al. 1994). Similarly, in Yoho's Kicking Horse Valley, cutting and burning failed to regenerate aspen.

West of Yoho's Kicking Horse entrance, the British Columbia government cut and burned two large areas to increase forage for wintering ungulates, primarily Elk. The cut-blocks are on steep south-facing slopes above the Trans-Canada Highway. Prior to treatment, both areas were predominately aspen with low to moderate conifer invasion, primarily Douglas Fir. The trees were felled and then burned in place. That is to say, the areas were not technically logged, as none of the trunks were removed and no roads were built. Thus, unlike logging areas, there is no vehicle access to these cut-blocks. In addition, an approximately 100 m strip of vegetation was left along the highway so that the cut-blocks are not visible from the pavement. This prevents hunters shooting into the cut-blocks from the road.

At one cut-block, I measured four uncut aspen stands, four felled aspen stands at the edge of the cut-block, and four felled aspen stands in the center of the cut-block. Uncut aspen stands had low sucker

densities and had not successfully regenerated. While 14 years after they were treated, aspen within the edge of the cut-block had slightly elevated sucker densities, successful regeneration was absent because ungulate browsing prevented any of those stems from growing more than 1 m tall. In the center of the cut-block, however, where browsing was less intense, aspen sucker densities were significantly higher and some stems had recently grown beyond the reach of ungulates (Figure 1).

Elk use the edges of cut-blocks more frequently than they do the centers because the animals are reluctant to venture far from cover where they can be shot (Lyon 1979; Edge and Marcum 1985; Edge et al. 1985; Brunt 1990: 88; Lyon et al. 1985). Although sportsmen cannot drive into these cut-blocks, the areas are still hunted because they are so close to Trans-Canada Highway. Although there are no data on aspen sucker densities immediately following treatment, it is likely that the low sucker densities now seen around the inside edge of these cut-blocks are also a result of ungulate browsing (Kay 1990; Bartos et al. 1994; Shepperd and Fairweather 1994).

Only in areas where ungulate numbers were low did logged aspen stands successfully regenerate. For instance, clear-cut logging and broadcast burning on British Columbia crown lands north of Kootenay Park stimulated aspen regeneration. Mean ($n = 18$) stem densities 15 to 25 years after logging were: (1) < 2 m tall = 3288/ha; (2) > 2 m tall but less than 5 cm DBH = 6131/ha; (3) 6–10 cm DBH = 2593/ha; (4) 11–20 cm DBH = 269/ha, and (5) > 21 cm DBH = 0. The same was true along the Ice River south of Yoho Park. Mean ($n = 8$) stem densities 12 to 14 years after logging were: (1) < 2 m = 4313/ha (2) 2 m $<<$ 5 cm DBH = 6647/ha; and (3) 6–10 cm DBH = 832/ha. Many of the regenerated stems had reached heights of more than 6 m and showed little evidence of ungulate bark damage (mean proportion of individual aspen trunks scarred = 2%) or browsing (mean percent aspen suckers browsed = 9%).

There was also a correlation between ungulate use and aspen regeneration in undisturbed stands. Where ungulate use was high, no stands were able to successfully produce new stems greater than 2 m tall, but where ungulate use was low, as measured by the mean percent aspen suckers browsed and the mean percent aspen bark damage, collectively termed the ungulate use index, aspen stands successfully regenerated without disturbance. A linear regression of the ungulate use index and aspen sapling density produced a correlation coefficient of $r^2 = 0.96$, which suggests a strong negative relationship between ungulate use and aspen regeneration (Figure 2). Even stands with high rates of conifer invasion were able to regenerate successfully if ungulate use was low.

Aspen on Mount Wardle displayed a similar regeneration pattern. Mount Wardle is located north-

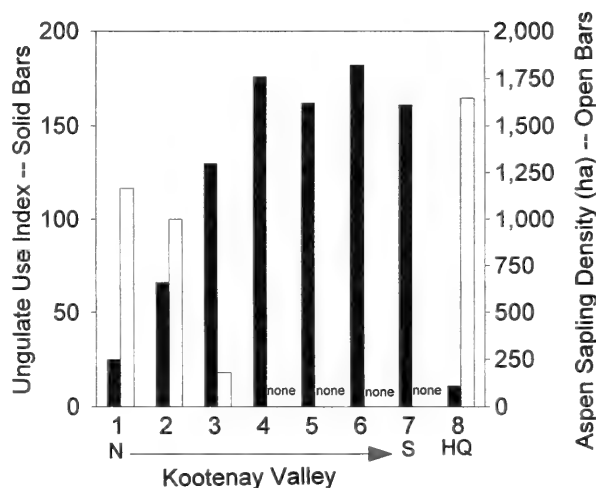


FIGURE 2. The relationship between ungulate use and aspen regeneration in Kootenay National Park. The ungulate use index (solid bars) is a combination of the mean percent aspen suckers browsed plus the mean percent aspen bark damage and is plotted with the density (ha) of aspen stems greater than 2 m tall but less than 5 cm DBH. Areas 1–7 are all in the Kootenay Valley from north to south, with one north of the park and seven south of the park while HQ is the area around park headquarters in the Columbia Valley. Where Elk use was low, undisturbed aspen stands had successfully regenerated at more than 1000 stems/ha but as ungulate use increased, stem density declined. At ungulate use levels above 140, stands failed to produce new stems greater than 2 m tall. Linear regression — Aspen Sapling Density (ha) = -9.36 (Ungulate Use Index) + 1567.73; $r^2 = 0.96$; $p < .01$. (1) Unlogged area north of the park including aspen stands KNP-131 to 133, 139, 146, 147, 153, and 156 to 158; (2) west Kootenay fire-road north — KNP-60 to 66; (3) west Kootenay fire-road south — KNP-86 to 99; (4) Highway 93 — KNP-80 to 86 and 100–102; (5) east Kootenay fire-road — KNP-27 to 42; (6) Cross River eastside fire-road — KNP-11 to 18; (7) south of park — KNP-7 to 10 and 51 to 54; and (HQ) park headquarters — KNP-43 to 50.

east of Kootenay Crossing in Kootenay National Park and its steep south-facing slopes support populations of Elk and Mountain Goats (*Oreamnos americanus*) during winter (Poll et al. 1984). Six aspen stands were measured on Mount Wardle beginning near the bottom and progressing upslope. Ungulate browsing decreased with elevation while aspen regeneration showed the opposite trend (Figure 3). Lower-elevation aspen stands had no regeneration greater than 2 m tall while upper-elevation stands had successfully regenerated without disturbance and were multi-aged. Elk use the lower slopes more intensely than they do the steeper, rockier, upslope areas. Mountain Goats neither strip the bark from aspen nor do they apparently find it very palatable. The oldest aspen in these stands were only $60 \pm$ years

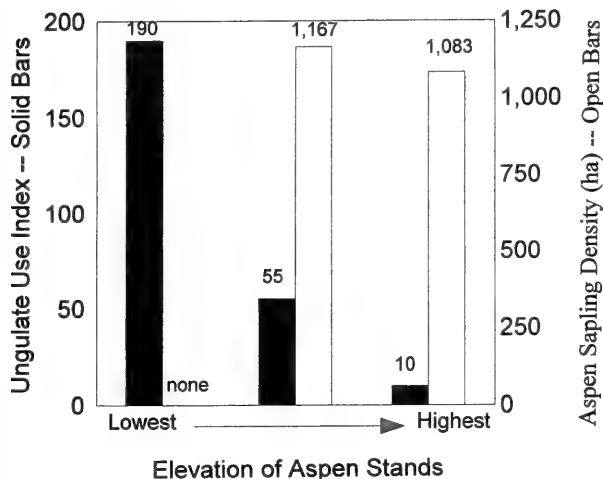


FIGURE 3. The relationship between ungulate use and aspen regeneration on Mount Wardle in Kootenay National Park. The ungulate use index (solid bars) is a combination of the mean percent aspen suckers browsed plus the mean percent aspen bark damage and is plotted with the density (ha) of aspen stems greater than 2 m tall but less than 5 cm DBH. Where Elk use was high at the base of the mountain, aspen stands had not successfully regenerated while further up the slope where Elk use was less, all aspen stands successfully produced new stems greater than 2 m tall. Linear regression — Aspen Sapling Density (ha) = -6.62 (Ungulate Use Index) + 1312.96; $r^2 = 0.91$; $p < .01$.

of age, but similarly aged trees were taller at the lower elevations. Thus, conditions are more conducive to aspen growth at lower elevations, but regeneration was better on the harsher sites. This suggests that climatic conditions are less important than ungulate browsing in determining whether or not stands can successfully regenerate.

Aspen in Kootenay and Yoho were difficult to age because many, and especially the older, stems had some type of heart rot or other disease (Peterson and Peterson 1992, 1995). This may be a natural phenomenon or it may be due to the high incidence of ungulate bark damage that has occurred in the parks (Hinds 1985). Cores without at least some heart rot were rarely encountered during this study. Many cores could not be read at all while in others, with only small bands of decayed wood, it was possible to establish approximate ages. That is to say, if there were x number of annual rings per cm before a short section of diseased core, I assumed that a cm of diseased core contained x number of growth rings. While this technique is not precise, it is the best that could be done under the circumstances. This was mainly a problem with the larger aspen as the smaller stems were usually not diseased. Thus, the younger stems were more accurately aged than the older aspen.

Because aspen “has a pronounced ability to express dominance, and overstocking to stagnation

of growth is extremely rare” (Perala 1990: 562), other studies have found a positive correlation of increasing age with increased stem DBH (Alder 1970:15–17; Masslich et al. 1988: 258; Kay 1990: 63). So it is not surprising that a linear regression of age in year and DBH in cms for all unlogged stands measured in Kootenay produced a significant positive correlation — age in years = 2.24 (DBH in cm) + 13.16; $r^2 = 0.69$; $n = 632$; $p < 0.01$. Thus for Kootenay in general, the smaller the aspen stems, the younger their age. Logged aspen stands north of the park were not included in this calculation because they had nearly double the DBH growth rate of unlogged stands which would have skewed the analysis. Instead, that regression was calculated separately — age in years = 1.45 (DBH in cm) + 6.22; $r^2 = 0.82$; $n = 147$; $p < 0.01$.

A linear regression of age in years and DBH in cms for all unlogged stands measured in Yoho also yielded a significant positive correlation — age in years = 2.24 (DBH in cm) + 29.54; $r^2 = 0.64$; $n = 121$; $p < 0.01$. This was similar to that obtained in Kootenay except the y-intercept was greater. This probably reflects the larger number of smaller-sized stems that were available for aging in Kootenay. In Yoho, only a few stands had successfully regenerated, while in Kootenay there were more sites that had successfully regenerated.

The aspen stand-age distribution for Kootenay and Yoho National Parks, or more correctly the age of

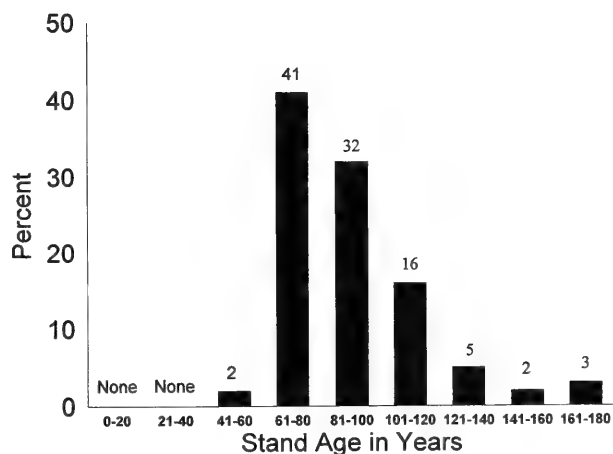


FIGURE 4. Age classes of aspen stands in Kootenay and Yoho National Parks. Fire suppression and ungulate browsing have had a dramatic impact on Kootenay and Yoho’s aspen communities. There have been virtually no stand replacing fires during the last 60 years while before then aspen stands were frequently regenerated by fire when Elk populations were low. There are few stands with trees older than 150 years because that is near the maximum longevity of individual aspen stems and because historically fire-return intervals were very short; i.e., by chance alone, old age trees are uncommon in areas burned by frequent fires (Johnson et al. 1995; Lesica 1996).

the oldest aspen trees in the stands, indicates that aspen commonly regenerated ca. 1816 to 1935 (Figure 4). This probably reflects a history of frequent stand replacing fires (Van Wagner 1978) and low ungulate populations. During the last 60 years, however, few aspen stands have regenerated.

Discussion

Aspen is declining in Yoho and Kootenay National Parks due to advancing forest succession, an absence of fire, and high ungulate population densities. Aspen, however, is not "seral," as that term is commonly used. It is often claimed that aspen "is an early successional tree species [which] ... often occupies recently disturbed sites" (Campbell et al. 1994). This, though, is not true because aspen does not grow from seed either in the southern Canadian Rockies or the western United States (Mitton and Grant 1996). That is to say, if a coniferous forest is burned, aspen will not establish from seed. The only way aspen will "appear" after a burn is if it is already there; i.e. the clones are already established. By eliminating conifers and at the same time stimulating aspen growth, aspen does become more visible after fire, but only when the species is already present. So aspen is not really "seral," instead the presence of aspen indicates a long history of disturbance, primarily frequent fires.

Moreover, previous fire-history studies (Masters 1990; Tymstra 1991) underestimated the importance of fire in maintaining aspen. For aspen, it makes a difference if clones are burned once every 60 years or once every couple of hundred years. As fire-return intervals lengthen, aspen is eliminated (Shepperd and Smith 1993: 167). Noble and Slatyer (1980: 16) found that a 20 to 130 year fire frequency was necessary to maintain aspen in western Montana forests. The fire-return intervals in the southern Canadian Rockies are now longer than that necessary to maintain aspen (Kay et al. 1994).

Since Kootenay National Park was established, for instance, the fire-return interval for the Kootenay Valley increased from 92 to 165 years (Masters 1990). As few aspen trees live more than 100 to 150 years, the near doubling of the fire-return interval has probably contributed to the declining trend of aspen in Kootenay National Park. Moreover, Masters (1990) noted that the fire cycle for the entire park between 1928 and 1988 was in excess of 2700 years, while between 1788 and 1928 it was but 130 years, and between 1508 and 1778 it was only 60 years — this is a 45-fold decrease in the area burned since early historical times. The same is true in Yoho where fire-return intervals are now beyond their range of historical variability, especially in montane areas where most of that park's aspen is found (Tymstra 1991). This lengthening of the fire cycle is due to modern fire suppression and the elimination

of native burning, not climatic factors (Kay et al. 1994; Kay and White 1995; Wierzchowski 1995; Rogeau 1996).

Aspen in Kootenay and Yoho is also declining due to repeated ungulate browsing, primarily by Elk. Where ungulate populations are low, aspen has regenerated without disturbance and stands are multi-aged. At most locations, though, Elk and other ungulates browse all the aspen suckers and prevent height growth. Furthermore, forest succession with large numbers of Elk is different from succession with only a few Elk. It is clear that many "seral" aspen stands in southern Canadian Rockies can produce new stems greater than 2 m tall without disturbance if ungulate browsing is low. Thus, even "seral" aspen can maintain its presence on a site while it "waits" for the next fire to remove the encroaching conifers. So by limiting aspen regeneration, Elk in Kootenay and Yoho have not only contributed to that species' decline, but repeated browsing may also have eliminated some clones that could not "wait" for the next fire. In Yellowstone, repeated ungulate browsing has eliminated approximately one-third of the aspen clones present at park establishment (Kay and Wagner 1996).

Although logging outside Yoho and Kootenay National Parks stimulated aspen sucker production, browsing still prevented aspen height growth and successful regeneration, except where ungulate populations were low. This suggests that even if fire had been allowed to play its historical role for the last 60 years, aspen may still have declined. The very persistence of aspen in the southern Canadian Rockies over the millennia, indicates that ungulate usage, and especially Elk browsing, was not as intense in the past as it is now; i.e., the ecology of aspen suggests that Elk and other ungulate numbers were probably much lower in pre-Columbian times than they are at present — a conclusion supported by historical wildlife observations and archaeologically recovered faunal remains (Kay and White 1995).

Under current conditions, aspen's position in the ecosystem will continue to diminish from historical levels, and species that depend on aspen will also decline. If present trends continue, Kootenay and Yoho will lose the aspen communities that they once contained. The decline of aspen is not unique to the southern Canadian Rockies, but is also occurring throughout the western United States (Cartwright and Burns 1994). As discussed elsewhere, I believe that this decline has a common cause, namely the elimination of aboriginal land management practices; i.e., prior to European influence aboriginal burning stimulated aspen regeneration and native hunting in combination with carnivore predation kept ungulate populations low (Kay 1994, 1995; Kay and White 1995).

Ecological Integrity

According to legislative directives, Canada is to manage her national parks "so as to leave them unimpaired for... future generations [and]... ecological integrity... of natural resources shall be [given] first priority...." (Woodley 1993). If we measure present ecological integrity by the state of the ecosystem that existed before European arrival, as others have proposed (Kay 1991a, 1991b; Woodley and Theberge 1992; Woodley 1993; Woodley et al. 1993; Wagner et al. 1995), then much of the southern Canadian Rockies today lack ecological integrity, especially if the condition and trend of aspen is used as an indicator of long-term ecosystem states and processes. Moreover, as coniferous forests replace aspen and grasslands, wildlife habitat is lost (Van Egmond 1990); i.e., fire suppression and a history of high ungulate populations work in concert to severely reduce ungulate carrying capacity in the future (Kay and White 1995).

Throughout North America, most national parks, wilderness areas, and nature reserves are managed to represent the conditions that existed in pre-Columbian times; i.e., so-called natural or pristine conditions. But what is natural? If Native Americans repeatedly fired the vegetation and in combination with other predators limited ungulate numbers, which, in turn, determined the structure of entire plant and animal communities, that is a completely different situation than letting nature take its course today (Wagner and Kay 1993; Kay 1995; Wagner et al. 1995). Moreover, Canada, like many countries, has chosen to use her national parks as baseline reference areas from which to judge the health of other, more developed ecosystems (Woodley et al. 1993). But again, what is natural? If ecological conditions in Canada's national parks are changing due to reduced predation on ungulates and lack of aboriginal burning, as the ecology of aspen and other data suggest, then are those parks the proper standard with which to measure ecosystem health and ecological integrity in other areas?

It must be remembered, though, that doing nothing, so called "natural regulation" or "hands-off" management, is really a value judgment and a decision that has wide-ranging consequences (Wagner et al. 1995). In Kootenay and Yoho, for instance, following the status quo means, among other things, that (1) Elk will continue to dominate the ungulate community, (2) aspen will continue to decrease and may eventually be eliminated, and (3) biodiversity will continue to decline as aspen communities are lost. In Banff National Park, the Minister of Canadian Heritage mandated Bow Valley Study recently recommended that Parks Canada implement an aggressive prescribed fire program and that steps should be taken to reduce the park's Elk herd so that aspen and other vegetation types can be maintained

at levels approaching their historical abundance (Bernard et al. 1995*; Page et al. 1996a, 1996b). I would suggest that Kootenay and Yoho National Parks implement similar active management programs if those park's biological diversity and ecological integrity are to be maintained.

Acknowledgments

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An Investigation of the Invasive Shrub European Buckthorn, *Rhamnus cathartica* L., near Saskatoon, Saskatchewan

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Introduced to Saskatchewan in the 1930s as a potential shelterbelt species, European Buckthorn (*Rhamnus cathartica* L.) is now a predominant understory shrub in riparian woodland, aspen groves and prairie shrub communities around Saskatoon. The age of the oldest specimen was 56 years. Approximately 90% of the fruits and seeds collected in seed traps were dispersed directly beneath the canopy of the mature shrubs. The mean germination rate of these seeds was 85% with a mean emergence time of 42 days. The buried seed bank beneath mature shrubs averaged 620 seed/m² and was composed entirely of European Buckthorn which favours the development of the characteristic monospecific ground cover. However, there was little evidence that the species is allelopathic. Cutting and application of "Round-up" to the stumps, or spraying "Garlon 4" to the basal bark, proved to be the most effective methods of killing European Buckthorn.

Key Words: European Buckthorn, *Rhamnus cathartica* L., introduction, spread, control, Saskatchewan.

European Buckthorn (*Rhamnus cathartica* L.) is a coarse shrub or small tree that typically grows to a height of 2 to 3 meters (Figure 1). It occurs naturally on calcareous soils throughout England and eastwards into Scandinavia and across Russia into western Asia; the species is common at lower elevations as far south as Morocco and Algeria (Maw 1981). Like other exotic invasive species it is a vigorous competitor that reproduces aggressively and can quickly displace native plants thereby altering the structure of natural communities. It first established in the northeastern United States, and was appearing in taxonomic collections by the 1880s (Wolf 1938). In Canada it is prevalent in southern Ontario, Quebec and the Maritimes where it is found along fences and roadsides, in open woods and on moist, well-drained soils adjacent to lakes and streams. In Manitoba it is mainly found in parks and gardens in urban centres. (Maw 1981).

European Buckthorn was introduced to Saskatchewan in the 1930s as a potential shelterbelt tree with initial trials conducted at the Dominion Tree Nursery in Sutherland, now a suburb of Saskatoon. The species was selected because of its hardiness and ability to tolerate a variety of soils and site conditions. Experiments were soon terminated once it was realized that European Buckthorn was an alternate host to oat crown rust (*Puccinia coronata*), a virulent disease that affects oat seed yield, quality, weight, and protein content (Dietz 1926; Harder and Chong 1983), but not before the species had escaped from cultivation.

European Buckthorn has invaded many sites in the area and is especially prevalent in riparian woodlands and in some aspen groves. It thrives in the shade of other trees and shrubs and has become the

dominant understory species at some sites. The female shrubs produce small drupes that each contain 2 to 4 hard seeds (White et al. 1993). The majority of the seeds remain beneath the parent trees, but the drupes are edible, and despite a bitter taste they are consumed and the seeds dispersed by birds. Buckthorn is commonly found along fencerows, beneath "perch" trees and at the edge of woods. All of these locations suggest bird dispersal. Waxwings (*Bombycilla cedrorum*, *B. garrulus*) which visit the Saskatoon area in large flocks in the winter and early spring are potential vectors. Mature European Buckthorn trees provide shaded microsites that favour prolific seedling establishment (Maw 1981). The ability of European Buckthorn to regenerate quickly after cutting and burning also favours its persistence (Mulligan 1952).

Various aspects of the biology, ecology and control of European Buckthorn in the Saskatoon area are described in this paper.

Methods

Moist, well-shaded sites provide ideal habitat for European Buckthorn, and around Saskatoon it is common at Wanuskewin Heritage Park (located 10 km north of Saskatoon) and Saskatoon Natural Grasslands (SNG) adjacent to the former Dominion Tree Nursery. It is especially prolific along the South Saskatchewan riverbanks, but becomes less prevalent south of Saskatoon where its growth appears to be limited by drier, sandy soils.

a) Age class distribution

Unlike other shrubs in the Saskatoon area, the leaves of European Buckthorn remain green long



FIGURE 1. European Buckthorn (*Rhamnus cathartica* L.). (From Clare, S. 1991. Ontario Ministry of Agriculture and Food. Queen's Printer for Ontario, 1991. Reproduced with permission).

after the native shrubs have lost their foliage. This characteristic was used to initially identify sites infested with European Buckthorn as the species is readily distinguished on colour aerial photographs taken in late fall. The basal diameters of approximately 500 shrubs were measured and the shrubs then felled. Discs taken from the cut stumps were polished with sandpaper and then treated with oil. Each disc was placed under a low-power binocular microscope and the annual rings counted. Age-diameter relationships were calculated and subsequently used to establish age-class distributions for the local populations.

b) Fruit fall

Three large female shrubs on Yorath Island (52° 05'N, 106° 43'W), approximately five kilometers south of Saskatoon, were used to monitor the fall of mature fruits. The fruits were collected in wooden trays (50 cm × 50 cm) with wire mesh bottoms; they were placed at 1, 2, 3 and 4 m along each of three transects radiating from the base of each tree. The trays were set out in October and retrieved the following spring.

c) Factors affecting germination

Seeds collected from the canopy and from the litter layer were used to determine germination rates and the size of the seed bank. Some seeds were sown into soil, others were placed in petri dishes and germination was defined as emergence of the shoot or radicle. Initial trials were conducted to determine if the seeds must be removed from the pulpy fruits before germination will occur. For these experiments the fruits were treated as follows: samples of 200 fruits were either left intact and placed on filter paper in petri dishes or were placed intact between wet paper toweling; in a third sample 200 seeds were manually removed from the fruits then placed on filter paper in petri dishes. Additional seeds removed from the fruits were kept submerged in distilled water for short (three weeks) and long (two months) periods in an attempt to simulate natural flooding regimes in riparian habitats. Germination was carried out under fluorescent lights set to a 16 hr photoperiod at room temperature. The material was checked daily and germinated seeds were counted and removed. Germination rates were compared with a control group of unsoaked seeds. The fruits used in these experiment were collected in March of 1995, and so had been subjected to the natural overwintering cycle.

d) Seeding numbers and seedbank

Seedling counts were made in 15 1 m × 1 m quadrats beneath a dense European Buckthorn stand. Initial counts were made in September 1995 and recounted in April 1996. Samples of the surface soil layer were collected to a depth of 10 cm using a 10 cm diameter coring tool to determine the size and composition of the viable seed banks beneath a dense European Buckthorn stand. The soil was transferred into plastic trays; germination conditions were as described above.

e) Allelopathic effects

The possibility that European Buckthorn is allelopathic was tested by applying root and litter leachate to seeds and seedlings of other species. A leachate column was constructed using a glass tube with a perforated base. Air-dried litter collected from a dense European Buckthorn stand in the spring of 1995 was placed in the leachate column and distilled water was passed through it. The leachate was collected in a bottle. In a subsequent experiment root leachate was produced by removing the roots from European Buckthorn seedlings and saplings and placing them in a blender with distilled water until liquefied. The suspension was filtered and bottled. Distilled water was used as the control in these experiments. Tomato, lettuce, and radish seeds were selected as test seeds because of their rapid germination rates and their relative sensitivity. Trays containing six seeds of the test species were set out on

the germination bench. Replicate litter and root leachates and distilled water treatments were used in each test which was repeated four times.

Similar experiments were conducted on seeds in petri dishes; in this case germination was defined as the emergence of the radicle. In a further test small European Buckthorn saplings with established root systems were planted in field soil in 15 cm plastic pots. The saplings were left for six days to adapt to conditions in the laboratory before adding four tomato and four lettuce seeds to each pot.

(f) Management

Potential control methods were tested at one field site. Here a sample of 120 European Buckthorn shrubs was randomly selected. Each tree was cut off at the base and subsequently treated with herbicide or fire; some were left untreated to serve as the control. In the herbicide treatment a 1:1 ratio of chemical to water was applied by wicking or wiping the cut face of the stump. "Round-up" (glyphosate) and "Killex" (2,4-D, mecoprop and dicamba) were evaluated in these trials. In the burning treatment stumps were girdled with a propane torch which applied a temperature of approximately 1000°C to the cambium layer for a duration of 2 to 3 minutes. Studies have shown that typical fire temperatures in shrubby vegetation in this area typically reach a maximum of 500–700°C for 20 to 30 seconds and soil temperatures increase only slightly (O. W. Archibold, L. J. Nelson, E. A. Ripley, and L. Delanoy. Fire temperature in selected vegetation communities of northern mixed prairies). The simulated fire applied in this study was therefore of greater intensity and longer duration than in a natural fires. In subsequent trials, a

5 cm wide band of Garlon 4 (triclopyr) mixed with diesel fuel was sprayed to one side of selected European Buckthorn stems about 30 cm above ground level. This streamline treatment was applied to dormant shrubs in late-December.

Results and Discussion

a) Age class distribution

The oldest European Buckthorn shrub recorded in the survey was 56 years old and located at Wanuskewin Heritage Park. This compared to maximum ages of 51 years at Petturson's Ravine and 44 years at SNG. Once the species is established *in-situ* seed production produces a vigorous young population (Figure 2). Although SNG is close to the point of first introduction to Saskatoon, the oldest shrubs were considerably younger than at Wanuskewin and Petturson's Ravine located several kilometers away. The reasons for this are unclear, but could be related to intensity of grazing, soil conditions, and availability of perch sites in native shrubs and aspen (*Populus tremuloides*).

b) Fruit fall

A total of 249 European Buckthorn fruits and an additional 174 seeds were collected in the seed traps. Approximately 90% of these fruits and seeds fell directly beneath the canopy of the female shrubs. This would favour the development of the dense understory of seedlings which is so characteristic of European Buckthorn stands.

c) Factors affecting germination

The results of the germination trials suggest that the seeds need to be removed from the fruits for germination to occur. In experiments with intact fruits

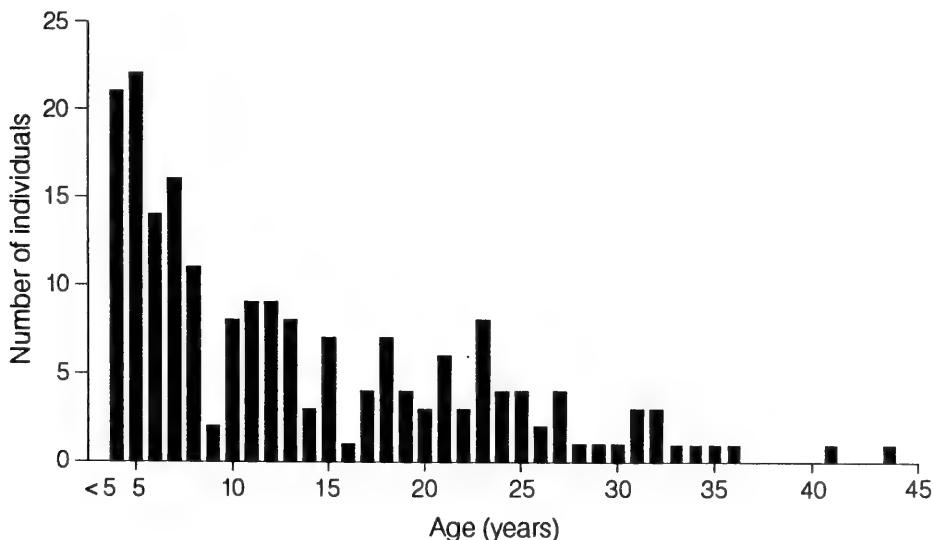


FIGURE 2. Buckthorn age-class distribution at SNG shows how the population density steadily increases once a few pioneering individuals become established. Current year seedlings average 124 m⁻² and are omitted.

no seedlings emerged. Seedling emergence for seeds extracted from the fruits began after 25 days. Peak emergence occurred after 34 to 40 days with a mean time to emergence of 42 days. The mean emergence rate for extracted seeds was $87.5 \pm 1.7\%$. Presumably under natural conditions the pulp rots away or is consumed by animals. This may delay the germination until the spring following fruit dispersal when the seedlings would have the entire growing season in which to become established.

The results of the immersion suggest that prolonged high water levels may be detrimental to seed germination. A slight decline in germination was noted in seeds following immersion for two weeks. The mean germination rate for these seeds was $77 \pm 2.5\%$ with a mean time to emergence of 44 days. No germination occurred in seeds that were immersed for two months prior to planting. Prolonged high water levels during spring runoff could therefore regulate the spread of European Buckthorn in low-lying riparian habitats. Areas with naturally high water tables, such as slough margins and springs may also be less prone to invasion.

d) Seedling numbers and seedbank

The number of seedlings recorded at the end of the first growing season averaged $110.8 \pm 16.0 \text{ m}^{-2}$. By early spring the following year this had increased to $123.7 \pm 19.0 \text{ m}^{-2}$, an average increase of $11.5 \pm 5.3\%$. One of the sample quadrats was adjacent to a game trail that traversed the stand and the soil was very compact. Compared to the other quadrats seedling density is low at this point (73 seedlings m^{-2} in 1995 and 74 seedlings m^{-2} in 1996), but even here European Buckthorn dominated the ground layer.

European Buckthorn seedlings emerged from all of the soil samples collected from beneath a European Buckthorn stand. The calculated density of viable seeds was 620 m^{-2} in the surface 10 cm of soil. Mean emergence time for these seedlings was 28 days, which was noticeably less than that for seedlings originating from freshly harvested seeds. The results indicate how prolific fruit production coupled with high germination rates could allow European Buckthorn to rapidly dominate an understory.

e) Allelopathic effects

No other species emerged from these soil samples which raised the possibility that European Buckthorn may have allelopathic properties which inhibit germination and growth of potential competitors. However, little evidence of allelopathy was found in the various experiments that were conducted. Tomato, lettuce and radish seeds sown in potting soil and treated with either litter or root leachate all exhibited 100% germination, with a mean emergence time of 19 days; this was considerably less than the 42 days noted for emergence in seeds treat-

ed with distilled water. Similar results were noted when the seeds were germinated on moistened filter paper. Germination was 100% in all seeds treated with leachates with average emergence times of 2 days for radish and tomato and 1 day for lettuce. This compared to emergence rates in distilled water of 50% for radish, 33% for lettuce and 17% for tomato; corresponding emergence times were averaged 3, 2 and 4 days, respectively. Germination of lettuce was 100% in the experiments using European Buckthorn saplings, and radish germination was reduced to 88%. The results of these various experiments suggest that allelopathy does not account for the dearth of species beneath European Buckthorn. However, the experiments did not examine the effects of leachates from the leaf canopy or on the various native species in the study area. The possibility that European Buckthorn may be allelopathic has also been suggested by Boudreau and Willson (1992) who noted that native and exotic species reappeared in treated areas within three months of cutting and application of herbicide.

f) Management

The results of the control trials indicated that a single-event fire was ineffective in controlling the growth of European Buckthorn, and that "Killex" also had only a minimal effect. The fire treated stumps reemerged in the spring and developed vigorously. The new leaves were larger than those on untreated shrubs and the crown was also denser than on untreated individuals of similar size. However, there is evidence that successive fires can reduce the density of European Buckthorn (Boudreau and Willson 1992; Heidorn 1991); it is particularly effective against seedlings, although the paucity of litter in such sites makes it difficult for the fire to carry through the stand. The stumps treated with "Killex" grew back in a similar fashion, as did the control stumps that had been left untreated. "Round-up" was the most effective control method. Only 6% of the stumps treated with "Round-up" showed signs of resprouting and these plants were much less vigorous than in other treatments. "Garlon 4" also curtailed growth in about 70% of the European Buckthorn treated with this herbicide. A small amount of new growth was noted in the remaining 30% of the treated shrubs at the end of the growing season following herbicide application; typically this new growth consisted of a single shoot less than 10 cm in height.

Conclusion

The control of European Buckthorn is an important issue for the Meewasin Valley Authority which manages the river bank and other natural areas around Saskatoon. Highest priority has been given to controlling European Buckthorn from conservation

areas. Control is conducted on a site-by-site basis with the goal of restoring the mix of native species. Based on the present study it is recommended that management efforts initially concentrate on the removal of female shrubs as this would reduce the number of seeds that are contributing to the seed bank. Careful monitoring of natural areas with "perch trees" and adjoining fencelines could help to reduce the spread of this vigorous species. The good results achieved with "Garlon 4" coupled with ease of application warrants further trials. As well as being cost-effective this method can also be used well into dormancy. This not only extends the working season, but can have the added advantage of eliminating the "brown-out" phase during which time unsightly dead leaves remain on the tree. Such treatment would also prepare the stand for a subsequent burn intended to kill seedlings.

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Status of the White-top Aster, *Aster curtus* (Asteraceae), in Canada*

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Douglas, George W., and Jeanne M. Illingworth. 1997. Status of the White-top Aster, *Aster curtus* (Asteraceae), in Canada. *Canadian Field-Naturalist* 111(4): 622-627.

In Canada, White-top Aster, *Aster curtus*, is restricted to southeastern Vancouver Island and some adjacent small islands. Eight of the 16 extant sites are located in the Greater Victoria area. Colonies at 12 sites have been confirmed in recent years but the status of colonies at four other sites remains unknown (Table 1). An additional six sites are likely extirpated. Confirmed colonies at these sites collectively represent the northern range limit of *A. curtus*. Threats to confirmed colonies vary in intensity. Although some colonies are protected to a certain extent from direct habitat destruction, introduced species pose a serious threat to the continued existence of most colonies particularly those that have small numbers of plants. Managing sites for *A. curtus* is difficult given the lack of information regarding the biology and ecology of this plant, its competitive interactions with other species, and factors controlling the establishment, growth and maintenance of colonies. Even if confirmed sites where this species occurs in Canada could be preserved, active management may be required to ensure the continued existence of the Canadian colonies.

Key Words: White-top Aster, *Aster curtus*, British Columbia, threatened, distribution, population size.

The White-top Aster, *Aster curtus* Cronquist, is a member of a genus of about 250 species, most of which occur in North America (Cronquist 1955). It is one of 23 species occurring in British Columbia (Douglas 1989, 1995) and about 52 occurring in Canada (Scoggan 1979). *Aster curtus* is not known to have any medicinal or economic uses.

Some western taxonomists (e.g., Ferris 1960; Peck 1961) have treated this taxon as *Seriocarpus rigida* Lindl. in Hook. rather than follow the lead of Cronquist (1955), who placed it in the genus *Aster*. It would appear that most recent taxonomists (e.g., Scoggan 1979; Argus and Pryer 1990; Jones 1980; Straley et al. 1985; Douglas 1989, 1995; Douglas et al. 1997; Kartesz 1994), however, agree with Cronquist's (1955) treatment.

Aster curtus is a leafy, erect plant, ranging from 10 to 30 cm tall with broadly lanceolate, alternate leaves 2.5 to 3.5 cm long (Figure 1). Both the lower and upper leaves are reduced. The 5 to 20 flower heads are borne on short stalks in a terminal inflorescence. The involucre bracts are narrow and the ray flowers are white, few and inconspicuous. The disk flowers are pale yellow with purple anthers.

Distribution

Aster curtus occurs on the west coast of North America from southwestern British Columbia to western Washington and northwestern Oregon. In

Canada, it is restricted to southeastern Vancouver Island and some adjacent small islands (Figure 2).

Habitat

Aster curtus tends to occupy very dry microsites where soils are shallow and sites are exposed or partially shaded by individual trees. Trees such as Garry Oak (*Quercus garryana*) and Arbutus (*Arbutus menziesii*) are often present, but do not form a closed overstorey. An open understorey of shrubs (e.g., Scotch Broom [*Cytisus scoparius*], Ocean Spray [*Holodiscus discolor*] and Common Snowberry [*Symphoricarpos albus*]) are also commonly found. They do not form dense thickets, as they do in other areas, possibly because the soils are too shallow. The vegetation tends to be dominated by a mixture of introduced grasses such as Early Hairgrass (*Aira praecox*), Orchardgrass (*Dactylis glomerata*), Hedgehog Dogtail (*Cynosurus echinatus*) and Sweet Vernalgrass (*Anthoxanthum odoratum*). The latter species are usually frequent in the meadows in which *Aster curtus* occurs. Soils vary from shallow, dark brown to brownish-red brunisols.

General Biology

Each year the shoots of *Aster curtus* emerge in April from the over-wintering rhizomes. In Washington, Gamon and Salstrom (1992) found that a typical colony covered a 1 to 2 m² area with 5 to

*This paper is based primarily on a COSEWIC status report by the authors. It has been revised to include more recent information. The species was designated threatened by COSEWIC in April 1996. The original report is available from the COSEWIC Secretariat, c/o Canadian Wildlife Service, Environment Canada, Ottawa, Ontario, K1A 0H3.

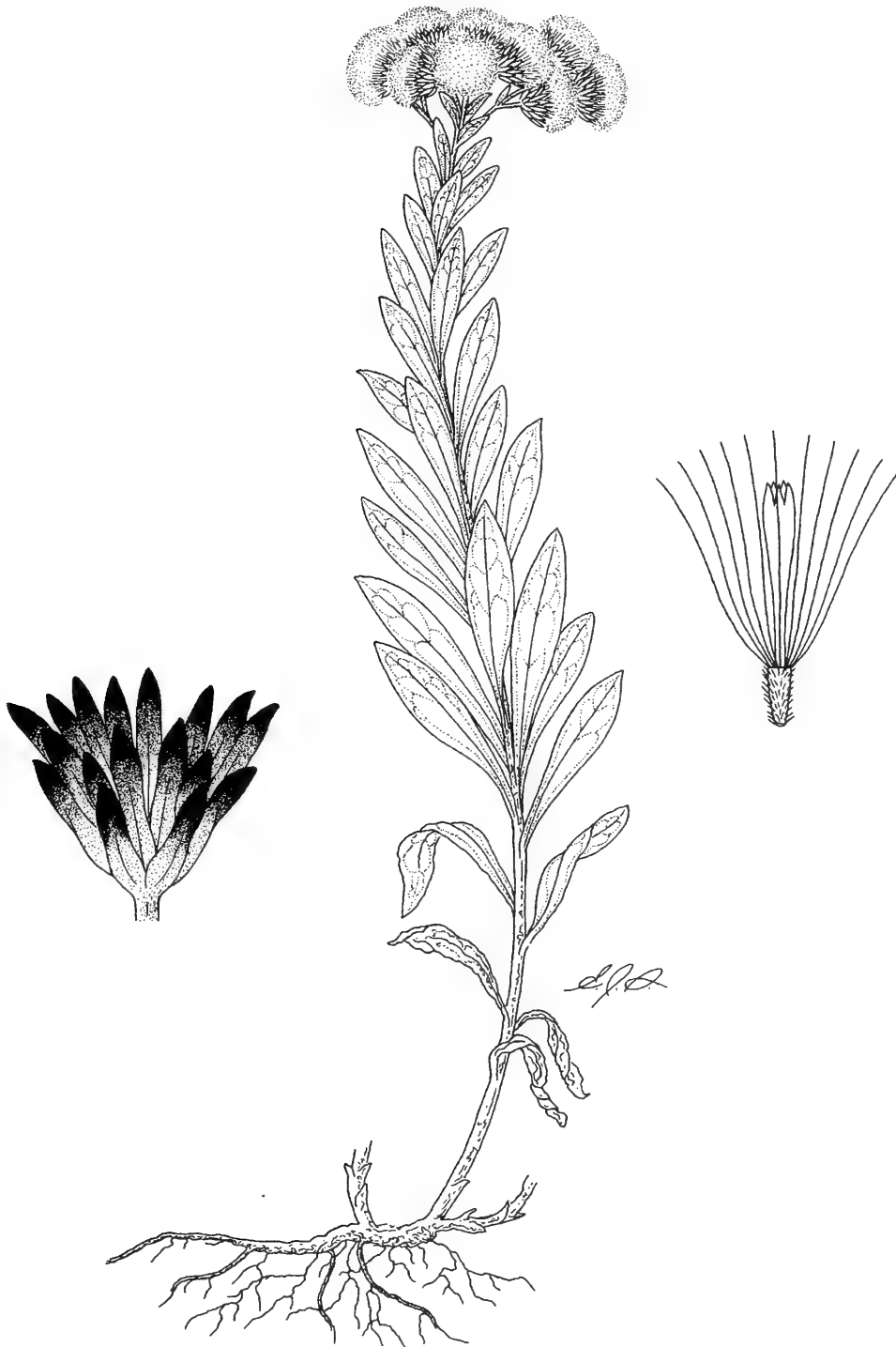


FIGURE 1. Illustration of *Aster curtus*. Line drawing by Elizabeth J. Stephen in Douglas (1995).

30% of the stems bearing flowers. Colonies surveyed in British Columbia in July and August had slightly higher counts of 30 to 50%. Seedlings were not observed in the field. *Aster curtus* probably reproduces primarily by vegetative means. Since seed viability is very low, growth of seedlings is extremely slow and the seedlings are poor competitors (Clampitt 1987), the successful establishment of seedlings is infrequent.

Population Size and Trends

Aster curtus has been collected or observed at 22 sites in Canada with all of these colonies located in British Columbia on southern Vancouver Island or adjacent islands (Table 1). Six of these sites (one in Nanaimo and five in Victoria) are considered extirpated. Twelve of the remaining 16 sites were either resurveyed or discovered during the present study. Colony areas are usually small with the three largest

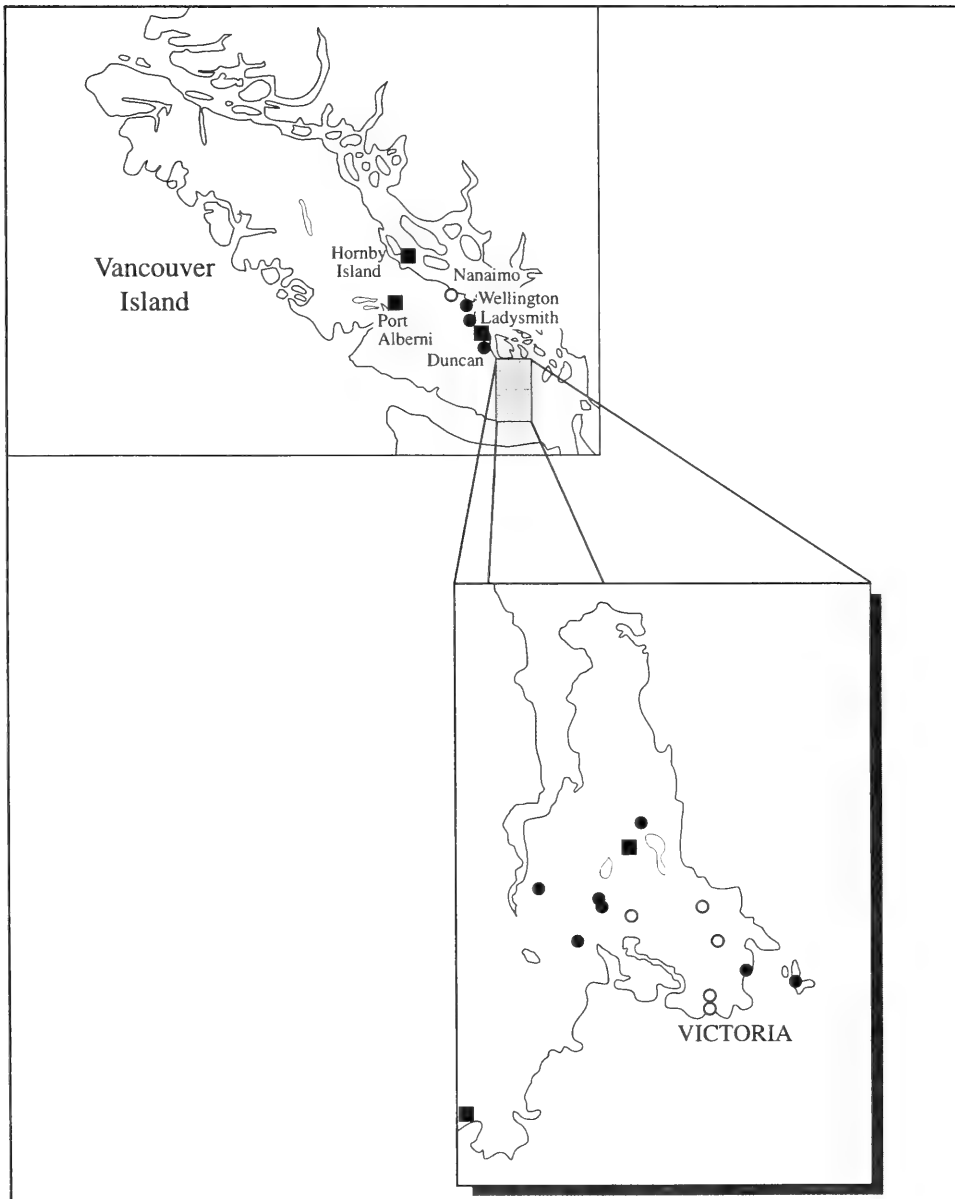


FIGURE 2. Distribution of *Aster curtus* in British Columbia. (○ – extirpated sites, ■ – unconfirmed sites, ● – recently confirmed sites)

ranging from 125 to 300 m². Individual plant stems were fairly high, considering the limited areas covered, ranging from 200 to 1200 stems/site.

Only two of the sites (Mount Tzuhalem and Uplands Park) have been observed with respect to colony trends. During a three-year time period the latter colonies maintained their size and stem numbers within 10% of their maximums. A slight decrease at Mt. Tzuhalem was due mainly to the efforts of members of a local natural history society who, during a *Cytisus scoparius* removal program, piled and burned the shrub on a sizeable *Aster curtus* colony.

Limiting Factors

The major threat to *Aster curtus* is habitat destruction. This is of particular concern in the

grass-dominated meadows often associated with the *Quercus garryana*-*Bromus* communities that are limited to the southeastern side of Vancouver Island and some of the Gulf Islands. Both types of vegetation are believed to have been much more common before colonization by European settlers. Their destruction has continued to the present resulting in the elimination of almost all sites occurring outside parks or ecological reserves. Historically, *Quercus garryana* communities and grass-dominated meadows have always been heavily influenced by human activity. Roemer (1972) believed that without human interference some of these stands would have eventually been replaced by Douglas-fir *Pseudotsuga menziesii* forests.

TABLE 1. Location of *Aster curtus* sites in Canada.

Collection Site	Last Observation	Collector	Colony (no. stems/area)
Nanaimo	1887	J. Macoun	Extirpated
Cedar Hill (Victoria)	1897	J. R. Anderson	Extirpated
Foul Bay (Victoria)	1914	J. Macoun	Extirpated
Gonzales (Victoria)	1924	G. Hardy	Extirpated
Lost Lake (Victoria)	1945	G. Hardy	Extirpated
Knockan Hill Park, west of (Victoria)	1968	H. Roemer	Extirpated
Little Saanich Mountain (Victoria)	1976	A. Ceska	Unknown
Maple Mountain (Duncan)	1976	A. Ceska	Unknown
South Wellington	1982	A. Ceska	15/5 m ²
Port Alberni	1983	W. Van Dieren	Unknown
Sooke	1985	A. Ceska	30/4m ²
Downes Point (Hornby Island)	1986	A. Ceska	20/5 m ²
Woodley Range (Ladysmith)	1992	C. Cadrin	500+/300 m ²
Trial Island (Victoria)	1993	G.W. Douglas	200+/30 m ²
Francis-King Park, south of (Victoria)	1993	M. Ryan	Unknown
Mt. Finlayson (Victoria)	1993	M. Ryan	200/4 m ²
Cordova Bay (Victoria)	1993	M. Ryan	600/36 m ²
Mill Hill (Victoria)	1994	J. M. Illingworth	1200+/250 m ²
Francis-King Park (Victoria)	1994	G. W. Douglas	450/16 m ²
Bear Hill Park (Victoria)	1995	J. M. Illingworth	300/40 m ²
Mt. Tzuhalem Ecological Reserve (Duncan)	1996	G. W. Douglas	1200/250 m ²
Uplands Park (Victoria)	1996	G. W. Douglas	600/40 m ²

The suppression of fire within the past century may have contributed to the demise of *Aster curtus* populations. Most of the sites in which *A. curtus* has been collected were likely maintained in the past as a result of periodic fires, both natural and unnatural. In the past, aboriginal peoples probably set fire to these stands to maintain them as an important habitat for wildlife and for the continued harvesting of Camas (*Camassia* spp.), a member of the Liliaceae (Roemer 1972; Turner and Bell 1971). Since that time, these sites have experienced little disturbance, resulting in the invasion and expansion of many other species, especially introductions.

The introduction of European species has resulted in substantial changes, not only to the grass-dominated meadows associated with *Quercus garryana*, but also to the rocky xeric sites north and west of Victoria where *Aster curtus* has been collected in the past. One of the most devastating species is *Cytisus scoparius* which has become a dominant shrub on xeric, exposed sites throughout much of eastern Vancouver Island and the Gulf Islands. Much of the vegetation is now dominated by introduced grasses. These species include *Aira praecox*, *Anthoxanthum odoratum*, *Cynosurus echinatus* and *Dactylis glomerata*.

Special Significance of the Species

Aster curtus is a member of a relatively small group of species with a restricted Pacific Coast range that have their northern limits in southern

British Columbia. The significance of these peripheral populations, especially with respect to their genetic characteristics, has yet to be studied adequately. This species may prove to be a fruitful subject for genetic research.

Protection

There is no specific legislation for the protection of rare and endangered vascular plants in British Columbia. The British Columbia Conservation Data Centre has ranked this species as S1³ and placed it on the Ministry of Environment, Lands and Parks Red list. This is the most critical category for imperiled rare native vascular plants in the province. In the remainder of its range, this taxon

³S ranks, for provincial or state rare elements, are those of The U.S. Nature Conservancy. The ranks are defined as follows:

- S1 – “critically imperiled because of extreme rarity (5 or fewer extant occurrences or very few remaining individuals) or because of some factor(s) making it especially vulnerable to extirpation or extinction”.
- S2 – “imperiled because of rarity (typically 6-20 extant occurrences or few remaining individuals) or because of some factor(s) making it vulnerable to extirpation or extinction”.
- S3 – “rare or uncommon; (typically 21-100 occurrences); may be susceptible to large-scale disturbances; e.g., may have lost extensive peripheral populations”.

has been ranked S2 by the Oregon Natural Heritage Program and S3 by the Washington Natural Heritage Program, where there are 24 and 48 known sites, respectively (Gamon and Salstrom 1992).

Some colonies of *Aster curtus* are protected to a certain extent by their location on public property. Of all the *A. curtus* colonies known in British Columbia, those located on Mount Tzuhalem and Trial Island receive the greatest degree of protection because of their location within ecological reserves. The Mount Tzuhalem Ecological Reserve encompasses 18 ha of *Quercus garryana* woodland, spring-flowering meadows, and rock outcrops which have been preserved to represent an example of *Q. garryana* woodlands and associated spring-flowering herbs. Unfortunately, *Cytisus scoparius* has become a dominant species at this site and threatens many herbaceous species, including *Aster curtus*. All of the plants in this reserve are located along trails thus there is some danger from trampling. The Trial Island Ecological Reserve probably provides the greatest degree of protection for any of the *A. curtus* populations. This reserve, despite its close proximity to Victoria, has very limited access since it can be reached only by boat and a government permit is required for landing.

The Woodley Range site, near Ladysmith, is presently on Crown Land with much of the site included within a forest harvest area. The presence of a number of rare plants, including the only recently confirmed site for *Lotus pinnatus* in Canada, has made this area a candidate for Ecological Reserve status. Until a reserve has been formally established, the continued presence of *Aster curtus* at the site will remain in jeopardy.

The Mount Finlayson site which is an extremely rich area for rare plants, is located west of Victoria and was designated as a Provincial Park in 1994. When management plans are in place, rare plants should receive a higher degree of protection than they previously had on private land.

A number of *A. curtus* colonies are in small regional parks in the Greater Victoria area. These include colonies at Bear Hill Park, Francis-King Park, Mill Hill Park and Uplands Park. These parks receive little active management, at least with respect to their rare plants. Park enhancement projects, road and trail developments and heavy recreational use by humans often result in the destruction of the native vegetation and rare plant species.

Evaluation of Status

Aster curtus is considered, by COSEWIC and the British Columbia Conservation Data Centre to be threatened in Canada and is known only from 16 extant colonies restricted to southeastern

Vancouver Island and some adjacent islands. Some colonies are limited to just a few hundred individuals and may be in danger of extirpation. The prognosis for this species is not good considering the threats posed by aggressive competitive species such as *Cytisus scoparius* which dominate many suitable habitats and directly threaten some colonies. Therefore, even if all colonies were protected from human interference, many colonies may eventually disappear as a result of aggressive competitive species. Likewise, much of the *Quercus garryana* vegetation in which *Aster curtus* is usually found has been extensively altered or destroyed, thus limiting the potential for new sites at which this species might become established.

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Notes

A Probable Case of Polyterritorial Polygyny in the Red-eyed Vireo, *Vireo olivaceus*

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Mountjoy, D. James. 1997. A probable case of polyterritorial polygyny in the Red-eyed Vireo, *Vireo olivaceus*. *Canadian Field-Naturalist* 111(4): 628–630.

A male Red-eyed Vireo (*Vireo olivaceus*) was observed to defend two territories separated by more than 100 m and the territory of another male. The polyterritorial male fed nestlings (Brown-headed Cowbirds, *Molothrus ater*) at a nest on one territory while associating with a female that may have had an active nest on the other territory. This observation represents one of a small number of cases of polyterritorial behaviour among North American passerines and the first report of probable simultaneous polygyny in the Vireonidae.

Key Words: Red-eyed Vireo, *Vireo olivaceus*, polyterritoriality, polygyny, mating systems.

The prevailing mating system for all species of the family Vireonidae is believed to be social monogamy (Hamilton 1962; Ford 1983; Ehrlich et al. 1988). Some “Least” Bell’s Vireos (*Vireo bellii pusillus*) are reported to be “sequentially polygynous” and “sequentially polyandrous”; i.e., they switch mates between nesting attempts; and simultaneous polygyny and simultaneous polyandry are suspected to occur occasionally (Brown 1993). Similarly, Black-capped Vireos (*Vireo atricapillus*) may be “sequentially polygynous” or “sequentially polyandrous”, and some females that switch mates for a second nesting attempt may continue feeding fledglings on the previous territory, which may be considered simultaneous polyandry (Grzybowski 1995). The Red-eyed Vireo (*Vireo olivaceus*) is perhaps the most abundant species in the genus *Vireo*, and has been relatively well studied (Lawrence 1953), but polygyny has not been documented previously in this species.

In this note I describe an instance of apparent polyterritorial polygyny in the Red-eyed Vireo. The male vireo defended two distinct territories (as indicated by responses to playback of recorded song) separated by the territory of another bird and unsuitable habitat. The polyterritorial male was paired and participated in a nesting attempt on one territory, and associated with a female that may have had an active nest on the other territory. A more complete account of these observations is outlined below.

On 19 May 1994, at Schramm Park State Recreation Area in Sarpy County, Nebraska (41°01'N, 96°15'W), I captured two Red-eyed

Vireos which flew into the same mist-net within approximately 10 s of each other. Playback of Red-eyed Vireo song lured the birds into the net, and the agitated response of the birds before they flew into the net indicated an obvious territorial response. A singing male had been noted in the area of capture (‘Territory A’) since 14 May, so one of the birds was probably this male, and the other bird a female. The two birds were not readily sexed on the basis of cloacal protuberance or brood patch development but the second bird to enter the net was smaller than the first bird in measurements of flattened wing chord, tarsus and exposed culmen although it weighed 15.7% more than the first bird. Each bird was banded before release with an aluminum Fish and Wildlife Service band and three colored plastic bands for individual identification, and subsequent behavioral observations confirmed that the first bird (#404) was a male and the second bird (#405) was a female.

On 20 June 1994, I discovered a vireo nest which contained two large Brown-headed Cowbird (*Molothrus ater*) nestlings (estimated to be 9–10 days old). The nestlings were being fed by male #404 and female #405, although the nest site was approximately 310 m to the southwest of the location where these birds had been captured in May, a distance considerably larger than the typical diameter of a Red-eyed Vireo territory (Lawrence 1953; Godard 1993; personal observation). This territory (‘Territory B’) was separated from Territory A by a clearing that was approximately 60 m wide and by the territory of another pair of Red-eyed Vireos adjacent to Territory

A. As a singing male had been noted throughout the intervening time in Territory A where the pair originally had been caught, I attempted to determine whether male #404 was still occupying that area. A singing male heard in Territory A on 21 June and 23 June was not seen well enough to determine whether it was banded. On 27 June playback of Red-eyed Vireo song was used to attract the male, and it approached closely enough to be seen well and was confirmed by its band combination to be male #404. Although this male was not positively identified by band combination on Territory A in the time period between 19 May and 27 June, there is no evidence that any other male occupied this territory and it is most parsimonious to assume that the male frequently heard singing on this territory was in fact male #404.

Although an active nest was not discovered on Territory A, it appeared that male #404 was paired to a second female there and that this male was probably involved in two overlapping nesting attempts. On 24 June I used play-back of Red-eyed Vireo song in an attempt to elicit a response from the male on Territory A, but the only bird that approached was an unbanded vireo that quivered its wings but did not sing. Wing-quivering is frequently observed in females that approach playback, but I have not noted it in males (Mountjoy, unpublished observations). On 27 June an unbanded bird, presumed to be a female, was associating with male #404 on Territory A, and I observed that this bird visited a particular group of trees several times. I did not find a nest then. On 29 June I noted that the commencement of song by the male near the suspected nest area resulted in the female promptly giving twittering contact calls from that group of trees. Later, the male also was seen approaching the suspected nest area, but the foliage within those trees was too dense to follow the bird further. On 22 January 1995, after most leaves had fallen, I returned to this area and found a nest of typical vireo construction in the group of trees which had been frequented by the vireos. The nest was suspended at a height of approximately 10 m in the fork of a branch of a Basswood (*Tilia americana*). The nest appeared to be largely intact and thus was probably constructed in the 1994 breeding season. No vireos of other species were detected in that area of the park during the breeding season, and it is presumed that this nest was built by the unbanded female observed with male #404.

It is not clear when the two territories were established, but it appears that Territory B was originally occupied by a male other than male #404. An unbanded male that frequently sang a distinctive song type was observed in this area between 11 May and 18 May but it apparently shifted its territory to the south by 20 May. On 20 May and subsequently, I noted a male singing in the Territory B area that did not sing the distinctive song type, but it is not known for certain whether this was male #404. Based on the

advanced stage of the nest in Territory B when it was found, however, the nesting attempt must have been initiated by 29 May or earlier.

Both male #404 and female #405 returned to the study area in 1995, but were paired with different birds. In 1995 (and again in 1996), male #404 occupied an area that was essentially the same as its second territory in 1994, and was not seen in the area of its original 1994 territory. Female #405 was discovered building a nest on 31 May 1995, approximately 70 m NNE of the location where it was captured in 1994.

The polyterritorial behaviour of male #404 is noteworthy as polyterritoriality has been documented in only 11 species of North American passerines (Ford 1995), although it appears to be a frequent spacing system in European passerines (Møller 1986). Polyterritoriality may be under-recorded in North American passerines. It has been suggested that polyterritoriality may be favored by low breeding densities and low male competition (Slagsvold and Lifjeld 1988). The present case appeared to be consistent with that pattern, as the upland forest dominated by oak (*Quercus* spp.), hickory (*Carya* spp.) and Eastern Red Cedar (*Juniperus virginiana*) in which Territories A and B were located was characterized by larger vireo territories and a higher proportion of unoccupied habitat than the lowland flood plain forest within the same park.

It was also unusual that female #405 moved with male #404 from the original territory to the second territory. It has been hypothesized that polygyny in polyterritorial species results from females being unaware of the second territory held by the male at the time of pairing (Haartman 1969), perhaps because search costs prevent females from surveying a wide area intensively. In the intensively studied Pied Flycatcher (*Ficedula hypoleuca*), males that have attracted a female in their first territory then establish a distant territory and try to attract a second female there (Slagsvold and Lifjeld 1988); females do not shift territories. Female #405 certainly was able to observe that male #404 was advertising on two separate territories, although this may not have been important if this bird was the primary female of male #404, and if males provide more parental care to primary nests than secondary nests. The observations presented here suggest that, at least in some cases, polyterritorial polygyny may result from a different pattern of behavior than the typical scenario of a secondary female being attracted to a later-established territory.

This appears to represent the first published evidence for the probable occurrence of simultaneous polygyny in any vireo species, but polygyny may occur somewhat more frequently than has been documented. Few studies have been made of species in this genus in which birds were marked for individual

identification, and it would be easy to overlook polygyny if birds were not individually recognizable. Several observations made at Schramm Park suggested that occasionally more than one female may nest on a Red-eyed Vireo territory, but as most females in the population are unbanded this has not been confirmed.

Acknowledgments

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The Northernmost Extension of the Moss *Pleurozium schreberi* (Brid.) Mitt. in the Canadian High Arctic

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Kuc, Marian. 1997. The northernmost extension of the moss *Pleurozium schreberi* (Brid.) Mitt. in the Canadian High Arctic. *Canadian Field-Naturalist* 111(4): 630–633.

The new northernmost locality of the moss *Pleurozium schreberi* (Brid.) Mitt. from the Alexandra Fiord area (79°42'W, 70°15'N) is discussed in respect to its recent and fossil records in the Canadian Arctic. An updated global range of the species is presented.

Key Words: *Pleurozium schreberi*, Alexandra Fiord, Canadian High Arctic, range extension.

A study of plants whose ranges terminate in the Arctic is one of the fundamental areas of research in plant geography. A review of the literature and examination of herbarium specimens reveals on the Canadian Arctic Archipelago 156 moss species belong to this category of plants, 67 of which are well known and 89 which need more investigation. This is half of the 339 moss species reported from this area without consideration of doubtful taxa, forms and varieties raised up to a rank of species, or records needing further examination. For these reasons the figures cited above differ slightly from analogous counts based on the Checklist of the Mosses of Canada II (Ireland et al. 1987).

Pleurozium schreberi (Brid.) Mitt. is one of those 67 well-known species, but it has a greater cognitive significance than other mosses because of its pre-Pleistocene fossil records which provide insight into the geological history of this region and suggest the origin of ranges of other moss species. It is an old historic element of which fossils are known from the mid-Tertiary (Jovet-Ast 1967, and literature cited therein). On the Canadian Arctic Archipelago *P. schreberi* is known from the late Pliocene (Kuc 1973; Matthews and Ovenden 1990; Matthews, Ovenden and Fyles 1990; Miller 1984; Ovenden 1993) in Beaufort Formation deposits. Its postglacial history is intriguing because the present range of *P.*

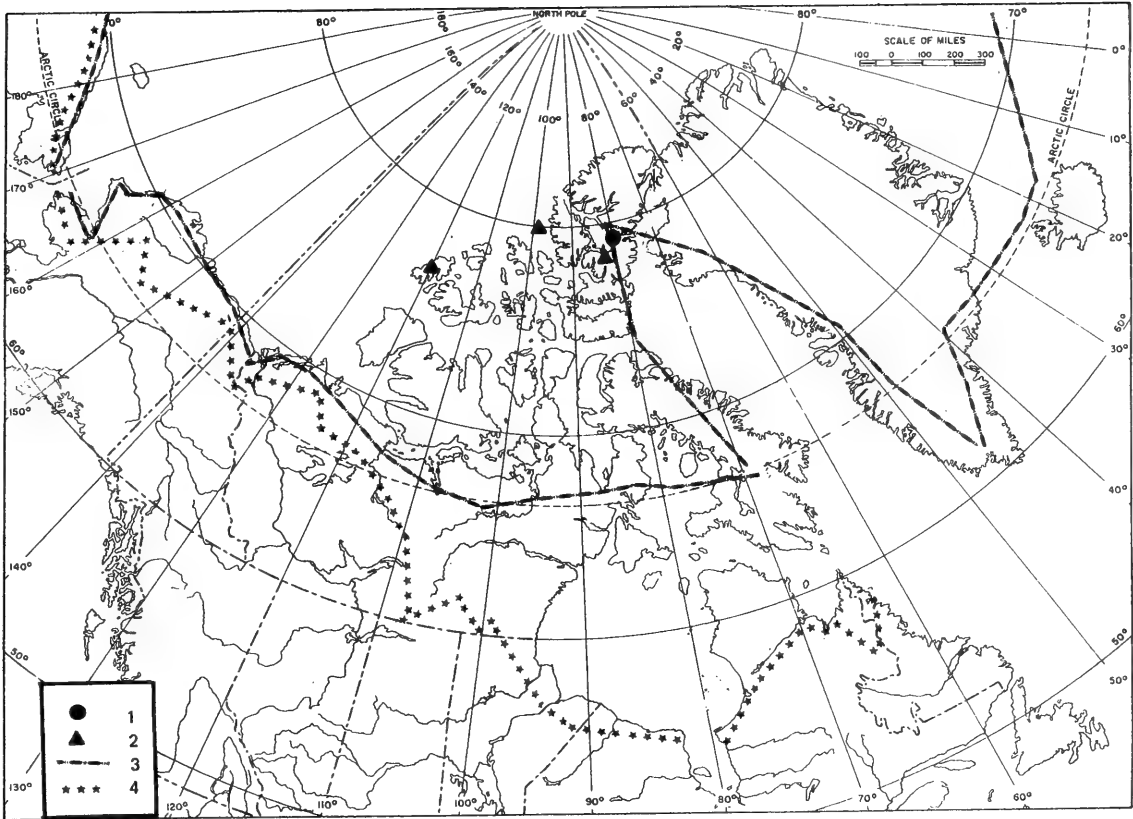


FIGURE 1. *Pleurozium schreberi* (Brid.) Mitt. on the Canadian Arctic Archipelago, past and present: 1 - Alexandra Fiord locality (cf. Kuc 1969); 2 - Pliocene (Beaufort Formation) localities; 3 - northern limit of *Pleurozium schreberi* (Brid.) Mitt. based on literature reports, herbarium specimens and the author's collections; 4 - polar tree limit.

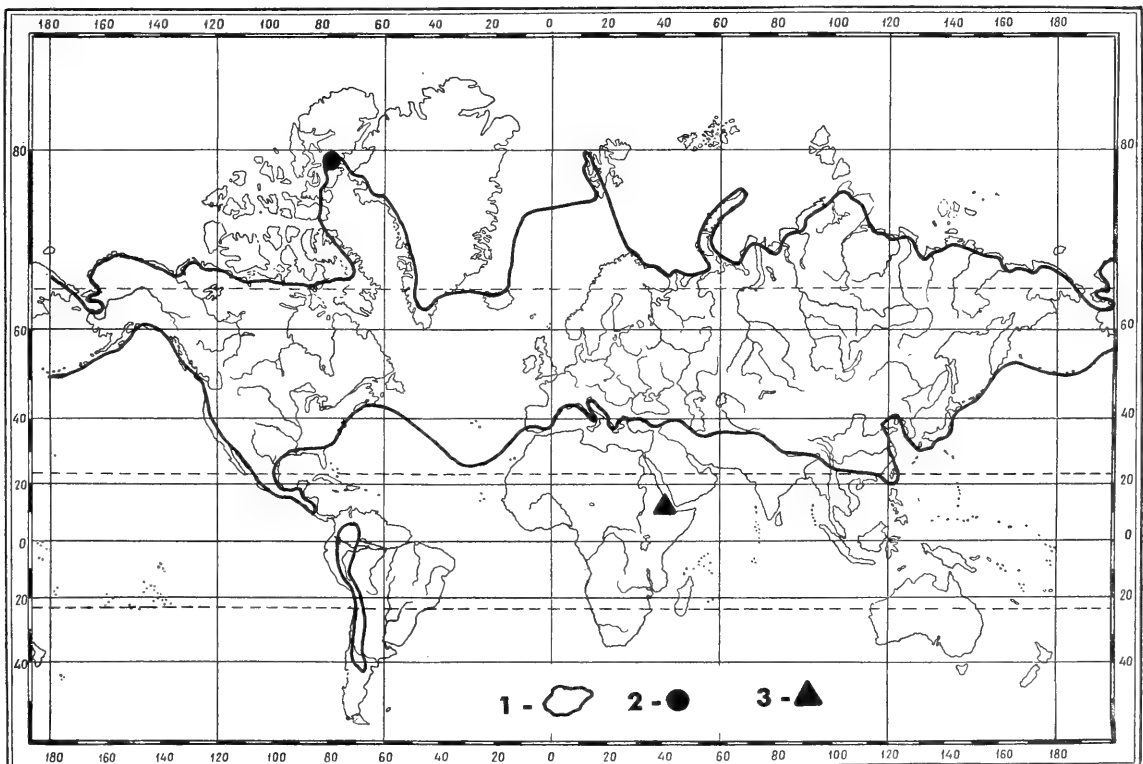


FIGURE 2. World-wide range of *Pleurozium schreberi* (Brid.) Mitt.: 1 - outer range line; 2 - Alexandra Fiord locality; 3 - isolated locality in Africa (Miehe and Miehe 1994). The outline of the northern and southern boundaries of the coniferous forest zone (Conodrymum) is shown by the heavy line.

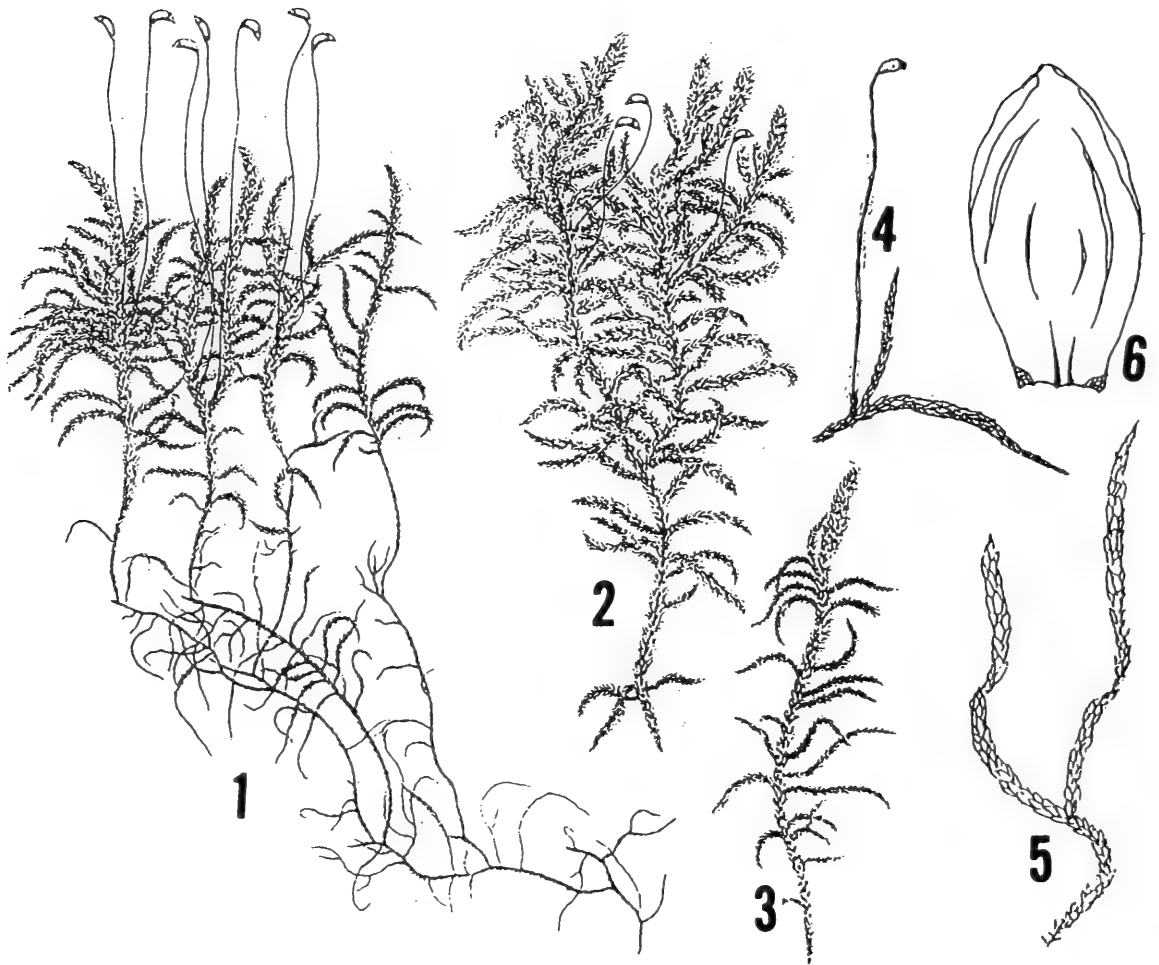


Figure 3. Habitual morphoses of *Pleurozium schreberi* (Brid.) Mitt: 1 - luxuriant specimens (5-10 cm tall, measured from herbarium specimens); 2 - average specimens (5-15 cm tall); 3 - depressed specimen (ca. 5 cm); 4 - strongly depauperate (fertile) Siberian specimen (2x); 5 - Alexandra Fiord specimen (ca. 2.5 cm long); 6 - leaf of Alexandra Fiord specimen (ca. 2.2 mm long). 1-3, after "Bryologia Europaea"; 4, after Gangulee (1978).

schreberi is greatly reduced, with a hiatus in the central and western Canadian Arctic, and in the southwestern parts which were ice-free during the last glaciation. *Pleurozium schreberi* is a wide-ranging moss, occurring mainly in the Holarctis, in particular the boreal forest zone. It also has isolated localities and distributional islands in the southern hemisphere, ranging from sea level (off active beaches) up to alpine zones, having its highest known extensions in the Himalayas in Bhutan at 5000 m and E. Nepal at 4600 m (Gangulee 1978).

Ecologically *P. schreberi* is a typical silvan of coniferous forests: an acidophilous, facultative sciaphilous, meso-thermophilous mesophyte. In high-arctic plant communities (Canadian Arctic, Svalbard, northern Siberia) it occurs usually woven into mesic and meso-hydric thicker moss-carpets, rarely forming small and loose pure stands. Arctic specimens with sporophytes are unknown.

The specimens reported here which I have identified as *P. schreberi* represent its northernmost range

extension. They were collected in the Alexandra Fiord area by Greg Henry in 1983, are nearly morphologically the same as average Low Arctic specimens. However, anatomically they represent extremely reduced forms with stems only 1-3 cm high, single or sometimes forked, with 2 or 3 annual rates, and with some leaves of upper stem-parts distinctly resorbed and pale. The stems grow erect, mingled in the 6 cm thick mesic-moss carpet with fertile *Oncophorus wahlenbergii*, and associated with *Calliargon sarmatosum*, *Drepanocladus revolvens* and *Racomitrium* sp. cf. *sudeticum* among mesic sedge meadows dominated by *Carex misandra* and *Dryas integrifolia*. From one *Oncophorus* tuft 22 stems of *P. schreberi*, or parts thereof, were extracted. Ten of them were used for sectioning and the remainder for other studies. Ecologically these particular specimens compare well to other collections of this species which have been found in the High Arctic, specifically from Spitsbergen (Kuc 1963). The specimens have been retained in my personal collection.

The significance of this discovery, apart from being a northernmost range extension in the Arctic, is that it points to the occurrence of the species between northern Ellesmere Island and southern Baffin Island from where it was reported by Steere (1947). Both Alexandra Fiord and Baffin Island localities correspond well with localities in Greenland suggesting that the expansion of *P. schreberi* in this area is due to the influence of the marine climate.

Historically, *Pleurozium schreberi* in the Canadian Arctic is a rather young, postglacial migrant. Its range may have been more extensive during the hypsithermal period of 5000 years ago and subsequently reduced during the Little Ice Age which lasted from 1450-1850 (Blanckesteijn and Hackebord 1993).

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Trichophyton mentagrophytes Ringworm Infection in a Northern Pocket Gopher, *Thomomys talpoides*

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Proulx, Gilbert, and Detlef K. Onderka. 1997. *Trichophyton mentagrophytes* ringworm infection in a Northern Pocket Gopher, *Thomomys talpoides*. *Canadian Field-Naturalist* 111(4): 633-634.

We report the capture of a Northern Pocket Gopher (*Thomomys talpoides*) in Alberta with a *Trichophyton mentagrophytes* ringworm infection. Although ringworm infections are common in rodents, this is the first reported case in a Northern Pocket Gopher.

Key Words: Northern Pocket Gopher, *Thomomys talpoides*, ringworm, *Trichophyton mentagrophytes*, fungus, Alberta.

Dermatomycosis (ringworm infection) has been reported in many animals and has a worldwide distribution (Georg 1954). It is a fungus infection of the

keratinized portion of the skin causing patchy areas of hair loss with thickened skin covered with yellow, dry crusts. The name "ringworm" is suggested by the

circular lesion that often develops from the outward growth of the fungi (United States Department of Agriculture 1976). The two species of fungi most commonly recovered from the hair coat of rodents are *Trichophyton mentagrophytes* and *Microsporium gypseum* (Clark et al. 1978). Dermatormycosis has been reported for the families Cricetidae, Microtidae, Chinchillidae, Erethizontidae, Capromyidae, Caviidae, and Muridae (McDiarmid 1962; Clark et al. 1978). However, to our knowledge, no cases have been reported for the Geomyidae.

In October 1994, a farmer from Gull Lake, approximately 120 km south of Edmonton, Alberta, captured a Northern Pocket Gopher, *Thomomys talpoides*, with dry cream-colored thickened skin void of hair. This covered most of the head and extended partially onto the neck. The lesion was about 3 cm in diameter. Microscopic examination revealed hyperkeratosis with focally large numbers of spores mixed in the proliferating skin cells as well as in the hair follicles and hair shafts. The spores were grown in a mycology culture on phyton yeast extract agar. They were identified by growth characteristics (i.e., rate of growth, color, texture, colony size, etc.) and microscopic morphology of the fruiting structures. The fungal spores were identified as *Trichophyton mentagrophytes*.

Northern Pocket Gophers spend most of their time underground (Proulx et al. 1995) where they are continuously exposed to mycotic organisms which occur as saprophytes in soil and organic debris (Migaki 1980). However, dermatormycosis is most often a latent infection and the incidence of clinical disease is low (Clark et al. 1978). While conditions which alter the immune system are usually necessary to predispose animals to such infections (Migaki 1980; Harkness and Wagner 1983), this pocket gopher was in good physical condition and no attempts were made to evaluate its immune competence. The lack of ringworm infection reports for the Northern Pocket Gopher, in spite of numerous investigations (Chase et al. 1982), suggests that

this type of infection may not occur frequently in this species.

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Abundance and Diversity of Ant (Hymenoptera: Formicidae) Assemblages in Regenerating Forests of Northern Saskatchewan

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Many communities have highest diversity under intermediate natural disturbance regimes. However, our observation of ant assemblages in plots regenerating from clear cutting in boreal forest 120 km NE of Prince Albert, Saskatchewan, seem to contradict this conclusion. Ants were more abundant in recently disturbed habitats and species more evenly represented in older stands. Disturbance may de-emphasize competitive advantage effects in ants, and affect the future communities in regenerated forest.

Key Words: Ants, Hymenoptera, Formicidae, pan-trapping, logging, disturbance, diversity, abundance, Saskatchewan.

Large scale clear-cut logging is fast becoming the main ecological disturbance regime throughout the Holarctic (Niemela et al. 1993), and investigations into subsequent community regeneration are sorely needed. Arthropod taxa are speciose, abundant, and vital to ecosystem functioning, thus they are excellent indicators of ecological change (Rosenberg et al. 1986; Pearson and Cassola 1992; Kremen et al. 1993). Carabid, staphylinid, dung and carrion beetles (Klein 1989; Holliday 1991; Buse and Good 1993; Niemela et al. 1993), and ants (York 1994; Andersen 1995) have been used recently to compare insect assemblages in habitats under various disturbance intensities; most results have supported the hypothesis that species diversity is highest in communities under intermediate scales of disturbance (the "intermediate disturbance hypothesis", Connell 1978). Since ants are dominant members of most insect communities (LaSalle and Gauld 1993; Majer et al. 1994) and are of tremendous importance to terrestrial ecosystems as soil nutrient cyclers, predators and mutualists (Holldobler and Wilson 1990; LaSalle and Gauld 1993), we chose to use them as indicators in a pilot study to examine the effects of logging disturbance on abundance and diversity of insects in areas regenerating from Jack Pine (*Pinus banksiana*) clear cutting in northern Saskatchewan.

Methods

We used pan traps to sample ants in mature Jack pine forest and regenerating clear cuts of various ages. The Meyomoot study area (54° 03' N, 105° 20' W) was located approximately 120 km NE of Prince Albert, Saskatchewan, in the Prince Albert Model Forest. This area included three regenerating plots (5, 10 and 15 years) and the corresponding *P. banksiana* leave block (the remaining mature forest from which trees were harvested). The fresh cut (0 years) and an adjacent leave block were located in a

second area, the Clarine Lake Demonstration Forest (53° 38' N, 105° 52' W), approximately 40 km N of Prince Albert.

The vegetation at both areas was characteristic of the boreal/mixed forest. *P. banksiana*, *Picea glauca*, *Populus tremuloides* and *Betula papyrifera* were dominant canopy trees, while common shrubs included *Shepherdia canadensis* and *Alnus crispa*. Qualitative observations of regenerating stands compared to old stands agree with general conclusions about vegetative cover, warmth and moisture in the Canadian boreal forest (Johnson and Green 1991): the floors of young stands were open and warm, whereas the floors of old stands were cool, damp and had thick mats of feather moss.

In each of the six plots we laid three pan traps 15 m apart along arbitrarily selected transects that ran perpendicular to the edge. The first trap was set approximately 40 m in from the stand edge to compromise between minimizing edge effects and maximizing topographic similarity between adjacent sites (Lenski 1982). The canary yellow pan traps (approximate dimensions: 24 cm × 28 cm × 4 cm) were inserted into the soil such that the pan lip was flush with the litter surface (Finnamore 1988). Each pan was partially filled with a dilute preserving solution (< 10% per volume ethylene glycol; household detergent added as a surfactant). We maintained the traps for 22 consecutive days in July/August 1993. The specimens were stored in 70% isopropyl alcohol.

Ants were identified to species, and counts of individuals per species were compiled for each trap. Abundance data were used to calculate Shannon-Wiener indices of species diversity, or "evenness" (Pielou 1975): $H' = -\sum p_i (\ln p_i)$.

Results

Differences in abundance due to microsite variation among positions of trap within a stand were

TABLE 1. Number of individuals per species captured at each site (ML = Meyomoot leave block, CL = Clarine Lake leave block, 5, 10, 15 = years since clear cutting.)

	Meyomoot				Clarine Lake		Total
	ML	15	10	5	CL	0	
<i>Camponotus herculeanus</i>	5	21	15	78	0	0	129
<i>Formica fusca</i>	8	40	74	136	2	0	260
<i>Formica aserva</i>	4	34	9	31	0	0	78
<i>Myrmica fracticornis</i>	10	15	15	42	2	8	92
<i>Leptothorax muscorum</i>	1	8	2	11	0	0	22
Total	28	118	115	298	4	8	
H'	1.43	1.48	1.08	1.34	—	—	

non-significant, therefore stand data were pooled (Table 1). Since sample sizes in both stands at the Clarine Lake site were so small we cannot be certain that the results are the effect of harvesting treatment, so we have excluded them from the analysis.

Only one site per age class was sampled in this study, so only qualitative comparisons may be made. *Formica fusca* were most abundant overall ($n = 260$), with an overwhelming representation in the 5-year age class. *Camponotus herculeanus* were next most abundant ($n = 129$), followed by *Myrmica fracticornis* ($n = 92$), *Formica aserva* ($n = 78$), and *Leptothorax muscorum* ($n = 22$). All ants combined were nearly three times abundant in the youngest age class as in the intermediate classes. Abundance in the mature leave block was minimal.

Shannon-Wiener indices were highest in the 15-year (1.48) and mature stands (1.43), and lowest in the 5-year (1.34) and 10-year (1.08) stands due to the predominance of *F. fusca*.

Discussion

Ants were most abundant in the youngest age class and most diverse in the older stages of recovery from disturbance; most of this effect seems due to the relative abundance of one species (*F. fusca*) in the younger age classes. These results contradict the intermediate disturbance hypothesis.

The effects of vegetation cover on low-lying habitats are of particular importance to this study because of the implications for ant behaviour. For example, ant foraging activity has been linked to vegetation structure through seed patch density and arrangement (Crist and MacMahon 1991). Also, mean foraging distance of *Pogonomyrmex occidentalis* varies with the percent of bare ground among different types of pastures (Crist and Wiens 1994). Whether the higher trap abundance of *F. fusca* in the younger age classes is the result of lower foraging efficiency (and therefore more time spent foraging, and a greater likelihood of being trapped) is open to speculation, but clearly vegetation removal had differential effects the surface abundance of this species.

Perhaps of greater interest in the implications of vegetation removal for this study was the observed change in ant species evenness. Competition hierarchies based on ant social organization and forager density are responsible for community composition and the spatial pattern of species distribution in ant assemblages (Fox and Fox 1982; Savolainen and Vepsäläinen 1988; Holldobler and Wilson 1990; Andersen 1991). The northern Saskatchewan ant assemblage includes species in three different levels of the competition hierarchy ["territorial" - *F. aserva* (Holldobler and Wilson 1990), "encounter" - *C. herculeanus* (Savolainen and Vepsäläinen 1988), and "submissive" - *F. fusca*, *M. fracticornis* and *L. muscorum* (Andersen 1991)]. It is curious that a submissive species had the greatest abundance in most recently disturbed habitat; this observation suggests that disturbance may de-emphasize the effects of competitive advantage in ants. Since changes to the competitive structure of ant assemblages may ultimately affect which species are successful in future communities, we believe further concern should be focused on causes and consequences of altering the relative abundance of insect species.

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Northern Record of the Water Shrew, *Sorex palustris*, in Alaska

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Cook, Joseph A., Chris J. Conroy, and James D. Herriges, Jr. 1997. Northern record of the Water Shrew, *Sorex palustris*, in Alaska. *Canadian Field-Naturalist* 111(4): 638–640.

Eight specimens of Water Shrew, *Sorex palustris*, collected in Alaska document the most northern extent of the species in North America.

Key Words: Water Shrew, *Sorex palustris*, distribution, Alaska.

Since the publication of Hall (1981) new specimens have defined further the range of the Water Shrew (*Sorex palustris*), including southeastern Alaska (MacDonald and Cook 1996), Ogilvie Mountains, Yukon Territory (Jarrell 1986), Healy, Alaska (MacDonald and Elliot 1984), and recent specimens reported here. During 12–14 July 1996, five female and three male Water Shrews, *S. p. navigator*, were collected at Big Windy Hot Springs (65° 13.65' N, 144° 30.01' W; elevation 480 m). Seven of these were immature based on tooth-wear and lack of testicular development or lack of embryos or placental scars. The eighth specimen may have been a second-year female based on tooth-wear and six placental scars (Conaway 1952). Trapping effort totaled approximately 120 trap nights (97 museum special and 23 cone pitfall traps). All specimens (Table 1) were preserved in 70% ethanol and deposited at the University of Alaska Museum (UAM).

Big Windy Hot Springs is 250 km NE of the published distribution of *S. palustris* in Alaska and the most northern record in North America (Figure 1). That site is on a tributary of Birch Creek that flows into the Yukon River, approximately 160 km NE of Fairbanks. Geothermal water emanates from springs and from dispersed seeps in granite cliffs 30 m N of the creek. Traps were located on the rocky slope

between the creek and cliffs, in mesic grass and White Spruce (*Picea glauca*) woodland. Surrounding vegetation is primarily White Spruce forest or White Spruce/Paper Birch (*Betula papyrifera*) forest. Six of eight shrews were captured in the grassland portion of the trapline, which had about 90% coverage of Reed Canary Grass (*Phalaris arundinacea*). This population of *P. arundinacea* is widely disjunct from the main North American distribution (Hulten 1968).

Three rodent species, *Microtus oeconomus*, *M. longicaudus*, and *Clethrionomys rutilus*, were also captured at this site. The historical biogeography of the mammalian fauna of the area is complex. Taxa were restricted to Beringia (e.g., *M. oeconomus* and *C. rutilus*) or thought to have moved north into central Alaska (e.g., *M. longicaudus*) following recession of the Laurentide ice sheet at the end of the Fraser glaciation (Hoffmann 1981). *Sorex palustris* appears to be a member of the latter group. The distribution of *M. longicaudus* in western North America is similar to *S. palustris* (Hall 1981) and both are now documented at the northern limit of their ranges in the Yukon River drainage. However, both *M. oeconomus* and *C. rutilus* are thought to have been present in Beringia and to have arrived in North America (from Asia) in the late Pleistocene (Hoffmann 1981; Lance and Cook in press).

TABLE 1. Summary of specimen data from collection notes and museum records. Alaska Frozen Tissue Number refers to the tissue collection administered by the UA Museum Mammal Department. Sex was determined by verification of either testes or uterine horns and/or embryos. All measurements (TL = total length; HF = hind foot, EFN = ear from notch) were made in the field prior to fluid preservation.

UAM Catalog Number	Alaska Frozen Tissue Number	Sex	TL-Tail-HF-EFN ≡ Weight(g)
34596	15869	F	139-67-20-7 ≡ 8
34597	15870	F	142-68-20-[6] ≡ 8
34598	15871	F	139-72-20-[6] ≡ 8
34599	15872	F	147-71-20-7 ≡ X
34600	15873	M	149-73-21-7 ≡ 9
34601	15875	F	139-68-20-[5] ≡ 8
34602	15874	M	151-73-20-[6] ≡ 8
34603	[no tissues]	M	144-73-20-[7] ≡ 9

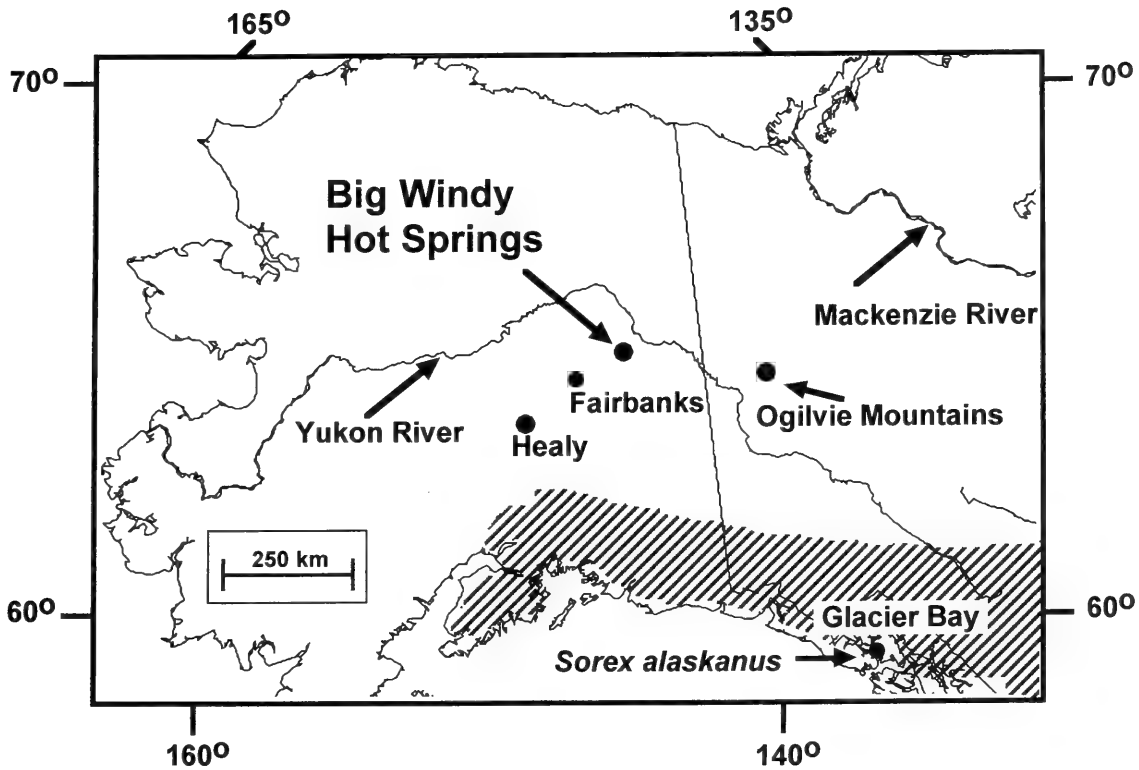


FIGURE 1. Extreme northern localities for *Sorex palustris* and type locality for *S. alaskanus*. Hatched area is distribution reported by Hall (1981; Map 22).

The Big Windy Creek record is consistent with Jarrell's (1986) suggestion that this species may be distributed widely in the Yukon River drainage. Intensive trapping in the vicinity of Galena and Ruby (ca. 700 km west of Big Windy Hot Springs) on the western Yukon River, however, has not revealed this species (Johnson et al. 1996*; Quade 1993*; UAM unpublished data).

The Water Shrew is rarely encountered in surveys of small mammals in Alaska and relatively few specimens are available for study. For comparison, there are 4897 specimens of Alaska species of *Sorex* archived at UAM; 21 are *S. palustris*. Excluding island endemics, only the recently discovered tiny shrew, *S. minutissimus* (Dokuchaev 1994) (four specimens), is represented by fewer specimens at UAM. This lack of material for *S. palustris* has limited the assessment of geographic variation and hampered studies of the ecology and status of Water Shrew populations in the subarctic. For example, a larger series of specimens representing a wide geographic region would allow evaluation of the status of the Alaska Water Shrew, *S. alaskanus* (Hutterer 1993). The Alaska Water Shrew is a species of conservation concern (MacDonald and Cook 1996) that is thought to be closely related (Jackson 1928) or conspecific (Hall 1981; Junge and Hoffmann 1981) with *S. palustris*. *Sorex alaskanus* is apparently endemic to Glacier Bay, Alaska, however, it is

represented by only three specimens (deposited at U. S. National Museum and Glacier Bay National Park; MacDonald and Cook 1996). Water Shrew populations in surrounding regions have been inventoried poorly. Given this paucity of specimens and unclear taxonomy, additional documentation is needed to determine the distribution and status of Water Shrews at the northwestern limit of their range.

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A Preliminary Evaluation of Four Types of Traps to Capture Northern Pocket Gophers, *Thomomys talpoides*

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Proulx, Gilbert. 1997. A preliminary evaluation of four types of traps to capture Northern Pocket Gophers, *Thomomys talpoides*. *Canadian Field-Naturalist* 111(4): 640–643.

A preliminary evaluation of four types of Northern Pocket Gopher, *Thomomys talpoides*, traps was carried out in alfalfa fields in fall 1991, when juveniles were similar in size to small-medium adults. After 192 trapnights, the ConVerT box trap was the most successful (35% of a total of 178 captures). It was followed, in order of decreasing success, by the Black Hole (25%), the Guardian (24%), and the Victor Easyset (16%). Because of the discrepancy observed between the capture success of various traps in fall, it is recommended that pocket gopher traps be further assessed under various environmental conditions and at different times of year, with young and full-grown pocket gophers.

Key Words: Alberta, alfalfa fields, capture success, Northern Pocket Gopher, *Thomomys talpoides*, traps.

Because density estimates of small mammal populations are usually derived from trapping results, knowledge of the capture success of various traps is essential (Smith et al. 1971; Wiener and Smith 1972; Rana 1982). Many trap models are available for the capture of Northern Pocket Gophers (Anonymous 1982) but data are lacking on their efficiency. The objective of this study was to assess the ability of four types of kill traps to capture Northern Pocket Gophers.

Methods

The study was carried out from 18 September to 4 October 1991 in Vegreville, Alberta. Tested kill traps were the Blackhole (F. B. N. Plastic, Tulare, California; \$13 CAN), the ConVerT (L. B. Bachelder, Calgary, Alberta; \$9 CAN), the Guardian (Guardian

Trap Co., San Leandro, California; \$12 CAN) and the Victor Easyset (Woodstream Co., Lititz, Pennsylvania; \$9 CAN) (Figure 1). All the traps require that pocket gophers push on a trigger to release a killing bar (ConVerT and Guardian traps) or snare wire (Blackhole) that hits the animals ventrally, or a pair of jaws (Victor Easyset) that strikes the animals sideways.

Four independent trapping areas were delineated in alfalfa fields where pocket gopher populations are commonly found in Alberta (Proulx 1996). In each trapping area, 96 burrow systems with fresh mounds, ≥ 10 m apart from each other, were selected. Two traps of a same model were set facing opposite directions (Marsh and Howard 1978) in the active tunnel of 24 burrow systems, according to the manufactur-

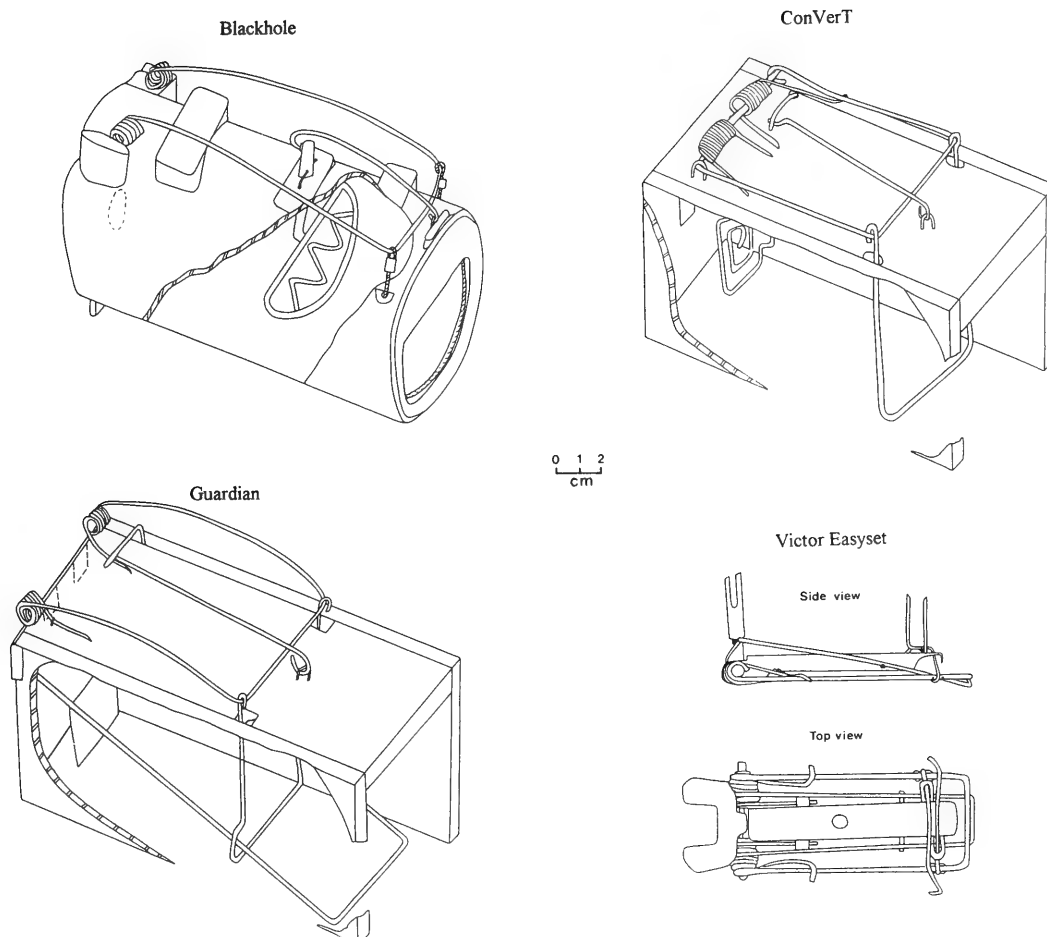


FIGURE 1. Diagrams of the Blackhole, ConVerT, Guardian and Victor Easyset traps.

er's instructions (Figure 2). Therefore, 48 traps of each model were set in each trapping area. Capture success was evaluated over one trapnight. There were 48 trapnights/trap model in each study area; each trap model was tested during 192 trapnights in four trapping areas. Animals were not classified according to their age or sex because of the difficulty in recognizing small male adults from large male juveniles, and separating male and female juveniles in the field without opening their body cavity.

The overall captures of the four trap models were analyzed with the Chi-square goodness-of-fit test (Siegel 1956). The capture success of traps for the four trapping areas was compared to each other with the Kruskal-Wallis one-way analysis of variance (Siegel 1956). A *t*-test was also used to compare mean capture success of traps (Dixon and Massey 1969). A 0.05 level of significance was used for all tests.

Results

A total of 178 pocket gophers were captured. There was a significant difference ($\chi^2 = 12.472$, $df = 4$, $P < 0.01$) in the success of capture of traps. The

ConVerT had the highest overall capture success (35%) and the Victor Easyset, the lowest (16%) (Table 1). The number of captures/trapping area varied significantly between traps (Kruskal-Wallis $H = 26.250$, $P < 0.05$). It was significantly greater in the ConVerT ($\bar{x} = 15.8$, $SD = 3.6$) than in the Victor Easyset (7.3 ± 2.1) ($t = 4.075$, $P < 0.005$). However, the mean capture success of these traps did not differ

TABLE 1. Number of Northern Pocket Gophers captured in the ConVerT, Guardian, Blackhole and Victor Easyset traps, in four trapping areas in Vegreville, Alberta, in fall 1991.

Trap	Number of captures				Total
	Trapping area				
	I	II	III	IV	
ConVerT	11	15	18	19	63
Blackhole	7	10	11	16	44
Guardian	8	9	9	16	42
Victor Easyset	5	6	9	9	29

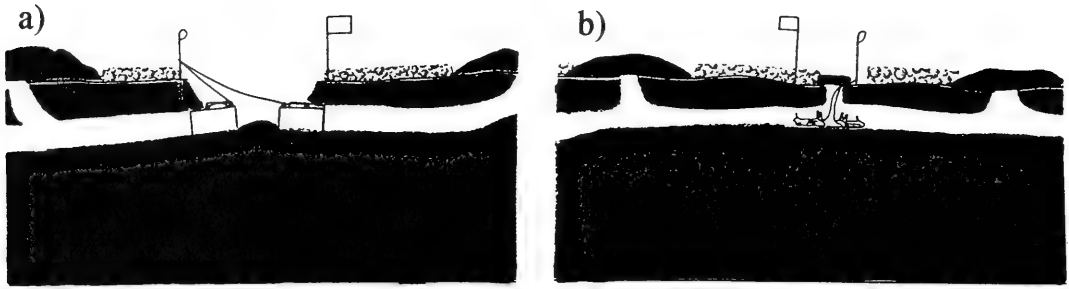


FIGURE 2. Trap set for a) the ConVerT, Guardian and Blackhole and b) the Victor Easyset.

significantly ($P > 0.05$) from that of the Blackhole (11 ± 3.7) and the Guardian (10.5 ± 3.7). Overall, one pocket gopher was captured every 3.2 trapnights in the ConVerT, compared to 4.8 and 4.9 trapnights in the Blackhole and the Guardian, respectively, and 7.1 days in the Easyset.

When visiting a trap site, a pocket gopher may push soil ahead of itself and fill up the trap with dirt; such plugging may either spring the trap before the animal is in line with the striking bar, snare or jaws, or interfere with the movement of the trap's striking components. In either case, the animal is not captured. Pocket gophers plugged two ConVerT and two Guardian traps, and therefore rendered them inoperative, during the 192 trapnights. On the other hand, 13 Blackholes and 23 Victor Easyset traps were plugged during the whole study period. Two pocket gophers captured in the Victor Easyset were able to free themselves from the closed jaws.

Discussion

The ConVerT was significantly more successful than the Easyset to capture Northern Pocket Gophers. The Easyset has a base that is raised approximately 1 cm above the floor of pocket gophers' tunnel. This base may constitute an obstacle since an animal is forced to climb on it in order to approach the trigger system; this may explain why so many Easyset traps were plugged by the pocket gophers. While the Easyset trap was quick to install, its jaws did not always hold their capture and escapes occurred.

Although the difference in the mean number of captures with the ConVerT and the Blackhole was not statistically different, the number of trapnights/capture was still noticeably lower with the ConVerT. The Blackhole took longer than other traps to set. It was necessary to cover its floor with dirt to entice animals to enter the trap; this had to be done without interfering with the movement of the snare cable. Also, the trigger mechanism often bent and became excessively sensitive. Because of its relatively high cost, the trap did not appear advantageous for extensive population studies.

The ConVerT was also more successful than the Guardian which required more trapnights to capture one animal. The greater success of the ConVerT over the Guardian may be attributed to its larger back hole that allows for more air and light to enter the pocket gopher tunnel and incite the resident animal to investigate the trap. The Guardian has two small openings at its back that are covered by a piece of tin; therefore, the air and light do not directly enter the burrow system. The Guardian is a stronger trap than the ConVerT and the trigger mechanism often needs repair after firing. Because of its stronger springs, the Guardian requires more force than the ConVerT to be fired (2.4 Newtons vs. 0.5 N; R. Drescher, Alberta Research Council, personal communication). The trap must therefore be hair triggered in order to capture the smaller animals.

The ConVerT is easy to set and relatively inexpensive. Because of its high success of capture, the ConVerT may be the most advantageous kill trap to use in the study of Northern Pocket Gopher populations. However, the capture success of the ConVerT and other trap models may vary at different times of year according to the sex, age, size and physiological state of the animals. It is therefore recommended that the capture success of pocket gopher traps be further assessed under various environmental conditions and at different times of year (i.e., during reproduction, juvenile dispersal, etc.), with small and full-grown pocket gophers.

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Estimating Fall Whole-body Weights of Muskrats, *Ondatra zibethicus*, from Skinned Weights

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Proulx, Gilbert. 1997. Estimating fall whole-body weights of Muskrats, *Ondatra zibethicus*, from skinned weights. *Canadian Field-Naturalist* 111(4): 643-645.

While mean body weights are useful in comparing the sizes of animals of different samples, a conversion factor to estimate whole-body weights from skinned weights has yet to be determined for Muskrats (*Ondatra zibethicus*) captured in fall by fur trappers. At Luther Marsh, Ontario, the mean ratio of skinned weight to whole-body weight was 0.76 in juvenile males, and 0.75 in all other age-sex classes. There was a significant difference ($P < 0.05$) between the mean whole-body weights, and between the mean skinned weights, of Muskrats of different age-sex classes. A linear regression of whole-body to skinned weights was determined for each age-sex class.

Key Words: Muskrat, *Ondatra zibethicus*, body weight, skinned weight, Ontario.

Large numbers of skinned Muskrats (*Ondatra zibethicus*) are commonly available from trappers in the fall (see Proulx and Buckland 1985, 1986) and mean body weights may be useful to assess the animals' condition and the suitability of their habitats (Kuehn 1985). However, a conversion factor to estimate whole-body weights from skinned weights has yet to be determined for fall-captured Muskrats. Such information would be useful to compare trapped animals of different sex and age classes, and to compare fur-trapped populations to protected ones for which only whole body-weights are available

through live-trapping. The objective of this study was to determine the relationship between whole-body and skinned weights.

This study involved 233 Muskrats (19 male and 24 female adults, and 109 male and 81 female juveniles) captured at Luther Marsh, 65 km north of Guelph, Ontario, from 26 October to 24 November 1979. All Muskrats were weighed to the nearest 25 g before and after skinning, and were aged by the dentition method (Sather 1954; Proulx and Gilbert 1988). Comparisons between age and sex classes of mean whole-body and skinned weights were done with an

TABLE 1. Whole-body and skinned weights (g) of adult and juvenile Muskrats captured at Luther Marsh, Ontario, in fall 1979.

Age	Sex	Number of animals	Weights					Ratio of skinned to whole-body weights $\bar{x} \pm E$
			Whole-body		Skinned			
			Actual	Calculated from regressions				
		$\bar{x} \pm SE$	Range	$\bar{x} \pm SE$	$\bar{x} \pm SE$	Range		
Adult	Male	19	1496 \pm 29	1225 - 1775	1497 \pm 21	1120 \pm 25	950 - 1325	0.75 \pm 0.01
	Female	24	1389 \pm 27	1125 - 1650	1389 \pm 26	1036 \pm 21	825 - 1275	0.75 \pm 0.01
Juvenile	Male	109	1034 \pm 16	650 - 1500	1030 \pm 16	779 \pm 11	500 - 1125	0.76 \pm 0.003
	Female	81	980 \pm 15	650 - 1250	981 \pm 14	735 \pm 11	500 - 950	0.75 \pm 0.004

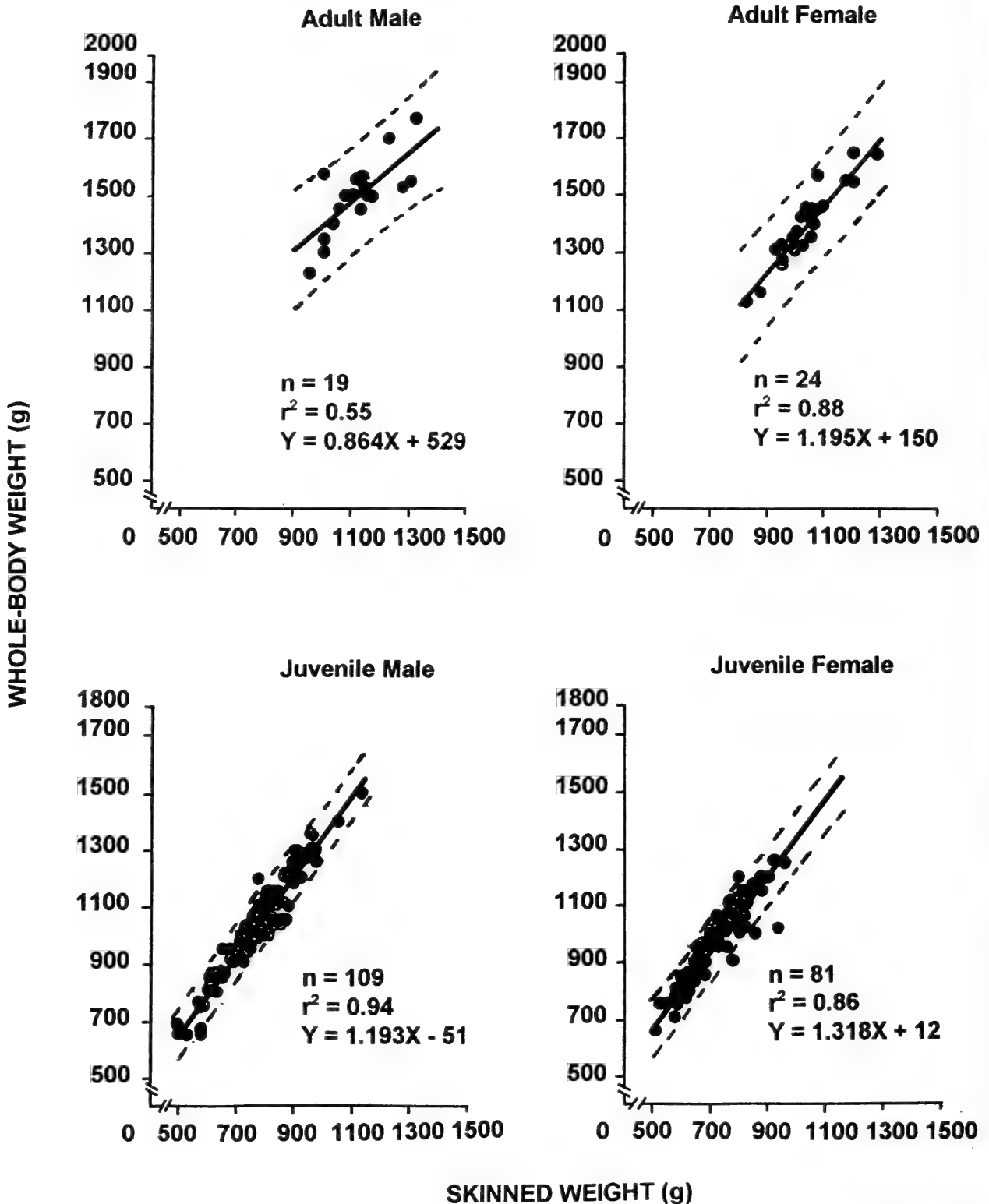


Figure 1. Relationship between whole-body and skinned weights, and 95% confidence limits of the Y value (dashed lines), of Muskrats captured in fall 1979 at Luther Marsh, Ontario.

analysis of variance and Student *t*-tests (Dixon and Massey 1969). A simple linear regression model was used to determine the relationship between whole-body and skinned weights (Kuehn 1985). A 0.05 level of significance was used for all tests.

There was a significant difference between the mean whole-body ($F = 93.885$; 3, 229 df; $P < 0.005$) weights of Muskrats of different age-sex classes (Table 1). The mean skinned weights were also different ($F = 100.914$; 3, 299 df; $P < 0.005$) among the

classes. The mean whole-body and skinned weights of adult males was significantly greater than any other class ($t = 2.677$, $P < 0.01$). Adult females were heavier than juveniles ($t = 9.585$, $P < 0.005$), and juvenile males were heavier than juvenile females ($t = 2.342$, $P < 0.01$) (Table 1). The mean whole-body weights were significantly ($P < 0.005$) greater than the mean skinned weights for all age-sex classes (Table 1).

The mean ratio of skinned weight to whole-body weight was 0.76 in juvenile males and 0.75 in all other age-sex classes (Table 1). There was no difference ($P > 0.05$) between the mean ratios. However, because of the difference in the mean weights of the age-sex classes, data were not pooled for the regressions of whole-body to skinned weights. The regression of whole-body to skinned weights for male adults was $Y = 0.864 X + 529$ ($r = 0.74$, $P < 0.001$), and for female adults, $Y = 1.195 X + 150$ ($r = 0.94$, $P < 0.001$) where Y = whole-body weight in grams and X = skinned weight (Figure 1). The regression of whole-body to skinned weights for male juveniles was $Y = 1.393 X - 51$ ($r = 0.97$, $P < 0.001$) and for female juveniles, $Y = 1.318 X + 12$ ($r = 0.93$, $P < 0.001$) (Figure 1). The mean difference between actual and calculated weights was 66 (SE = 12) g and 53 (± 16) g in male and female adults, respectively, and 35 (± 3) g and 38 (± 4) g in male and female juveniles, respectively. These differences corresponded to 3.4 to 4.4 % of the actual mean whole-body weights of age-sex classes. The calculated mean whole-body weights did not differ ($P > 0.05$) from the actual ones for all age-sex classes (Table 1).

This study showed that a mean ratio of skinned to whole-body weight of approximately 0.75 may be used for all age-sex classes in comparative studies involving live-captured Muskrats and carcasses originating from habitats similar to those of Luther Marsh (see Proulx and Gilbert 1983). This ratio was similar to the 0.78 and 0.79 estimated by Dozier (1945) for winter-captured males and females, respectively, and 0.76 to 0.79 reported by Piérard and Bisailon (1982) for spring-captured Muskrats of different age and sex classes. This ratio probably varies among seasons as the leather becomes light and papery later in the trapping season (Anonymous 1983), and fat reserves may be depleted over winter (Piérard and Bisailon 1982). The regressions devel-

oped for fall-captured animals should be applied cautiously in other seasons. The mean differences observed between calculated and actual whole-body weights were small and similar to those reported in a study of Fisher (*Martes pennanti*) carcasses (Kuehn 1985). Overall, the regressions resulted in estimated mean whole-body weights that were representative of the real world.

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Coyote, *Canis latrans*, Depredation of a Mute Swan, *Cygnus olor*, Nest

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A Coyote (*Canis latrans*) was observed interacting with a pair of nesting Mute Swans (*Cygnus olor*) on four different occasions over a three day period. The Coyote consumed two eggs, one broken egg was removed by the nesting swans, and the fate of the fourth egg was unknown. On the third day of interactions, the swans abandoned their nest and were observed loafing on an adjacent beach. Because of continued expansion of both Mute Swan and Coyote populations over the past 40 years, their ranges now overlap. Coyotes can have an effect on individual nesting pairs, but their potential effects on the expanding swan population are unknown.

Key Words: Coyote, *Canis latrans*, Mute Swan, *Cygnus olor*, nesting, egg depredation, Connecticut.

Mute Swans (*Cygnus olor*) were imported into the United States from Europe between the late 1800s and early 1900s (Allin 1981; Madsen 1983; Phillips 1928). In the Atlantic Flyway, Swans were introduced along the Hudson River in 1910 and on Long Island in 1912 (Bull 1964). Swans were first documented in Connecticut in the mid-1950s (Allin 1981) and current populations are estimated at 1900 (P. Merola, Connecticut Wildlife Division, personal communication). Nearly concurrently, Coyotes (*Canis latrans*) were first documented in Connecticut in the early 1960s and presently are distributed statewide with an estimated population of 1500 - 3000 (P. Rego, Connecticut Wildlife Division, personal communication). As a result, Swan and Coyote ranges currently overlap.

Adult male Mute Swans have a wingspan of 2.4 m (Willey and Halla 1972) and can weigh up to 11.4 kg; adult females weigh about 9.6 kg (Bellrose 1976). Because of their large size and aggressiveness, swans have few predators other than humans (Allin et al. 1987). There are no published reports on depredation of Mute Swan eggs. Here, we document Coyote depredation of a swan nest.

Observations

Since 1989, a pair of Mute Swans nested in a salt marsh adjacent to Mumford Cove in Groton, Connecticut. The nest site was along the edge of a tidal creek in a salt marsh and was surrounded by water on three sides. Swans successfully hatched two eggs in 1993 and three eggs in 1994 at this site. Prior to 1 May 1995, we observed a nesting pair of swans in this area and it was determined by other observers residing in a residential community adjacent to the salt marsh, that the swan nest contained four eggs. Detailed observations were provided by four residents of the community who observed the nesting swans for several years. We queried observers indi-

vidually, and descriptions of the occurrences were consistent among all witnesses.

On 1 May 1995, a Coyote was observed approaching the Swan nest. As the Coyote approached, the female swan came off the nest and approached the Coyote, while the male swan remained at the nest aggressively flapping its wings. The Coyote ran directly to the nest and successfully obtained an egg which was carried to a rock outcrop approximately 70 m away and consumed. After consuming the egg, the Coyote attempted to obtain a second egg but was driven away by the swans. These events occurred at about 10:00 h and lasted for approximately 20 min.

On 2 May, a similar situation occurred at about 10:00 h. A Coyote approached the nest. The female swan stood by the nest posturing as the male attempted to defend the nest by aggressively flapping its wings. After about 5 min, the Coyote retreated and left the area. Shortly afterwards, an egg, possibly broken during the confrontation, was pushed out of the nest by the female swan.

On 3 May, a Coyote was observed approaching the swan nest at about 06:00 h and successfully maneuvered around the swans, obtained an egg and carried it into the woods. The fate of the fourth egg was unknown. Later on 3 May, the pair of swans abandoned the nest site, and were observed loafing at a nearby beach. The swans did not re-nest.

Discussion

The expanding Mute Swan population along the Atlantic Flyway and the potential effects on aquatic habitat and native waterfowl species are concerns to some biologists (Allin et al. 1987). Mute Swans can reduce significantly the amount of aquatic vegetation occurring in some habitats (Allin et al. 1987; Chasko 1986). Because some swans are aggressively territorial (Eltringham 1963), they may exclude native waterfowl species (Kania and Smith 1986).

Swans have few natural predators, which partially accounts for the rapid expansion in numbers and distribution of feral populations (Allin et al. 1987). Reports exist on depredation of cygnets (Gelston and Wood 1982), but our review of the scientific literature showed no clear documentation of egg depredation. This note reports the first case of Mute Swan eggs being depredated by Coyotes.

With the continued expansion of both Mute Swan and Coyote populations during the past 40 years, their ranges now overlap. Because swans are large birds and both sexes assist in defending nest sites, they may be able to deter successfully most potential nest predators. However, Coyotes are successful predators and opportunistic feeders that occupy a wide variety of habitat types. We document that Coyotes can affect individual nesting pairs, but their potential effects on the expanding swan population are unknown.

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Hybridization of Thinhorn and Bighorn Sheep, *Ovis dalli* × *O. canadensis*

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Hoefs, Manfred, and Uli Nowlan. 1997. Hybridization of Thinhorn and Bighorn sheep, *Ovis dalli* × *O. canadensis*. *Canadian Field-Naturalist* 111(4): 647–648.

On 3 June 1994 a female lamb was born at the Yukon Game Farm from crossing of a Dall's ram (*Ovis dalli dalli*) with a Rocky Mountain Bighorn (*Ovis canadensis canadensis*) ewe. At 18 months of age this hybrid was backcrossed to a Bighorn ram to establish hybrid fertility, which was confirmed with the birth of a healthy lamb on 22 May 1996.

Key Words: Dall's Sheep, *Ovis dalli dalli*, Bighorn Sheep, *Ovis canadensis canadensis*, hybridization.

While interspecific hybridization is uncommon in nature among large mammals (Gray 1972), it has frequently been observed in *Ovis*, and it may have played a major role in the evolution of this genus (Bunch and Workman 1988). In this short review we have used Mayr's (1964) concept of hybridization, who defined it as any crossings of separate gene

pools. Natural hybridizations have been documented for several subspecies of Urial Sheep (*Ovis orientalis* ssp.) in Iran (Valdez et al. 1978), and for two subspecies of Thinhorn Sheep (*Ovis dalli* ssp.) in Yukon (Hoefs and Barichello 1984). Most genotypes of wild sheep have hybridized with domestic sheep (*Ovis aries*), either accidentally by sharing the same

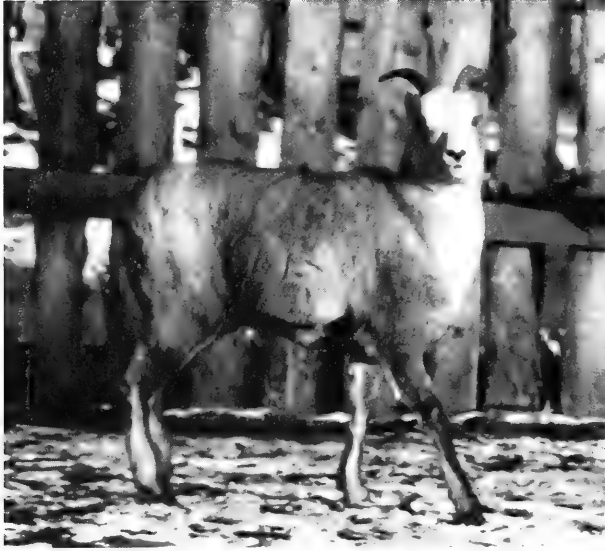


FIGURE 1. Female hybrid Dall's Sheep \times Bighorn Sheep, *Ovis dalli dalli* \times *Ovis canadensis canadensis*, 18 November.

range or by human manipulation. Crosses of domestic sheep with European Mouflon (*Ovis orientalis musimon*) have been reported by Uloth (1976) and Türcke and Tomiczek (1982), those with Bighorn sheep (*Ovis canadensis*) by Pulling (1945) and Young and Manville (1960). Experimental hybridizations have been carried out between Bighorn rams and Argali-Mouflon ewes (*Ovis ammon* spp \times *O. orientalis musimon*) (Bunch and Workman 1978). Hybridizations have affected most genotypes of sheep (Gray 1972); they were generally successful and resulted in fertile offspring. Only two species of wild sheep appear to have escaped hybridizations, and these are the sheep to the north: Siberian snow sheep (*Ovis nivicola*) and American Dall's sheep. No doubt, the fact that their ranges are disjunct from those of other sheep, and that husbandry of domestic sheep has rarely been attempted in their subarctic and arctic habitat are relevant in this context.

We report here on an accidental hybridization, which occurred at the Yukon Game Farm at Whitehorse, where both Dall's Sheep and Bighorn Sheep are held for display and propagation purposes. In November 1994, a Dall's ram escaped from his enclosure, jumped into a paddock with Bighorn ewes and bred one of the ewes. This mating resulted in a healthy vigorous female lamb being born on 3 June 1994. Its colouration was intermediate between the

two parents and resembled Yukon's "Fannin" sheep - a natural cross between Dall's and Stone's sheep (Figure 1). This hybrid developed exceptionally well and surpassed her mother in size and weight at 18 months of age. To establish hybrid fertility she was backcrossed to a Bighorn ram at that age. This mating was successful with the birth of a healthy male lamb on 22 May 1996 which resembled typical Bighorn lambs in colouration.

Of interest from the natural history point of view is the fact that these two species, which share a common ancestor, became separated during the last glacial advance, the Wisconsin, perhaps for more than 100 000 years. The northern population survived in the Beringia Refugium, the southern one in the Wyoming and Mojave desert areas and evolved into *Ovis dalli* and *Ovis canadensis* respectively (Cowan 1940; Geist 1985). This period of separation, however, was insufficient to develop a reproductive barrier. Should these species continue to expand their ranges and establish contacts intergradation can be predicted.

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Ptilidium californicum, a New Liverwort for Alberta

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Priddle, D. Ross. 1997. *Ptilidium californicum*, a new liverwort for Alberta. *Canadian Field-Naturalist* 111(4): 649–650.

Ptilidium californicum (Aust.) Underw. was collected 3–6 August 1996 in Waterton Lakes National Park. It has not been reported previously for Alberta.

Key Words: *Ptilidium californicum*, liverwort, Waterton Lakes National Park, Alberta.

During the summer (August 3–6) of 1996 I collected bryophytes in Waterton Lakes National Park. One discovery was *Ptilidium californicum* (Aust.) Underw. which is previously unreported for Alberta. Mosses and liverworts are rather poorly known for this portion of the province, the important previous collections being those of W. B. Schofield and H. A. Crum in the summer of 1955 (unpublished) and those of C. D. Bird in the early sixties (Bird and Hong 1969). R. J. Belland and J. Doubt also collected in Waterton in the summer of 1996.

The genus *Ptilidium* is represented by two other species in Alberta: *P. pulcherrimum* and *P. ciliare*. *P. californicum* is easily distinguished from the other two species by its relative lack of cilia on the leaf margins (Figure 1). Where *P. pulcherrimum* has ca. 25 cilia per leaf and *P. ciliare* has up to 50 or more cilia per leaf, *P. californicum* has only 1–4. Both *P. pulcherrimum* and *P. ciliare* are holarctic in distribution, with the latter also found as a rarity in southernmost South America and New Zealand (Schuster 1966). *P. californicum* on the other hand is Circum-Pacific. (Figure 2).

P. pulcherrimum is very common in Alberta, being found on “every rotten log in the Boreal forest” (D. H. Vitt, personal communication). *P. ciliare* has arctic affinities and is less common especially in the south-

ern portion of the province where it is found at high elevations, often in boulder fields (Vitt et al. 1988). There are excellent illustrations of both *P. ciliare* and *P. pulcherrimum* in Schuster 1966, but illustrations of *P. californicum* are hard to find, those in Frye and

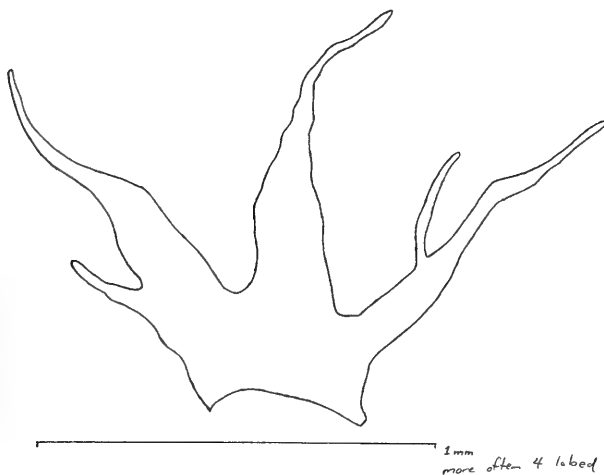


FIGURE 1. Leaf of *Ptilidium californicum* (Aust.) Underw. drawn from RP 1585, Salt Spring Island.

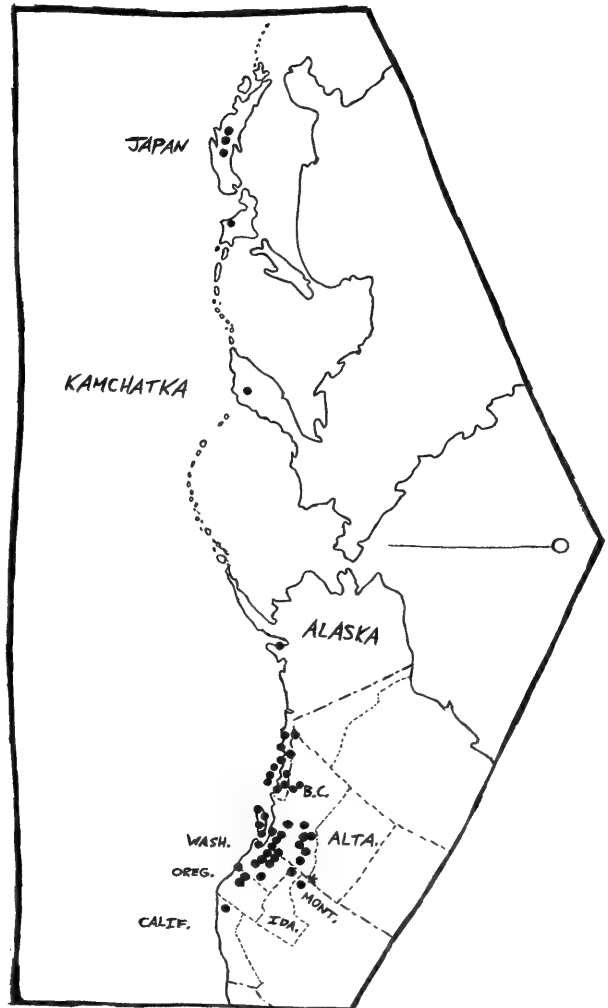


FIGURE 2. Distribution of *Ptilidium californicum* (Aust.) Underw. (prepared from specimens in the University of British Columbia herbarium with the addition of the type location in California; “on both sides of the Continental Divide” in Montana (Bird and Hong 1975); and Kamchatka (Korotkevich 1963).

Clark 1937-1947 being perhaps the most available.

My specimen of *Ptilidium californicum* was found at Lost Lake (49°09'N, 114°09'W) on a decorticated log in spruce/fir forest near the lake shore (1861m elevation). The specimen (RP 2001) has been verified by W. S. Hong at the College of Great Falls, Montana, where a duplicate has been deposited, and by R. J. Belland at the University of Alberta where the specimen has been deposited in the Cryptogamic Herbarium (ALTA).

This species joins a long list of bryophytes (e.g., *Dichodontium olympicum* Ren. & Card., *Thamnobryum neckeroides* (Hook.) Lawt., *Porella cordaeana* (Hueb.) Moore (unpublished data)), as well as vascular plants: *Xerophyllum tenax* (Pursh) Nutt. (Bear Grass), *Isoetes bolanderi* Engelm. (Bolander's Quillwort), *Cypripedium montanum* Dougl. ex Lindl. (Mountain Lady's-slipper) (Packer and Bradley 1984)), that barely extend into Alberta in Waterton Lakes National Park and are therefore "rare" in the province.

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A Case of Helping Behavior at a Brewer's Sparrow, *Spizella breweri*, Nest

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Gill, M. J., and P. G. Krannitz. 1997. A case of helping behavior at a Brewer's Sparrow, *Spizella breweri*, nest. *Canadian Field-Naturalist* 111(4): 650-652.

A single case of helping behavior was recorded in a breeding population of the sagebrush subspecies of Brewer's Sparrow in the Okanogan Valley, Washington State. This is the first report of cooperative breeding in the Brewer's Sparrow.

Key Words: Brewer's Sparrow, *Spizella breweri*, helping behavior, cooperative breeding, Okanogan valley, Washington State.

Although reported in two species of the Emberizini (Chipping Sparrow, *Spizella passerina*, by Middleton and Prescott 1989; Bobolink, *Dolichonyx oryzivorus*, by Beason and Trout 1984), cooperative breeding has not been reported in the Brewer's Sparrow, *Spizella breweri*, despite many intensive studies of its ecology (Dawson et al. 1979; Reynolds 1981; Petersen et al. 1986; Wiens et al.

1986). In most species, cooperative breeding involves helpers-at-the nest (Emlen and Vehrencamp 1983). We document the first case of helping behavior in the sagebrush subspecies of Brewer's Sparrow.

While observing sixteen active nests as part of a larger study of Brewer's Sparrow breeding ecology, three adults were observed attending a single nest on a study site just south of the United States-Canada

border (48° 58' N, 119° 24' W) in the Okanogan Valley. On 12 June 1995, a color-banded male, a color-banded female and an unmarked adult were seen simultaneously attending a nest containing two, one day-old nestlings. The banded male and female were holding food within 5 m of the nest. Concurrently, the unmarked adult was brooding the nestlings, and flushed from the nest when we approached. All three adults began alarm-calling, but did not behave aggressively toward each other. After we retreated from the nest, both the banded male and female brought food to the nestlings. This was the only occasion we observed all three individuals together. The adult male, captured and color-banded on 1 June, was observed at each visit, calling and defending a territory encompassing the nest. The adult female was also captured and banded on 1 June, 20 m from the nest. Although never seen incubating the eggs, she was observed calling within 50 m of the nest on a number of occasions. An unmarked adult, presumed to be the same one seen on 12 June, was observed incubating the four eggs of this nest on numerous occasions. It is unlikely that any of these Brewer's Sparrows were involved with another nest as no other active nests were found within 35 m at the time, and their activity was centered around this particular nest. The nest later failed from unknown causes between 13 and 15 June.

No observation of copulation was observed between any of the three adults, making it difficult to determine which individual was the helper. As the marked male and unmarked adult were seen visiting the nest before and after hatching, we assumed that they were the parents. The marked female was presumed to be the helper, as she was observed only visiting the nest after hatching. Most reported helpers are younger than the breeders, usually being the breeders' reproductively mature offspring (Brown 1978). This presumed helper was assessed as reproductively mature when captured, and she was seen nesting with a marked male in an adjacent territory after the original nest's failure.

There are few records of sexually mature helpers in migratory species (Beason and Trout 1984). Most other cooperative breeding migratory species such as Barn Swallows (*Hirundo rustica*) and Chimney Swifts (*Chaetura pelagica*) involve young-of-the-year as helpers (Dexter 1952; Myers and Waller 1977; Beason and Trout 1984). Prior to this case, the Chipping Sparrow, Bobolink, and Hooded Warbler (*Wilsonia citrina*) (Tarof and Stutchbury 1996) were the only reported migratory, North American species, known to have sexually mature adults as helpers. Helping behavior was considered rare for Chipping Sparrows and Hooded Warblers, as only one instance was observed in each study, while considered more common in the Bobolink, with three cases recorded out of 14 nests observed.

Emlen and Vehrencamp (1983) identified a shortage of territory openings as an ecological determinant of nest helpers in avian species. Sagebrush grassland, the preferred habitat of this subspecies of Brewer's Sparrow, was limited in this area to our 15-ha site, and was surrounded by orchards and antelope bitterbrush habitat. The sagebrush areas of the study site were completely occupied by territories of Brewer's Sparrow (Gill, unpublished data). This may have been an indication of a shortage of territory openings that caused at least one sexually mature adult to become a helper when unable to establish her own territory. Understanding the relationship between habitat fragment size and the proportion of helpers in a population may provide insight into the potential consequences of habitat fragmentation.

As it took several days of intensive observations of the nest before all three adults were seen simultaneously, it is possible that other instances of nest helpers on this study site went undetected. More studies involving marked breeding individuals may increase the number of migratory species that are found to exhibit helping behavior.

Acknowledgments

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Non-melanic Schizochroism in Alberta Evening Grosbeaks, *Coccothraustes vespertinus*

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Hudon, Jocelyn. 1997. Non-melanic schizochroism in Alberta Evening Grosbeaks, *Coccothraustes vespertinus*. *Canadian Field-Naturalist* 111(4): 652-654.

Evening Grosbeaks (*Coccothraustes vespertinus*) lacking all melanin pigments in their plumage have been reported in the last few winters at feeders across Alberta. The birds are completely brilliant yellow, except for primarily white wings and tail and dark eyes. The uniformity of the yellow color on the head of color variants is surprising considering that the black feathers of the crown of typical male Evening Grosbeaks normally contain little carotenoid pigments, about 4% the concentration of yellow pigments in the yellow feathers of the forehead (and about 17% the concentration in the greenish-olive feathers of the hindneck). The dearth of carotenoid pigments in the crown feathers of typical Evening Grosbeaks suggests that heavy deposition of melanin in those feathers somehow reduces concomitant deposition of carotenoids. Because the color change reported here is highly reminiscent of that which led to creation of the yellow form of the canary from a primarily green ancestor at the end of the seventeenth century, it may involve a homologous or functionally related gene.

Key Words: Evening Grosbeak, *Coccothraustes vespertinus*, canary, non-melanic schizochroism, plumage coloration.

Large yellow, and rather showy, finches resembling large canaries with unusually large bills have been reported in the last few winters at feeders across Alberta, generally in the company of Evening (*Coccothraustes vespertinus*) and Pine grosbeaks (*Pinicola enucleator*). One such bird was observed at a feeder outside St. Paul in the winter of 1991-1992. A similar looking bird was photographed in Peace River in September 1992. Another one was seen at a feeder in North Star 23 December 1993, and another, or the same one, was at a feeder in nearby Manning from the first week of January until 12 April 1994. I am not aware of other yellow birds having appeared since.

The photographic evidence suggests that perhaps as many as three different individuals may have been involved. The bird in St. Paul had some duskiness on the forehead, a lighter back and sides of the breast, and some black at the tip of some of its secondaries. The bird from Peace River had a uniformly brilliant yellow body and almost immaculately white wings. Finally, the birds from North Star and Manning both were uniformly brilliant yellow with some yellow on the greater secondary coverts and the base of outer secondaries. North Star is only about six km from

Manning, so these two observations likely involved the same individual. Feather replacement (molt) might have altered plumage coloration slightly over the years, but the probability that a single variant individual was recorded three years in a row at well-spaced locales in Alberta is remote.

The birds conformed well to Evening Grosbeaks in size and shape, including that of the bill. In fact, except for the absence of dark pigments (melanins), the birds match perfectly male Evening Grosbeaks, with yellow on the scapulars, forehead, back, rump and underparts. In contrast, female Evening Grosbeaks lack yellow pigments on the head, throat, and underparts.

The unique appearance of the birds, their close resemblance to male Evening Grosbeaks, and their habit of flocking with Evening Grosbeaks strongly suggested that the birds were Evening Grosbeaks that failed to deposit melanin pigments in their feathers. The black eyes of the birds suggested that the birds were otherwise capable of producing melanins. The light color of the bill and legs in typical birds, as in the variant birds, did not permit detection of changes in these structures. Birds such as these that fail to deposit one type of pigment in their plumage

but retain other pigment types are called schizochroic (Rensch 1925). When the ensuing coloration is yellow, the birds may be referred to as xanthochroic (Rensch 1925), although this term is usually reserved for situations in which the normal plumage pigments are actively replaced by yellow pigments (Harrison 1963). In situations where the absence of melanin pigments leaves carotenoid pigments phenotypically apparent, the term non-melanic schizochroism is preferred (Harrison 1963).

The uniformity of the yellow color on the head of schizochroic Evening Grosbeaks is somewhat surprising, considering that typical male Evening Grosbeaks have largely dark heads, including a completely black crown, and thus would not normally need to deposit bright carotenoids over part of the head. Does this imply that carotenoid pigments are deposited alongside melanin pigments in the black feathers of typical birds but are not visible there? To address this question I quantified the amount of carotenoid pigments in the yellow, greenish olive, and black feathers of the forehead, hindneck and crown, respectively, of an adult male Evening Grosbeak in winter plumage (a window kill of 10 December 1989). The carotenoid pigments were extracted in acidified pyridine as described by Hudon and Brush (1992) and transferred to hexane in a separatory funnel. The concentrations of carotenoids in the various extracts were determined by measuring the absorbance of the extracts at 440 nm, the peak of absorption of the carotenoid mixture present in the Evening Grosbeak, as described by Hudon and Brush (1992).

The yellow forehead feathers of the male Evening Grosbeak had approximately 3.5 times the concentration of carotenoids (0.64 mg/g of feather) found in the greenish-olive hindneck feathers (0.18 mg/g of feather), and about 23 times the concentration of carotenoids in the crown feathers (0.028 mg/g of feather). This suggested that the carotenoid pigments were not deposited uniformly on the head of typical birds, unlike in the variant birds. The fact that the yellow feathers were pigmented from about two-thirds to half of their length, whereas the black feathers (and greenish olive feathers) were pigmented from about half to only a third of their length could account for at most a 50% reduction in carotenoid pigments in the crown and hindneck feathers. The dearth of carotenoid pigments in the black feathers of normal male Evening Grosbeaks suggests instead that heavy melanin deposition somehow reduces concomitant deposition of carotenoid pigments in those feathers. Thus, whereas the deposition of black pigments in the Evening Grosbeak may be under direct genetic control, the deposition of carotenoid pigments on the head appears to be partly or largely under the epigenetic (indirect) control of melanin deposition, through currently unknown physiological mechanisms.

The intensification of carotenoid pigmentation on the crown of the variant Evening Grosbeak is intriguing, considering that the elimination of melanin pigments from the plumage of other birds does not generally alter the quality of the carotenoid patches (examples given by Deane 1876; Rensch 1925; Howell 1952). This suggests that there are various ways to combine carotenoid and melanin pigments to produce multicolored plumages. In instances where the melanin pigments do not contact the carotenoids, e.g., the yellow superciliary spot of the White-throated Sparrow, *Zonotrichia albicollis*, and where inhibition of carotenoid deposition by melanin pigments is not possible, the position of carotenoid patches must be specified in the genome precisely even in normal birds. In many instances where melanin pigments contact carotenoids (e.g., the red nuchal patch of the Northern Flicker, *Colaptes auratus* or red poll of the Common Redpoll, *Carduelis flammea*), melanins do not appear to inhibit carotenoid deposition, and in fact appear to be supplanted by the carotenoids. In contrast, in the Evening Grosbeak, the yellow forehead patch and superciliary appear to be specified largely by the avoidance of deposition of melanins from these specific areas of the plumage. Perhaps in instances where peculiar color patterns are produced, as in the Evening Grosbeak, it is easier to produce them with melanin pigments than it is with carotenoid pigments. There are numerous examples of fine and complex plumage patterns involving melanin pigments, compared to only a few involving carotenoid pigments.

The resemblance of the yellow Evening Grosbeaks to yellow canaries, down to the largely white wings and tail, was striking. Of course, both species are cardueline finches, and presumably have somewhat similar genetic make-ups. Canaries in the wild also are multipatterned birds of primarily greenish hue. The yellow variety of canaries seems to have appeared rather suddenly from such green individuals in captivity at about the end of the seventeenth century (Davenport 1908). Perhaps a mutation in a homologous or functionally related gene also took place in the Evening Grosbeak. Given proper breeding (assuming that the color change is hereditary), the new color variety of the Evening Grosbeak could probably be maintained indefinitely in a pure state. In the canary, the green (wild) allele is incompletely dominant over the yellow (mutant) allele, and has a variable expressivity, so that crossing of green and yellow individuals yields birds with variable blotches of green on a basically yellow plumage.

The indication that there probably were several yellow Evening Grosbeaks in central Alberta in the early 90's suggests that an allele coding for lack of melanins in the plumage is present in the gene pool of the species, and that yellow birds may appear again. Although to my knowledge there are no previous

reports of non-melanic schizochroic Evening Grosbeaks from Alberta, schizochroic Evening Grosbeaks have been described in other parts of the range of the species before. These include a female in Pullman, Washington that had a bright yellow nape, back and tips of breast feathers (but a light gray head and throat), and light gray wings and tail (Svihla 1933); a bird in Connecticut (29 October 1957) that had a brilliant yellow head (except for a few black speckles on the crown), neck, back and underparts, but seemingly normal black and white wings and tail (Saunders 1958); a similar-looking male in Wolfville, Nova Scotia (25 November 1958) that had brownish-olive blotches on the back, yellowish-olive feathers on the breast and upper abdomen, and extra white on the wings and tail (Tufts 1961; Godfrey 1967). Helleiner (1979) reported two more, and perhaps as many as seven, in Nova Scotia in 1970–1977. An “all yellow” bird like those described here, was reported from North Hornell and Hornell, New York, seen in late November 1968 (Groesbeck 1969). Finally, Ron Pittaway had a yellow bird also like the ones described from Alberta at his feeder in Minden, Ontario, in the mid-1980s (personal communication). These multiple occurrences imply either that the mutation(s) that cause(s) the variant color recur(s) frequently in the species or that birds carrying the mutation(s) wander widely, as the species is well known to do. The marked differences in appearance of variant birds suggest that different alleles of the mutation, perhaps even different genes, are involved, while the fine differences between individuals of the same “gestalt” could be due to differences in genetic background.

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An Example of Endurance in an Old Wolf, *Canis lupus*

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An 11 to 13-year-old Arctic Wolf (*Canis lupus arctos*) was observed chasing a young Arctic Hare (*Lepus arcticus*) for 6 to 7 minutes and catching it. This provides an example of the degree of endurance of which an old wolf is capable.

Key Words: Wolf, *Canis lupus*, Arctic Hare, *Lepus arcticus*, endurance, predation, hunting behavior, caching.

Many descriptions of Wolves (*Canis lupus*) hunting have been published (Murie 1944; Crisler 1956; Mech 1966; Mech and Frenzel 1971; Peterson 1977; Carbyn and Trottier 1988). However, none has pro-

vided a specific example of the endurance of which a known-old Wolf is capable. The observation of a female Wolf chasing, following, and tracking a White-tailed Deer (*Odocoileus virginianus*) for 21

km over a 130-minute period provides some insight, but that pursuit did not take place at high speed, and it involved a 2.5-year-old Wolf (Mech and Korb 1978).

I describe here a chase by an 11 to 13-year-old, male Arctic Wolf (*C. l. arctos*) of an Arctic Hare (*Lepus arctos*) that gives new insights into Wolf endurance. Wolves rarely live > 13 years in the wild and 16 in captivity (Mech 1988). I first observed the Wolf in this account on Ellesmere Island, Northwest Territories, Canada, during 1986 as a member of a pack that I habituated to my close presence (Mech 1988, 1995). The Wolf was distinguishable by a large wound on his left shoulder during 1986 and 1987 and by his behavior toward me from 1986 through 1996 as I observed him at distances of < 2 m (Mech 1995).

In 1986, this Wolf must have been at least 1-year old because of his size, and his behavior seemed to be mature enough for a 2 or 3-year-old animal, but he was not the dominant male of the pack. Because it is unlikely for a Wolf to remain in a pack more than three years, unless it assumes the breeding role (Gese and Mech 1991), this Wolf was probably not more than 3-years old in 1986.

In 1988, this Wolf which I called "Left Shoulder" became the breeding male in the pack, and he maintained that role through summer 1996; the only other males in the pack from 1988 to 1996 were his offspring (Mech 1995). In 1996, Left Shoulder's lower canine teeth were broken or worn to 1/3 to 1/2 their normal length.

I made the following observation of this Wolf through binoculars from about 200 m away on 25 July 1996. The terrain consisted primarily of low hills covered by snow-free, bare soil and scree, with low hummocks in valleys. No vegetation was higher than a few cm.

The Wolf and his mate had been hunting young hares intermittently from 0045 to 0250 when the female headed back toward their den some 8 km away. The male slept from 0312 to 0535 and then arose. He walked NW approximately 100 m and suddenly veered E toward a crouching leveret about 10 m away and more-or-less upwind of him. He walked by the hare, passing 3–7 m by it and got about 7 m beyond, turned, and went back toward it. The hare then jumped up, and the chase began.

The Wolf chased the hare for 6–7 minutes and almost caught it several times, but the hare's ability to make quick turns helped it elude the Wolf since the Wolf could not turn so sharply. The chase went back and forth, up and down gently sloping hills covering a distance with a maximum radius of an estimated 300 m. At times, the hare was as far as an estimated 30 m ahead of the Wolf. Finally at 0544 the hare seemed to tire and slow down, and the Wolf pounced on it.

The Wolf then rested, standing and panting from 0544 to 0551, when he lay down. He continued to lie and pant until 0606 when an associate of mine inadvertently disturbed him. The Wolf arose, carried the hare off, and cached it. He then slept from 0632 to 0712, and then left the area. I later dug up the cache and found that the leveret weighed 1.45 kg.

This observation indicates that even an old Wolf can persist in a long pursuit at high speed for several minutes. That such a chase taxed the Wolf was evidenced by the animal's 22-minute rest before caching his quarry and his 40-minute sleep after that. In comparison, a yearling female Wolf observed chasing a young Arctic Hare on 10 July 1993 for 3 minutes rested 11 minutes before she began eating the hare.

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Predation Attempts on Incubating Common Loons, *Gavia immer*, and the Significance of Shoreline Nesting

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It has been suggested that loons (*Gavia* spp.) nest close to water to facilitate quick escape from predators. However, predation on incubating loons has never been documented. We document two predation attempts on an incubating pair of Common Loons (*G. immer*) by a mature Bald Eagle (*Haliaeetus leucocephalus*).

Key Words: Common Loon, *Gavia immer*, Bald Eagle, *Haliaeetus leucocephalus*, nesting behavior, predator.

Loon (*Gavia* spp.) eggs and chicks often fall victim to avian, mammalian, and underwater (e.g., turtles, fish) predators (McIntyre 1977; Götmark et al. 1990). However, very little is known about predation on adult loons (McIntyre 1988). It has been suggested that loons nest close to deep water to facilitate escape from predators (Olson and Marshall 1952; McIntyre 1983), yet predation on nesting adults has never been reported. We describe such attacks by Bald Eagles (*Haliaeetus leucocephalus*).

From a distance of 100m, using a 25X spotting scope, we witnessed a Bald Eagle attack a color-marked, incubating, Common Loon (*G. immer*) at the Turtle Flambeau Flowage in north-central Wisconsin (46°0'N, 90°10'W) during a time-budget study on reproductive behavior (Paruk, in preparation). The loon was identified as a male by call; only males yodel (McIntyre 1988). At 18:50 on 24 May 1995, the loon had been incubating two, 7- and 8-day-old eggs for 5 h on a nest was located at the edge of a floating bog, surrounded on three sides by 0.8 m high vegetation (*Carex* spp., *Spirea tomentosa*). The loon's mate was not in sight. As a mature Bald Eagle approached overhead, the loon became alert, raised its neck to an "upright" position, and emitted a three-note wail. Seconds later, the eagle dove to within 1.5 m above the loon. The loon remained on the nest. As the eagle swooped a second time, the loon dove into the water directly in front of the nest and submerged itself. The eagle immediately landed on the loon's back and held the loon underwater 0.5 m from the nest's edge. The loon struggled and splashed, but the eagle remained on top of it for 20 s until the loon freed itself and surface-rushed across the water. The loon swam in semi-circles approximately 8 m in front of the nest and gave 15–20 three-note wails and the initiation of one yodel. The eagle remained motionless on the water between the loon and the nest for 2 min, then took flight.

Once the eagle was out of sight, the loon dove briefly around the nest area, moved 200 m away,

preened for about 2 min, then swam out of sight. The eggs remained undisturbed on the nest until 1 h later when the loon's mate returned and took over incubation. The eagle did not return before we left the site 30 min after sundown. The male loon resumed incubation duties the following day. No injuries to the loon were visible at that time, nor three weeks later when the loon was inspected in the hand (personal observation).

Later, on 10 June 1995, one day before the loons' eggs hatched, a mature Bald Eagle flew within 5 m of the incubating female loon of this pair, driving her from the nest. She resumed nest-sitting once the eagle was out of sight, approximately 20 min later.

Prior to these observations, only one record described eagle predation on an adult-sized loon on breeding grounds, an immature, parasitized, and oiled Pacific Loon (*G. pacifica*) swimming in open water (Hatler 1974). It appears that eagles also attempt to take healthy loons as the pair we witnessed was in sufficient health to fledge two chicks that breeding season.

These observations provide support for the hypothesis that edge-nesting facilitates escape by loons from predators. Loons' legs are positioned posteriorly on the body and as a result they travel poorly on land but are excellent divers. The nest belonging to the pair we witnessed was located immediately adjacent to water 0.5 m in depth. Had these loons not reached deep water so quickly, they may not have escaped.

Selective advantages for specific behaviors are often difficult to test in the field due to recent habitat alterations, human disturbance, and changes in population densities. There are 11 pairs of Bald Eagles, 22 pairs of Common Loons, plus non-breeders of both species at the Turtle Flambeau Flowage (B. Bacon, Wisconsin DNR, personal communication), thus the potential for eagle-loon interactions is high. The eagle-loon ratio on this 9040 ha impoundment may approximate conditions

that preceded recent declines of both species across their North American ranges and which existed during the period when nest site selection evolved. The placement of loon nests close to deep water probably has several selective advantages; these observations provide support for one of them, reduced risk of predation.

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A Simple Technique to Capture Breeding Adults and Broods of Surf Scoters, *Melanitta perspicillata*

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We used mist nets strung above and below the water surface to capture pairs prior to and during nest initiation, and to capture ducklings during brood-rearing. We discuss possible modifications of this technique to improve its effectiveness for capturing Surf Scoters and other diving ducks.

Key Words: Surf Scoters, *Melanitta perspicillata*, capture, mist nets, Lake Malbaie, Québec.

Reproductive and ecological studies of waterfowl are greatly enhanced by the presence of marked individuals. Recent recognition of the importance of individual differences in behavior highlights the need to have individually marked birds. Capturing broods with parent(s) is also important in genetic studies. Entanglement nets and mirror traps, have been used to capture diving ducks at various stages of their life cycle (Johnson 1972; Brown 1981; Savard 1985; Breault and Cheng 1990; Kaiser et al. 1995). In 1995, we captured Surf Scoters at Lake Malbaie, Québec (664 ha, 47° 34' N, 71° 00' W) located 90 km north of Québec City in the Laurentides Wildlife Reserve (Reed et al. 1995). We modified mist net techniques (Breault and Cheng 1990) to allow the capture of breeding adults and juveniles Surf Scoters (*Melanitta perspicillata*) with minimal disruption of breeding events. This simple way to capture Surf Scoters will allow more detailed

studies on the ecology of this relatively unstudied species (Bellrose 1976).

Methods and Results

Mist nets set up near the lake shore to capture adults.

Captures were attempted between 1 June and 5 July at four sites frequented by feeding scoters. Two nets (12 × 2.6m, 121 mm mesh) were set up end to end, extending perpendicularly from the shore. The two nets formed a straight line 24 m long, extending from approximately 5 m from shore in shallow areas (<1.5 m) toward the center of the lake. The technique, originally developed to capture seabirds over open water (Kaiser et al. 1995; Burns et al. 1995) was modified by replacing the floating devices designed to support the poles by less obtrusive poles planted directly in the lake bottom. We used three copper poles (2 cm in diameter by 3.5 m high) painted black, and pushed firmly into the sandy lake bottom. Two

anchors with black guy ropes were attached to the top of each pole to ensure stability. The bottom of the net was < 1 m below the water surface to ensure the capture of diving individuals, the top of net was above water. Two people took less than 25 min to set up the net from a boat or with chest waders, and approximately 10 min to remove it.

Captures occurred during daylight hours. Pairs of breeding scoters were allowed to approach the net of their own accord, but had to be driven by boat over the last 20 m, then flushed when < 5 m from the net. We usually selected a single pair for the drive but we once drove three pairs together, capturing four birds. A single boat equipped with a 9.9 horsepower motor was used. During the drive, the boat was kept parallel to the shore and reverse gear was often used to maintain proper orientation and slow forward motion to ensure that the birds did not flush until close to the net. The scoters had to be driven into the wind to ensure that they took flight toward the net. At about 50 m from the net we gradually accelerated, positioning the boat so that at about 10 m from the net, it was behind the scoters facing the net. When the birds got within 5 m of the net they were flushed toward the net. Very few birds dove when they reached the net and usually flew into it. Each drive lasted less than 30 min. A total of 22 birds (5 males, 17 females) were captured.

Submerged mist nets to capture broods.

From 20 July to 24 August 1995, we used the same basic technique with mist nets to capture broods, except that the net was submerged. A similar technique was developed by Breault and Cheng (1990) using underwater nets to capture diving birds, but our net was mounted on poles. The net was positioned perpendicular to the shore, extending 24 m outward from a point about 20 m from shore because broods tended to swim away from the shore at the approach of a boat. We used 2.5 m long metal rods passed through the bottom mesh to anchor the bottom of the net to the lake bed. The upper 30 cm of the net extended above the water surface. To capture

Class I ducklings (Gollop and Marshall 1954), we used mist nets with 40 mm mesh size and for Class 2 and 3 ducklings, we used 120 mm mesh size.

We drove individual broods, concentrating on manoeuvring the adult female toward the net. It proved difficult to drive broods and therefore required the use of a second boat or canoe, especially with older ducklings (Class II - III) still accompanied by the female. When within 1-2 m of the net the brood was rushed to force the birds into the net. Usually the first ducklings caught in the net generated confusion among the remaining ducklings who dove and entangled themselves in the net. Quick action was required to remove the entangled ducklings. This technique was most efficient for small broods. On most occasions the adult female and some ducklings escaped. Usually the adult female and the escaped ducklings re-united quickly nearby; on several occasions we were able to re-approach the escaped members of the brood and successfully release the captured individuals back into the brood. A total of 26 ducklings and 2 adult females were captured (Table 1) with no injury or mortality. Although based on a small sample of 10 broods, efficiency appeared greater with smaller broods and when broods were not accompanied by an adult.

Discussion

When using mist nets perpendicular to the lake shore, adult Surf Scoters were easily approached by boat and usually took off at close range, flying close to the water surface. This allowed us to drive individuals or pairs towards the capture site before pushing them in the net direction. Mist nets are relatively inexpensive and easy to use. They are also a safe method to capture birds because no injuries or mortality occurred during our capture sessions. Because of the proximity of a forested background, nets may be less visible to flying waterfowl thus enhancing the efficiency of the technique. It would probably work well for other waterfowl species like mergansers. On lakes where water depth or substrate make it difficult

TABLE 1. Juveniles Surf Scoters captured using underwater mist nets in 1995.

Number of broods	Brood composition		Age of brood*	Ratio**	Efficiency
	Female	Brood size			
1		1	3	1/1	100%
1		3	3	2/3	67%
1	1	4	1c	3/4	75%
1	1	6	1a-1b	1/6	17%
3	1	8	1a-1b-2a	9/24	38%
2	1	9	1c-2a	3/18	17%
1	1	10	1b	7/10	70%

*Age classes following Gollop and Marshall (1954).

**The ratio represents the number of ducklings captured versus the number of ducklings initially present in the brood.

to drive the poles into the lake bottom, nets could be mounted on floating rafts as described by Kaiser et al. (1995) and Burns et al. (1995).

Capture of adult male diving ducks in spring is usually difficult. Savard (1985) used mirror traps successfully with goldeneyes but that technique is not effective with waterfowl like scoters that are not territorially aggressive. Our technique allowed the capture of breeding male Surf Scoters and pre-laying and laying females, enabling us to mark individuals without disturbing females at the nest site and thus avoiding nest abandonment. The technique could also be used to capture molting birds.

In 1994, we conducted two attempts to capture broods by driving them towards funnel traps of nylon netting leading into a chicken-wire holding pen. These traps were set in open water, approximately 10 m from shore. In both attempts, the broods were reluctant to approach within 100-200 m of the trap, despite repeated attempts to drive them slowly using 2-3 boats. Reluctance to approach the trap appeared to be related to its greater visibility compared to mist nets. Less conspicuous leads and a more efficient trap door would possibly improve the efficiency of that technique.

Underwater mist nets proved effective for capturing ducklings. The bottom of the net had to be well anchored to the lake bottom with stones or metal poles because otherwise the first duckling trapped would rise to the surface with the net, creating an opening for other ducklings to swim through. We believed that some ducklings from large broods had escaped in this way during early attempts when the net was not anchored to the lake bed. It appeared that when the female left her ducklings (advanced age classes or separated during the drive) the catch efficiency increased.

Our approach for ducklings proved effective because Surf Scoter broods or crèches showed less reluctance to approach the unobtrusive nets than funnel traps. Furthermore, mist nets are easily and quickly set up, are less time-consuming, and require fewer boats than funnel traps. The main drawback is that sometimes several ducklings fail to become entangled and most adult females would break through the net and escape. Underwater mist nets could also be used to capture molting birds. The technique could be improved by carefully choosing

mesh sizes in relation to the size of the ducklings, and by backing that net with one of greater strength and larger mesh size to ensure capture of adult females accompanying the broods.

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Range Extension of the Rainbow Smelt, *Osmerus mordax*, in the Hudson Bay Drainage of Manitoba

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Remnant, Richard A., Paul G. Graveline, and Ronald L. Bretecher. 1997. Range extension of the Rainbow Smelt, *Osmerus mordax*, in the Hudson Bay drainage of Manitoba. *Canadian Field-Naturalist* 111(4): 660-662.

Rainbow Smelt, *Osmerus mordax*, were captured in experimental gillnet surveys of three hydroelectric generating station forebays of the lower Nelson River during August, 1996. Six smelt were captured in Limestone and Long Spruce forebays, while a seventh specimen was collected from the stomach of a Walleye, *Stizostedion vitreum*, captured in Stephens Lake. These specimens represent the most downstream captures of Rainbow Smelt in the Hudson Bay drainage of Manitoba. Rainbow Smelt captured in Playgreen, Sipiwesk, and Split lakes between 1994 and 1996 also are reported here. The movement of Rainbow Smelt to, if not into, Hudson Bay appears imminent.

Key Words: Rainbow Smelt, *Osmerus mordax*, exotic fish, zoogeography, Hudson Bay drainage, Manitoba.

Rainbow Smelt, *Osmerus mordax*, were captured in three hydroelectric generating station forebays of the lower Nelson River, Manitoba, during August, 1996. These captures were made as part of experimental gillnet (3.8 - 12.7 cm stretched mesh) surveys of Stephens Lake (56° 23' N, 94° 55' W), Long Spruce Forebay (56° 23' N, 94° 30' W), and Limestone Forebay (56° 26' N, 94° 11' W), three reservoirs created behind hydroelectric generating stations on the lower Nelson River (Figure 1). One Rainbow Smelt was captured in Limestone Forebay and five smelt were captured in Long Spruce Forebay. Fork lengths of these six smelt ranged from 84 to 101 mm. Additionally, one Rainbow Smelt was found in the stomach of a Walleye, *Stizostedion vitreum*, collected from Stephens Lake.

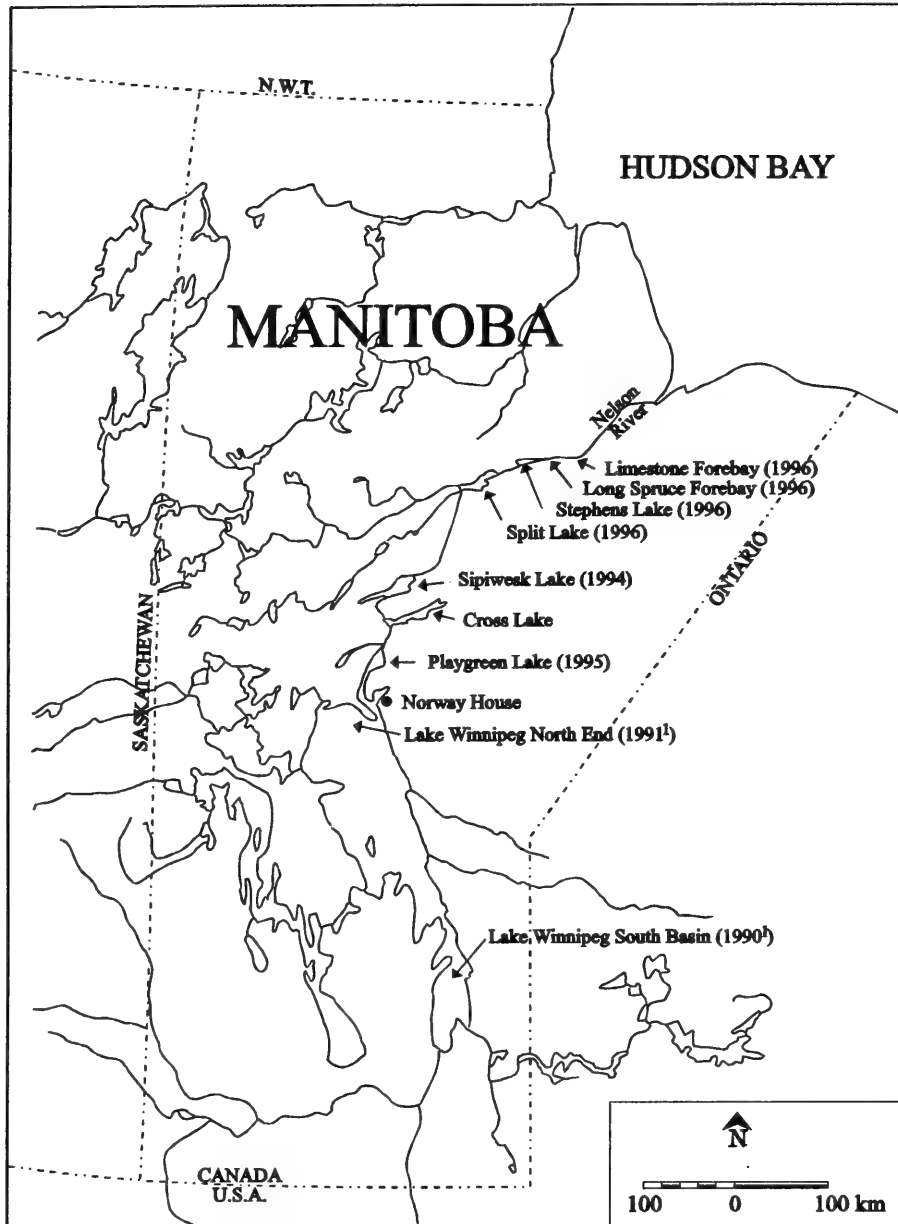
Rainbow Smelt were identified by external characteristics and the presence of vomerine teeth. All specimens were frozen immediately and stored. Identifications were verified by K.W. Stewart, Department of Zoology, University of Manitoba. Subsequently, all specimens were fixed in 10% formalin and deposited in the collection of the Manitoba Museum of Man and Nature (specimen numbers 1.5-740 to 1.5-746).

The first specimens of Rainbow Smelt collected in Manitoba were reported from the South Basin and north end of Lake Winnipeg in 1990 and 1991, respectively (Campbell et al. 1991). Potential origins of Lake Winnipeg smelt were dealt with by Campbell et al. (1991). Since 1993, Rainbow Smelt have been encountered sporadically by commercial fishermen from Norway House while fishing the North End of Lake Winnipeg (North/South Consultants Inc. unpublished data). The first specimens of smelt were confirmed from Playgreen Lake (54° 00' N, 98° 15' W) in fall, 1995 (North/South Consultants Inc., unpublished data). Smelt have never been captured in five years (1992 - 1996) of monitoring of the Cross Lake (54° 45' N, 97° 30' W)

fish community (W. Bernhardt, North/South Consultants Inc., personal communication). Rainbow Smelt were recovered from stomachs of Northern Pike, *Esox lucius*, caught in Sipiwesk Lake (55° 05' N, 97° 35' W) in 1994 (D. MacDonald, Manitoba Natural Resources, personal communication), representing the first verification of specimens captured downstream of Lake Winnipeg. Two Rainbow Smelt were captured in experimental gillnets (3.8 - 12.7 cm stretched mesh) set in Split Lake (56° 08' N, 96° 15' W) in 1996 (D. MacDonald, Manitoba Natural Resources, personal communication).

Prior to 1996, Rainbow Smelt had not been captured in seven years of gillnet surveys of lower Nelson River forebays (B. Horne, North/South Consultants Inc., personal communication). Smelt accounted for 0.64% of the experimental gillnet catch (n = 935) in the three lower Nelson River forebays during 1996. However, given the size of the captured smelt, they were not fully vulnerable to capture in the gillnets used, and likely were more abundant than gillnet catches indicated.

Remnant (1991). An Assessment of the potential impact of the rainbow smelt on the fishery resources of Lake Winnipeg. Unpublished MNRM practicum, University of Manitoba, Winnipeg. 170 pages) predicted that Rainbow Smelt would move down the Nelson River from Lake Winnipeg and inhabit water bodies such as Split and Stephens lakes. The smelt in the lower Nelson River were captured 525 km downstream of the outlet of Lake Winnipeg only six years after they were first documented in Lake Winnipeg. A similar phenomenon was observed in the Missouri River. In 1971, adult Rainbow Smelt were introduced into Lake Sakakawea, North Dakota, and seven years later they were captured in the lower Missouri River in Missouri (a river distance of approximately 1600 km), following population buildup and passage through four major reservoirs (Mayden et al. 1987).



1 - Source: Campbell et al. (1991).

FIGURE 1. Location and collection year of first confirmed specimens of Rainbow Smelt in Manitoba waterbodies.

Historically, Rainbow Smelt were restricted to coastal waters and a few isolated freshwater lakes in eastern North America (Scott and Crossman 1979). Smelt were introduced to the Great Lakes in the early 1900s, and from the Great Lakes they have been intentionally or accidentally introduced into other water bodies (Evans and Loftus 1987). The capture of Rainbow Smelt in the lower Nelson River prompts speculation about the potential of the species to colonize Hudson Bay. Franzin et al. (1994) predicted that Rainbow Smelt would thrive in coastal Hudson Bay, establishing populations in the larger tributaries. Whether or not Rainbow Smelt colonize Hudson Bay is still speculation, however,

with the recent capture of smelt only 175 km upstream of the bay, movement to, if not into, Hudson Bay appears imminent.

Acknowledgments

Work which reported specimens of Rainbow Smelt collected in Playgreen Lake and lower Nelson River gillnet surveys was funded by Manitoba Hydro as part of their ongoing biophysical monitoring programs in northern Manitoba. Kenneth W. Stewart, Department of Zoology, University of Manitoba, verified the identification of specimens. The authors also thank Don MacDonald, Manitoba Natural Resources, 59

Elizabeth Drive, Thompson, Manitoba, R8N 1X4, for providing unpublished information from Sipiwek and Split lakes. A special thanks is due commercial fishermen from Norway House for retaining their specimens of Rainbow Smelt. Kenneth W. Stewart and an anonymous reviewer provided constructive criticism of a draft of the manuscript.

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Distribution Records for the Threespine Stickleback, *Gasterosteus aculeatus* Linnaeus (Pisces: Gasterosteidae), in Manitoba

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McKillop, W. B., and W. M. McKillop. 1997. Distribution records for the Threespine Stickleback, *Gasterosteus aculeatus* Linnaeus (Pisces: Gasterosteidae), in Manitoba. *Canadian Field-Naturalist* 111(4): 662–663.

A 1996 collection in northern Manitoba extended the range of *Gasterosteus aculeatus* Linnaeus inland in Manitoba, west of Hudson Bay, approximately 300 km from the coast.

Key Words: Threespine Stickleback, *Gasterosteus aculeatus*, distribution, colonization, Tyrrell Sea, Hudson Bay, Manitoba.

Gasterosteus aculeatus Linnaeus has been collected from both coasts of North America and along the northwestern coasts of Hudson Bay and James Bay (Lee et al. 1980; Scott and Crossman 1973). Recent expeditions to northern Manitoba have allowed us the opportunity to make dip net collections of invertebrates and small fish on the coast and in many of the province's northern lakes (McKillop 1996). The fish were deposited in The Manitoba Museum, and K. W. Stewart and W. B. Preston have determined that these collections contained the only representative of the Threespine Stickleback held in Manitoba, although the species had been collected in the province in 1966 (Canadian Museum of Nature [NMC] 66-223). This site (Figure 1, Site 1) was on the Caribou River at the southeastern end of Long Lake at 59° 24'N, 95° 18'W. In 1996 we found a single specimen at Nueltin Lake (Figure 1, Site 2) in northwestern Manitoba.

The single specimen (The Manitoba Museum [MMM] 1.5-722) collected at Site 2 in 1996 is of special interest as it not only extends the species distribution to the west in the province but also raises the questions of migration and colonization. A previous collection (NMC 66-224) (Figure 1, Site 3) from Northwest Territories at 60° 23'N, 95° 45'W included one specimen from the Thlewiaza River, the outflow to the coast from Nueltin Lake. Site 3 is 94 m above sea level, 57 km from the coast and approximately 70 km upriver. Site 2, at Nueltin Lake, is 277 m above sea level, 310 km (over 400 km upriver) from the coast at 59° 52'N, 100° 08'W. The specimen is a mature male with a total length of 41 mm. It is a fully plated morph with 31 plates (Bakker and Sevenster 1988) and a caudal keel. In alcohol, it is greenish/beige dorso-laterally and silvery on the sides and below. The specimen was collected at the base of a waterfall flowing from Bagg Lake into

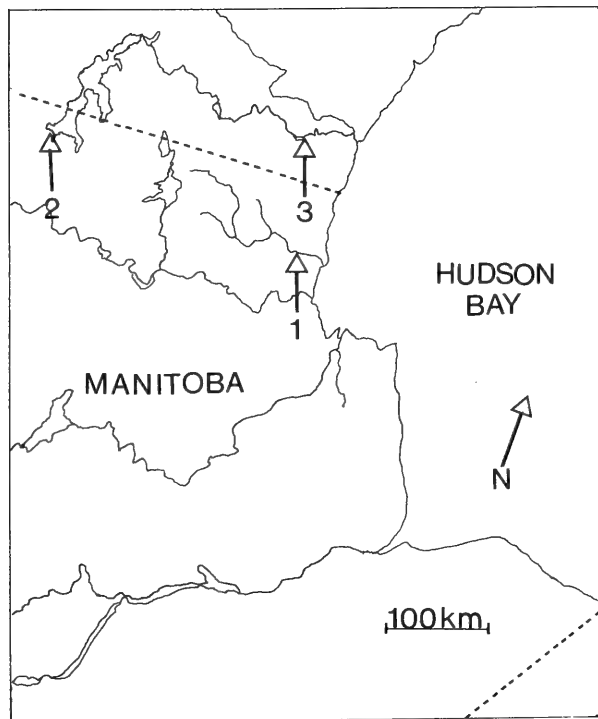


Figure 1. The Nueltin Lake collection (site 2) in relation to the downstream collection in Northwest Territories (site 3) and the previous collection in Manitoba (site 1).

Nueltin Lake, in a quiet, sandy-bottomed backwater, approximately one-half metre in depth, with some aquatic vegetation.

Gasterosteus aculeatus probably spread into the Tyrrell Sea from the Atlantic Ocean shortly after the ice retreated along the Labrador coast about 8000 years BP (McPhail and Lindsey 1970; Crossman and McAllister 1986). Hagen and Moodie (1982) reported the species taken up to 410 km from the sea on the east coast, much farther inland than the specimen reported here.

Certainly the Nueltin Lake population is not anadromous due to the great distance and physical barriers along the Thlewiaza River. Recent colonization from the Hudson Bay coast by human transport is unlikely. It is more probable that the species migrated up the Thlewiaza River during the late Holocene, shortly after deglaciation (about 7000 years BP). At that time the Tyrrell Sea extended approximately 120 km farther inland in the Thlewiaza River valley than the present location of the Hudson Bay shoreline, and was less than 140 km from Nueltin Lake (Dyke and Prest 1986). It was also approximately 183 m above the present level of Hudson Bay. Today, Nueltin Lake is 277 m above modern sea level, or 94 m higher than the elevation of the Tyrrell shoreline. Because little isostatic rebound had occurred by 7000 years BP, there probably was even less elevation difference, possibly as

little as a few tens of metres (E. Nielsen, personal communication 1996).

This would suggest that the species, while rarely collected, is distributed more broadly and much farther inland than previously thought. It should be noted that few collections of any type have been made in this area, and those that have been made used methods that do not effectively sample small fish.

Acknowledgments

We thank Manitoba Heritage Grants and the Manitoba Museum of Man and Nature Foundation for providing grants to support the numerous northern expeditions. K. W. Stewart of the University of Manitoba provided taxonomic determination and also made important improvements to the manuscript. W. B. Preston of The Manitoba Museum allowed access to the specimen. G. E. E. Moodie of the University of Winnipeg and B. Coad of the Canadian Museum of Nature provided additional help for which we are grateful. E. Nielsen of Manitoba Mines and Energy provided information regarding sea levels. Special thanks are extended G. Young for providing editorial suggestions.

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Hyssop-leaved Loosestrife, *Lythrum hyssopifolia* L. (Lythraceae), New to Canada

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Blaney, C. Sean, Michael J. Oldham, and Anton A. Reznicek. 1997. Hyssop-leaved Loosestrife, *Lythrum hyssopifolia* L. (Lythraceae), new to Canada. *Canadian Field-Naturalist* 111(4): 664–665.

Hyssop-leaved Loosestrife (*Lythrum hyssopifolia* L.) is added to the Canadian flora on the basis of a 1992 collection from near Belleville, Hastings County, Ontario. This European adventive is otherwise known in the Great Lakes region only from historical records from southeastern Michigan and central Ohio. Elsewhere in North America, it occurs primarily on the east and west coasts.

Key Words: Hyssop-leaved Loosestrife, *Lythrum hyssopifolia*, Lythraceae, new record, distribution, Ontario.

Hyssop-leaved or Annual Loosestrife (*Lythrum hyssopifolia* L.) is widespread in its native Europe, though local in the north where it occurs primarily as a casual weed (Tutin et al. 1968). In North America it was introduced into the United States in the early 1800s and is now naturalized along the United States Atlantic Coast from Maine to Pennsylvania and on the Pacific Coast from Washington to California (Shinners 1953). According to Gleason and Cronquist (1991) it occurs mostly on wet soil, especially around salt marshes, in northeastern North America. In the Great Lakes states, *L. hyssopifolia* is known only from old records from Michigan and Ohio. The sole Michigan specimen is an 1832 collection from Detroit and the species has not been seen since in the state (Stuckey 1978; Voss 1985). In Ohio it was collected from wet fields near the town of Thatcher in Pickaway County between 1935 and 1955 (Blackwell 1970; Andreas 1989; Cooperrider 1995). It has not been reported previously from Ontario (Morton and Venn 1990) or Canada (Boivin 1966–1967; Scoggan 1978–1979).

In June of 1992, *Lythrum hyssopifolia* was collected from a ploughed, unsown field about 6 km northwest of Belleville, Sidney Township Municipality, Hastings County, Ontario, 44° 12' 00" N, 77° 26' 15" W (C.S. Blaney s.n., DAO, MICH, NHIC - herbarium of the Natural Heritage Information Centre, Peterborough). At the time of collection it was locally abundant, though we do not know if it has persisted at the site since then. The habitat of the Ontario population is similar to that reported for England, where native populations of *L. hyssopifolia* are now restricted to a single locality in south Cambridgeshire. In that area, *L. hyssopifolia* occurs in seasonally wet depressions in grain fields where flooding and ploughing prevent establishment of perennial species (Preston and Whitehouse 1986). Elsewhere in Europe the habi-

tat is reportedly disturbed or seasonally flooded ground (Tutin et al. 1968).

Two other *Lythrum* species occur in Ontario. The exotic wetland weed *L. salicaria*, Purple Loosestrife, and the rare native *L. alatum*, Winged Loosestrife. The former is a tall perennial with opposite or whorled leaves, pubescent stems (at least in the region of the inflorescence), showy, terminal, spike-like inflorescences, and petals 7 to 11 mm long. *Lythrum alatum* is a glabrous, branched perennial, with flowers borne in the axils of small linear bracts on the upper half of the plant, and petals 4 to 7 mm long. *Lythrum hyssopifolia* is a small, glabrous, simple or loosely branched annual, with flowers borne all (or almost all) of the way to the base of the plant in axils of small, more or less linear leaves, and petals 2 to 3 mm long. All three species have purple or pink (occasionally white) flowers.

In contrast to *Lythrum salicaria*, which has become a serious weed of North American wetlands (Thompson et al. 1987, Mal et al. 1992), *L. hyssopifolia* has poor competitive ability (Preston and Whitehouse 1986). It is unlikely therefore, that the species will behave as an aggressive invader.

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Addendum

Since this article was accepted for publication, the following new information can be provided.

1. The site of the original 1992 collection was revisited on 4 July 1997 by Blaney and Oldham, and *Lythrum hyssopifolia* was still present. Distribution and abundance at the site had not changed significantly between 1992 and 1997. Several thousand *L. hyssopifolia* plants were observed growing along the moist edges of a soybean (*Glycine max*) field, adjacent to a wetland. Associated plant species were typical of agricultural field edges in southern Ontario (*Poa compressa*, *Agrostis stolonifera*, *Artemisia biennis*, *Equisetum arvense*, *Juncus bufonius*, *Phleum pratense*, *Trifolium aureum*). *Lythrum hyssopifolia* was virtually absent from drier parts of the cultivated field and was not in direct association with the soybean crop. An additional specimen was collected (M.J. Oldham 19866 & C.S. Blaney, duplicates to be distributed to regional herbaria).
2. The date of the original collection was 1 July 1992 (not June 1992).
3. A recent publication (Callaghan, D. A. 1996. The conservation status of *Lythrum hyssopifolia* L. in the British Isles. Watsonia 21:179–186.) provides additional information on the species in Britain.

Received 4 July 1997

News and Comment

Notices

Canadian Species at Risk April 1997

This 19-page booklet contains the latest update of the decisions of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) for all species designated in the five "risk" categories and two other non-designated categories ("not at risk" and "indeterminate"). Current geographical occurrence (for Canada, by province, territory, or ocean) are included for each species.

Thirty-one species, 27 of them considered for the first time, were designated at the April 1997 COSEWIC meetings [* indicates four previously designated species whose status was re-examined, but not changed from their previous assignment category]:

EXTIRPATED (2)

- Sage Grouse, *Centrocercus urophasianus phasio*, British Columbia population
- Karner Blue Butterfly, *Lycaeides melissa samuelis*, Ontario

ENDANGERED (4)

- * Vancouver Island Marmot, *Marmota vancouverensis*, British Columbia
- * White Whale [Beluga], *Delphinapterus leucas*, Quebec: St. Lawrence River population
- Maritime Ringlet Butterfly, *Coenonympha tullia nipisiquit*, New Brunswick
- Long's Braya, *Braya longii*, Newfoundland

THREATENED (5)

- Sage Grouse, *Centrocercus urophasianus urophasianus* (Prairie population), Alberta and Saskatchewan
- Banff Springs Snail, *Physella johnsoni*, Alberta
- Fernald's Braya, *Braya fernaldii*, Newfoundland
- False Hop Sedge, *Carex lupuliformis*, Ontario, Quebec
- Apple Moss, *Bartramia stricta*, British Columbia

VULNERABLE (6)

- Pacific Great Blue Heron, *Ardea herodias fannini*, British Columbia
- Eastern Hognose Snake, *Heterodon platirhinus*, Ontario
- Western Silvery Minnow, *Hybognathus argyritis*, Alberta
- Cultus Pigmy Sculpin, *Cottus* sp., British Columbia
- Monarch Butterfly, *Danaus plexippus*, All provinces
- Fernald's Milk-vetch, *Astragalus robbinsii* var. *feraldii*, Newfoundland, Quebec

SPECIES EXAMINED AND DESIGNATED IN THE NOT AT RISK CATEGORY (8)

- * Sharp-shinned Hawk, *Accipiter striatus*, All provinces and territories
- Common Loon, *Gavia immer*, All provinces and territories
- Yellow-billed Loon, *Gavia adamsii*, Alberta, British Columbia, Manitoba, Northwest Territories, Quebec, Yukon Territory
- Eastern Silvery Minnow, *Hybognathus regius*, Ontario, Quebec
- Chain Pickerel, *Essox niger*, New Brunswick, Nova Scotia, Quebec
- MacLean's Goldenweed, *Haplopappus macleanii*, Yukon Territory
- Pacific Rhododendron, *Rhododendron macrophyllum*, British Columbia
- Wood's Sagebrush, *Artemisia rupestris* ssp. *woodii*, Yukon Territory

SPECIES EXAMINED AND DESIGNATED IN THE INDETERMINATE CATEGORY BECAUSE OF INSUFFICIENT INFORMATION (6)

- Dwarf Sperm Whale, *Kogia simus*, Pacific Ocean
- Chiselmouth, *Acrocheilus alutaceus*, British Columbia
- Spinynose Sculpin, *Asemichthys taylori*, Pacific Coast
- Gatineau Tadpole Snail, *Physella parkeri lachfordi*, Ontario(?), Quebec
- Rabbit-brush Godenweed, *Ericameria bloomeri*, British Columbia
- Impoverished Pinweed, *Lechea intermedia* var. *depauperata*, Saskatchewan

The complete list of all designations can be obtained from COSEWIC Secretariat, c/o Canadian Wildlife Service, Environment Canada, Ottawa, Ontario K1A 0H3; Telephone 819-997-4991; Fax 819-953-6283; e-mail: sylvia.normand@ec.gc.ca

The Boreal Dip Net

Volume 2, Number 1, Winter-Spring 1997. This publication is the Newsletter of the "Canadian Amphibian and Reptile Conservation Network" a new name for the group previously known as the "Working Group on Amphibian and Reptile Conservation in Canada". This 12-page issue includes a news item on the progress with fund-raising for the group, including three new benefactors, two artists donating paintings and a company donating 10% of profits on a T-shirt with "Native Frog" logo. A summary report covers the network meetings at the University of Calgary, 5-7 October 1996. A feature article discusses "Are amphibian populations disappearing? A task force status report 1996-1997" and covers six years of world evaluations. "Contaminants, deformities and lots of hypotheses" by Christine A. Bishop and "News from eastern Canada" by Carolyn Seburn [covering monitoring, conservation, and research], and minor news items plus an announcement and call for papers for October 1997 meetings in Nova Scotia complete the issue.

The Ontario Chorus

Volume 1, Number 3, January 1997. Four pages and a two-page inset on recording site locations. A brief summary of the cool spring of 1997 ("And you thought you had it bad") is followed with a note on web sites, notice of National Wildlife Week (6-12 April), summary of "The Marsh Monitoring Program" in the Great Lakes basin, and an "Appreciation Corner" of acknowledgment to volunteers.

Program and Abstracts: 1st Annual Meeting of the Working Group on Amphibian and Reptile Conservation in Canada and 6th Annual Meeting of the IUCN/SSC Task Force on Declining Amphibian Populations in Canada (DAPCAN)

These meetings were held at the University of Calgary, 5-7 October 1996, and co-sponsored by the Ecological Monitoring Co-ordinating Office, Environment Canada, Burlington, Ontario. Abstracts cover of 31 papers by 44 contributors.

The *Boreal Dip Net*, *Ontario Chorus*, and *Program and Abstracts* are distributed by The Canadian Wildlife Service, Canada Centre for Inland Waters, Environment Canada, P.O. Box 5050, 867 Lakeshore Road, Burlington, Ontario L7R 4AF.

Froglog: Newsletter of the Declining Amphibian Populations Task Force

Number 22, June 1997, contains notes on "Disease, stress, and amphibian declines" by Cynthia Carey, DAPTF Climate and Atmospheric Change Working Group; "The DAPTF in Prague": activities scheduled during the Prague meeting of the World Congress of Herpetology; "Workshop on amphibian deformities at Shenandoah National Park" by Martin Ouellet; "Limb deformities in the anurans of Quebec: Abstract [from a paper in *Journal of Wildlife Diseases* 33: 95-104 by M. Ouellet, J. Bonin, J. Rodrigue, L.-J. DesGranges, and S. Lair. 1997. Hindlimb deformities (ectromella, ectrodactyly) in free-living anurans from agricultural habitats]; Recent amphibian declines in lower Central America by Karen R. Lipps; Extract from Alytes; DAFTF Reports; Froglog Shorts; Publications of interest.

Froglog is available from Editor John Wilkinson, Department of Biology, The Open University, Walton Hall, Milton Keynes, MK7 6AA, United Kingdom; e-mail DAPTF@open.ac.uk and on the World Wide Web at the following URL: <http://acs-info.open.ac.uk/info/newsletters/FROGLOG.html>

Rana-Saura: Amphibian population monitoring program; Atlas of amphibians and reptiles of Quebec

Volume 4, Number 1, May 1997, contains the latest progress on the monitoring program and the Atlas, including goals, numbers of participants, new records. For more information contact David Rodrigue, Saint Lawrence Valley Natural History Society, 21125 ch. Ste-Marie, Ste-Anne-de-Bellevue, Quebec H9X 3L2; e-mail: ecomus@total.net

Canadian Association of Herpetologists Bulletin

Volume 11, Number 1, spring 1997, contains reports on Herpetology at University of Guelph (Jim Bogart), University of Windsor (Stephen Hecnar) and Redpath Museum, McGill University (David Green). There are also "Work in Progress" reports from Marc J. Mazerolle, Donald F. McAlpine and Patrick Garcia. Meetings reported on are the Workshop on Amphibian Deformities at Shenandoah National Park (15-6 April 1997); the then anticipated Fifth International Congress of Vertebrate Morphology (12-17 July 1997)

at University of Bristol, United Kingdom; and the Canadian Herpetology Conference to be held at Wolfville, Nova Scotia (3-5 October 1997). Conservation Status Ranks of the Amphibians and Reptiles of Manitoba are given by James R. Duncan, Manitoba Conservation Centre, Winnipeg. There are three brief notices of Publications of Interest. Five recent Canadian herpetological theses are listed (and abstracts given for each): Stephen J. Hecnar, Ph.D. 1997. University of Windsor, Windsor, Ontario (*Supervisor*: Dr. Robert T. M'Closkey) Species Richness, Species Turnover, and Spatial Dynamics of Amphibian Communities; Sheri Watson, M.Sc. 1997. Department of Biological Sciences, University of Calgary, Alberta (*Supervisor*: Dr. Anthony Russell) Food Level Effects on Metamorphic Timing in the Long-toed Salamander, *Ambystoma macrodactylum krausei*; Raymond A. Saumure, M.Sc. 1997. McGill University, Montreal, Quebec (*Supervisor*: Dr. Roger Bider) Growth, Mutilation, and Age Structure of Two Populations of Wood Turtles (*Clemmys insculpta*) in southern Quebec; Karen Leigh Graham, M.Sc. 1997. University of Guelph (*Supervisor*: Dr. J. P. Bogart) Habitat Use by Long-toed Salamanders at Three Different Scales; Ben Porchuk, M.Sc. 1996. University of Guelph (*Supervisor*: Dr. R. J. Brooks) Ecology and Conservation of the Endangered Blue Racer Snake (*Coluber constrictor foxii*) on Pelee Island, Canada.

Membership in the Canadian Association of Herpetologists / Association Canadienne des Herpetologistes is \$10.00 for regular members and \$5.00 for students payable to Dr. Patrick T. Gregory, Treasurer CAH/ACH, Department of Biology, University of Victoria, Victoria, British Columbia, Canada V8W 2Y2.

Recovery: An Endangered Species Newsletter

The spring 1997 (received 2 September) issue of this publication by the Canadian Wildlife Service, (coordinated by Chuck Dauphine, CWS; designed by West Hawk Communications, Ottawa; ISSN 0847-0294) contains a lead article on the addition of three butterflies to the list of species at risk in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) - the Monarch, the Karner Blue, and the Maritime Ringlet. A RENEW (Recovery of Nationally Endangered Wildlife) update covers a multi-species recovery plan targeting the Acadian Flycatcher and the Hooded Warbler. There is an Essay section - "Protecting species behind the trees" by Simon Nadeau and Jean-Pierre Martel, an Editorial "The challenge of protecting species" by Sheila Forsyth, and three features on the Canadian federal Endangered Species Protection Act (Bill C-65) which failed to receive complete consideration in the last Parliament and died on the Order Paper with the session's dissolution at the call for a new election in June ("Federal Act halted in Parliament", "How Canada makes a law" both by Deborah Gudgeon Harris; and "A comparison of provincial laws by Theresa Aniskowicz); a COSEWIC update ("Mapping the 'hotspots'" by Erich Haber) two book reviews (The 1996 IUCN Red List of Threatened Animals; Canada's Biodiversity: The variety of life, its status, economic benefits, conservation costs and unmet needs); and a Featured Species ("The return of the 'pancake turtle'" by Michelle Fletcher) on the Spiny Softshell, *Apolone spinifera*, in Ontario.

Recovery is available free in either English or French (sous le titre *Sauvegarde*) from Canadian Wildlife Service, Environment Canada, Ottawa, Canada K1A 0H3.

Amphipacifica: Journal of Systematic Biology

Volume 2, Number 3, Pages 1 to 140, is dated 15 May 1997 and contains two major research articles: "The Amphipod Superfamily Eusiroidea in the North Pacific Region. II. Family Calliopiidae. Systematics and Distributional Ecology" by E. L. Bousfield and E. A. Hendrycks (pages 3-66) and "The Amphipod Superfamily Corophioidea on the Pacific Coast of North America. Part V. Family Corophiidae. Corophiinae, new subfamily. Systematics and Distributional Ecology" by E. L. Bousfield and P. M. Hover (pages 67-139). The issue concludes (page 140) with a list of errata for *Amphipacifica*. A two-page editorial begins the issue and includes tributes to the editor's late and lamented colleagues Leo Margolis 1927-1997 and Jan H. Stock 1931-1997.

The editorial (page 1) notes the change from quarterly to occasional publication for the journal due to ill-health and hospitalization of the editor, E. L. Bousfield. Here, and in a loose sheet inclosed, Ed's health problems, despite his strong post-operative recovery, are cited for the greatly regrettable decision to step down from journal production, and either hand it on if willing hands are found, or terminate it if not. Appended on page 140 is a list of 13 yet unpublished manuscripts which have completed station lists and plates of North Pacific amphipod taxa which are available from the retiring editor.

In its two volumes, seven issues and a supplement, *Amphipacifica* has provided a notable service in making lengthy monographic papers on systematics and phylogeny of amphipods available to contemporary and future workers. Colleagues owe an immense debt to Bousfield for his initiative in providing a publication outlet for this material, up to a decade after his formal retirement from National Museum of Canada (now

Canadian Museum of Nature) which long ago terminated publication of its scientific series where such material was once presented in what were, to some at least, more enlightened times.

Enquiries can be made to Dr. E. L. Bousfield, Managing Editor, Amphipacifica Research Publications, 611-548 Dallas Road, Victoria, British Columbia V8V 1B3 e-mail: <elbousf@islandnet.com>

Swift Fox Symposium: 18-19 February 1998

This symposium will be held in conjunction with the Fifth Prairie Conservation and Endangered Species Workshop, Saskatoon Inn, Courtyard Room, 2002 Airport Drive, Saskatoon, Saskatchewan.

Swift Fox conservation in North America took on new dimensions when the United States Fish and Wildlife Service listed the species as a candidate for consideration under the Endangered Species Act. In Canada, the species disappeared from the prairies during the early 1940s and subsequent re-introduction efforts have been successful. Recent conservation efforts and research projects are currently in various stages of completion in the United States and Canada. It is, therefore, timely to convene a symposium on the species to produce a "state-of-the-art" perspective.

This will be the first North America-wide approach to fostering information exchange, gathering current updates on distribution, legal status, taxonomy, population dynamics, dispersal, habitat selection, diseases, and conservation issues of this species. Its objective is subsequent publication of a substantive, peer-reviewed proceedings from the symposium.

For further information contact the conveners:

Canada:

Lu Carbyn
Canadian Wildlife Service
Room 200, 4999-98 Avenue
Edmonton, Alberta T6B 1X3
e-mail: lu.carbyn@ec.gc.ca

USA:

Marsha Sovada
Northern Prairie Science Center
8711 - 37th Street SE
Jamestown, North Dakota 58401
e-mail: marsha_sovada@nbs.gov

Sponsors: Biological Resources Division, United States Geological Survey; Canadian Wildlife Service, Environment Canada.

Meeting information will be posted under "Announcements" on the Northern Prairie Research Center's Home Page: <http://www.npsc.nbs.gov>

Sea Wind : Bulletin of Ocean Voice International

This thoughtful and newsy publication on the world marine environment now starts its second decade.

Volume 11, Number 1, 52 pages, January-March 1997, contains a report on the 1997 Annual Meeting of Ocean Voice International, its Annual Report for 31 March 1996 to 23 March 1997, a listing of the Table of Contents and an Index for *Sea Wind*, Volumes 6 to 10, 1992-1996 [the index of Volumes 1-5, 1987-1991, was published in *Sea Wind* 6(1): 29].

Volume 11, Number 2, 36 pages, April-June 1997, contains items on: The Burnum Burnum Declaration [January 1988, possession of England on behalf of aboriginal peoples: making a "Koompartoo" - a fresh start]; Eco-friendly Ornamental Fish to be Marketed [net-caught from the Philippines]; Swamping Dynamite for Nets: Community Resources Management in Columbia; Sagasa - Ija Ija Aho Aho: Yours in Yours and Mine is Mine; The Maltese Marine Environment; The Marine Aquarium Fish Council Certification and Market Incentives for Ecologically Sustainable Practices; Studies to Save Seahorses; Sea News; Conferences; On the Net; Book Nooke.

Volume 11, Number 3, July-September 1997 (dated 10 August 1997, received 10 September 1997) 140 pages, is a Special Issue — *Global Freshwater Biodiversity: Striving for the integrity of freshwater ecosystems*, by Don E. McAllister, Andrew L. Hamilton, and Brian Harvey, produced for International Fisheries Research, International Development Research Centre, P.O. Box 8500, Ottawa, Ontario, Canada K1G 3H9. The contents include sections on: Fresh Waters, Their Biodiversity & Biological Resources; Human Impacts on Freshwater Biodiversity; Key Gaps, Obstacles and Alternatives; Main Players in the Field; Key Meetings in 1997-98; Strategies and Options; Key Sources of Information (including electronic and paper) and an Appendix of Fish Species Diversity by Country.

Sea Wind is available through membership in Ocean Voice International P. O. Box 37026, 3332 McCarthy Road, Ottawa, Ontario, Canada K1V 0W0; e-mail: mcall@superaje.com [World-Wide Web site: <http://www.ovi.ca>].

Canadian Botanical Association Lawson Award to William J. Cody

The Canadian Botanical Association at its annual meeting banquet in Montreal, Quebec, 6 August 1997, presented William J. Cody with a Lawson Medal honouring outstanding achievement for his monographic treatment *The Flora of the Yukon Territory*, published in 1996 by the National Research Council, Canada.

Global Biodiversity: Canadian Museum of Nature

Volume 7, Number 1, Summer 1997, is 48 pages and contains papers on "Biodiversity, ecodiversity, sociodiversity -- three aspects of diversity, Part 2" by Pierre Dansereau; "Privatization of crop seeds: The public aspect" by Claude Andre St-Rierre, Andre Comeau, and Benoit Cauthier; "Developing a biodiversity database in Leicestershire" by Ingrid Birker and Ian Evans; "Facing the challenge of invasive alien species in North America" by Ian E. Efford, Constantino Macias Garcia, and James D. Williams. The Portrait of Biodiversity this issue is of the Desert Pupfish (*Cyprindon macularius*). The Forum section contains "The looming threat to the fair sharing of benefits: What can be done to stop it?" Don E. McAllister. News contains two Biodiversity Reports: "Incentives for landowners" and "Consultation on Canada's Sustainable Development Strategy" as well as sections on Biodiversity News (including notice of appointment of a new "President" for the Canadian Museum of Nature, Joanne DiCosimo, formerly Executive Director of the Manitoba Museum, who assumed her new post 1 July 1997), Cyberdiversity, and Biodiversity Meetings. Reviews contains the Book and Periodical Niche with reviews of one CD-ROM and eight books. The issue begins with The Editor's Notebook "Cloning and engineering sheep" by Editor D. E. McAllister; and concludes with The Last Word: "A promising new framework to control desertification" by Pierre Marc Johnson, IUCN Councillor for North America, and A few words about the Canadian Museum of Nature (publisher).

Volume 7, Number 2, Fall 1997, is a special 64-page ecoforestry theme issue guest-edited by Herb Hammond, Director of the Silva Forestry Foundation in British Columbia. The lead editorial "Why ecoforestry?" by Hammond is followed by eight theme papers: "What is ecoforestry?" by Herb Hammond; "The necessity of protecting ecoscapes" by J. Stan Rowe; "Ecoforestry at Windhorse Farm: Profile of a working operation" by Jim Drescher and Mark Kepkay; "Bringing ecoforestry to the BC Forest Service" by Jim Smith; "Forests, indigenous peoples, and biodiversity" by Russel Lawrence Barsh; "Threats to woodland caribou and the boreal forest" by W.O. Pruitt, Jr.; "Rethinking paper: Non-wood fibres poised for a comeback" by Heather Rosmarin; and "Cloning planet Earth: What can natural selection tell us about the economics of biodiversity?" Viewpoint by Tom Green. Also included are "A Portrait of Biodiversity (Boreal forest cube)" and Part 3 of "Biodiversity, ecodiversity, sociodiversity - Three aspects of biodiversity" by Pierre Dansereau. A "News" section includes Biodiversity news, Cyberdiversity, and Biodiversity meetings. The issue concludes with a "Reviews" section containing the Book and Periodical Niche.

The mailing address for *Global Biodiversity* is Canadian Museum of Nature, P. O. Box 3443, Station D, Ottawa, Ontario K1P 6P4. Items for publication or review consideration should be addressed to the attention of the Managing Editor Cartherine Ripley (e-mail: <cripley@mus-nature.ca>) to subscribe, place ads, or support the publication contact Advertising and Production Manager Anne Winship, or Subscription Manager Susan Swan (e-mail: <sswan@mus-nature.ca>).

FRANCIS R. COOK

A Tribute to Harold Archie Senn, 1912-1997

WILLIAM J. CODY

Biological Resources Division, ECORC, Agriculture and Agri-Food Canada, Wm. Saunders Building, Central Experimental Farm, Ottawa, Ontario K1A 0C6

Cody, William J. 1997. A tribute to Harold Archie Senn, 1912-1997. *Canadian Field-Naturalist* 111(4): 671-675.

Harold Senn was born 12 January 1912 in Caledonia, Ontario and died in Victoria, British Columbia, 22 January 1997. He attended primary and high school in Caledonia following which he enrolled in McMaster University at Hamilton, Ontario, where he obtained an Honors B.A. in Science and Biology in 1932. He continued study at McMaster to obtain a M.A. degree in Botany in 1934. At the suggestion of his professor, Lulu Gaiser, Harold went to the University of Virginia, Charlottesville, Virginia to study under Orland E. White at the Blandy Experiment Station. There he worked on the cytotaxonomy of the genus *Crotalaria*, and received his Ph.D. in 1937. For part of 1937 and again in 1938 Harold was at the Harvard Botanical Station in Soledad, Cuba. Between visits to Cuba he worked at the Arnold Arboretum, Boston, in association with Harvard University.

In 1938, Harold joined the Botany and Plant Pathology Division, Department of Agriculture, Ottawa as an assistant to Herbert Groh. With a particular interest in cultivated plants, he soon became Custodian of the Dominion Arboretum and Botanic Garden and in December 1938 published the first Index Seminum which listed 1499 seed lots, mainly from the arboretum and garden. This was the forerunner of what is now the Gene Bank Resources of Canada. His interest in Canadian botany is well documented in his continuation of *A Bibliography of Canadian Plant Geography* which was initiated by John Adams in 1928 in the Transactions of the Royal Canadian Institute.

Harold became head of the Botany Unit and through his initiative the Vascular Plant Herbarium began to expand in specimens and in usefulness as a taxonomic tool. He was instrumental in the hiring of exceptional new staff who conducted meticulous studies of cultivated plants and the flora of Canada thus making Agriculture Canada's Botany Division a world centre for plant systematic research. Ray Moore arrived in 1944 to work on the cytotaxonomy of *Buddleia*, *Caragana* and *Medicago*. Jim Calder joined the group in 1946 and soon began studying the plants of northern Canada and then conducted a systematic survey of the plants of British Columbia, which culminated in the *Flora of the Queen Charlotte Islands*. Clarie Frankton also joined the

staff in 1946 where he soon took over the responsibilities for the Canadian Weed Survey from Herbert Groh and producing the *Weeds of Canada* in 1955 (revised in 1970). Bill Cody also came in 1946 and soon began his studies of the plants of northern Canada which contributed to *Vascular Plants of Continental Northwest Territories, Canada and Flora of the Yukon Territory*. Bill Dore arrived in 1947 to work mainly on Canadian grasses, which culminated in his *Grasses of Ontario*. Wray Bowden also joined the Botany and Plant Pathology Division in 1947 as a cytotaxonomist and conducted extensive studies on the genus *Lobelia*, the Triticeae and northern grasses. Bernard Boivin came in 1948 and spent many years in the western provinces collecting plant specimens, which culminated in his *Flora of the Prairie Provinces*, but he also wrote *Enumération des plantes du Canada*. Gerry Mulligan also joined the unit in 1947 and became a specialist in the family Cruciferae and introduced weedy species. John Bassett arrived in 1948 and became a specialist on weedy species in the families Plantaginaceae, Chenopodiaceae and Urticaceae and also resident pollen expert, producing *An Atlas of Airborne Pollen Grains and Common Spores of Canada*. Jack Gillett who, after three summers as a student assistant joined the Botany Unit in 1949 became a specialist of the family Gentianaceae, and also conducted many botanical surveys across Canada. Some of these scientists appointed and directed by Harold were pioneers and innovators in new cytotaxonomic techniques, and it was in his time that the herbarium began to become one of the largest in North America assuming world-wide importance. In addition to his scientific administration responsibilities, Harold served as president of the Professional Institute of the Public Service of Canada in 1951 and 1952.

In 1959, Harold was an organizer and vice-president of the IX International Botanical Congress which took place in Montreal as well as chairman of the field-trips committee which set up field trips all across Canada and in the Arctic. Also in 1959 he became the first director of the new Plant Research Institute at the Central Experimental Farm. Harold left the department in 1960 to become a Professor of botany and Director of the new Biotron facility at the University of Wisconsin, at Madison, Wisconsin.

Harold joined the Ottawa Field-Naturalists' Club in 1939 and was elected to the Council in 1940. He became acting editor of *The Canadian Field-Naturalist* in 1942 for Volume 56 (7 and 8 & 9) and served as editor until the completion of Volume 69 in 1955, a total of 13¹/₄ years for 74 issues comprising a total of 2681 pages. He was the longest serving editor when he stepped down (still second only to Francis Cook). Previously Arthur Gibson (1909-1920: 11.9 years) and Douglas Leachman (1928-1938: 10 5/9 years) had served more than ten years. It is interesting to note also, that Harold was one of eight editors who worked at the Central Experimental Farm and federal Department of Agriculture (the others being J. Fletcher, F. T. Shutt, W. T. Macoun, J. A. Guignard, A. Gibson, R. A. Hamilton and T. Mosquin).

As Director of the Biotron his first responsibility was the development of a National Science Foundation controlled environment facility for plants and animals. This involved obtaining over six million dollars from the National Institute of Health and the Ford Foundation in order to build a facility with capabilities for environmental control that was unique world-wide. This included the recognition of the need for humidity, carbon dioxide and atmospheric contamination control in the early years of controlled environment research. Mechanisms were installed to control wind speed, atmospheric pressure, electromagnetic fields and to provide high radiation levels to duplicate sunlight. The construction of this facility required the development of many new and different technologies, the proper functioning of which required extensive monitoring. Consequently Harold could often be found sleeping through the nights in the Biotron to ensure that the systems kept operating and research was not lost.

Harold continued as Director of the Biotron until his retirement from the University of Wisconsin in 1978. He was awarded Emeritus Professor status and retired to Victoria, British Columbia.

After arriving in Victoria Harold devoted his time to his life-long love of gardening, with a special interest in Rhododendrons. His garden, which measured about 23 X 37 metres contained about 150 species and varieties of Rhododendrons from around the world, most of which were grown from seed. Many of these were transplanted to the University of Victoria's Finnerty Gardens under the direction of fellow Rhododendron enthusiast Dr. Herman Vaartnou in July 1993 because of a deterioration in health of both Harold and his wife Betty. According to his daughter Norma, the garden is still very interesting even after so much was transplanted.

Harold died in Victoria, British Columbia, on 22 January 1997. He is survived by his wife Betty in Victoria; son, daughter-in-law and grandchildren, James, Jong Soon, Joseph and Daniel of Platteville, Wisconsin; and daughter Norma of Aldergrove, B.C.

Harold was a fellow of the Royal Society of Canada (FRSC), a Life Member of the Agriculture Institute of Canada and a member of The Ottawa Field-Naturalists' Club for 58 years. He was a significant leader in the development of biology and especially systematic botany in Canada and contributed substantially to the outstanding international reputation that Canada developed for plant systematic research.

Acknowledgments:

I appreciate the information provided by Theodore Tibbitts on Harold's life at the Biodome, Francis Cook's comments on his years as Editor of *The Canadian Field-Naturalist* and Paul Catling's suggestions on an earlier version of this tribute.

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Harold A. Senn, 1959. Agriculture and Agri-food Canada photograph.

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Book Reviews

ZOOLOGY

Field Guide to the Birds of the Middle East

By R. F. Porter, S. Christensen, P. Schiermacker-Hansen.
1996. T. & A.D. Poyser, London, England. 460 pp.,
illus. + plates. £29.95.

Some years ago, I coloured in a blank world map with the areas covered by the field guides in my collection. Over time I have conscientiously worked towards filling the gaps revealed by this process. Finally, I achieved almost full coverage. Only one patch of white remained; the Middle East. It stayed that way for many years, but the gap has finally been filled. This new book, then, is a historic document. Field guides are now available that will give you a portable reference for any region of the world. The challenge for future authors is to bring them all up in quality to match the best of North America or Europe.

The region covered by *Birds of the Middle East* is a triangle from northern Turkey, southwestern Yemen to southeastern Iraq, probably the most politically troubled regions on earth. This region has its own resident and migratory fauna and has vagrants from Europe, Africa and India. So, despite the often dry and hostile terrain, it has a rich list of birds for the intrepid traveller.

The book begins with the colour plates, where each significant plumage (male, female, etc.) is depicted. The illustrations are by four artists and the quality of the artwork itself is, characteristically, very high. In general, the shape, attitude and colour distribution of the feathers is representative of the species shown. The main illustration of a standing or sitting bird is often accompanied by small paintings of the species in flight. This sometimes makes for crowded plates, but this is a minor issue. White birds, such as egrets and terns, disappear against the white backgrounds used for all plates. The Peterson series solved this problem years ago, by using a neutral gray background in such cases. Some illustrations are a bit over-coloured from my experience. This is most noticeable in shore birds like Curlew Sandpiper. I suspect that the illustrators often worked with museum skins as their major or only guide. The depictions of vagrants, like Redpoll, (Bohemian) Waxwing and Snowy Owl do not capture the feel of the bird as well as those of the local species. Some of the less common birds depicted do not fit the patterns of the expected subspecies, and are more illustrative of a common subspecies. Lilac-breasted Roller, Little Green Bee-eater, and White-collared Kingfisher are

three such species. The Kingfisher also raises another issue. I found many English names used in this book are different from those in general use. Most authors use Mangrove Kingfisher for *Halcyon chloris*, for example. Some names are easy to convert (Red-headed Falcon vs. Red-headed Merlin), while others are more confusing (Purple Gallinule is not the species from North America but the Purple Swamphen). Alternative names are given in the text, but even here there is little consistency. For example, the divers are given their North American loon titles while the alternative for Lapwing and White-winged Black Tern is their correct name (Northern Lapwing and White-winged Tern). The authors have also missed the split of Black-headed Penduline Tit (*Remiz macronyx*) from Penduline Tit (*Remiz pendulinus*) - both birds occur in the area covered. I was also unhappy with the illustrations of the extremely similar Great Tit (*Parus major intermedius*) and Turkestan Tit (*P. bokharensis*). The fine points that separate these two birds are not well shown.

Opposite each set of illustrations are an equivalent set of range maps and a short note on status. The range maps are clear and large enough to read easily. Although I believe these maps are accurate, given the level of turmoil in the region, I wonder if any one knows the real status and distribution.

The text follows the plates. This is not the arrangement that I prefer. I believe one of the major reasons for the popularity of the National Geographic guides is its arrangement of text and illustration side by side; it is so convenient to use. The text, though, is well organised and provides precise information to help in identification. I generally find that my description of bird song rarely matches that of others. The vocal descriptions in this book are an exception; I thought they captured well the sounds as I hear them.

Most of my criticisms are minor and can easily be overcome. They are far outweighed by the contribution this book makes to world coverage and the overall quality of the work achieved. This is a good book to buy for the collector and the traveller to the Middle East and the countries around the periphery. Actually there is still one place that needs its own field guide; Afghanistan! Any volunteers?

ROY JOHN

754 Woodpark Road S.W., Calgary, Alberta T2W ZS4

The Historical Atlas of Breeding Birds in Britain and Ireland: 1875–1900

By Simon Holloway. 1996. T. & A.D. Poyser, London, England. 476 pp., illus.

A group of us recently started to write the Birds of Saskatoon. This involves digging into a disparate accumulation of data sets, collected with mostly unknown protocols for a variety of objectives. We soon realised the limitations and problems with dealing with 40 and 50 year old data. Simon Holloway's information is mostly over 100 years old, and I raise my cap to him for even trying.

Holloway has scoured the references to obtain a vision of bird life in Britain at the end of the last century. His book is patterned after the more recent atlases of breeding and wintering birds. A page of text is followed by a large map showing distribution by county. Each bird is illustrated with an engraving from the period - a delightful touch! The author, while he concentrates on the stated period of the book, cannot but help make comparisons to earlier times and the current status.

Let us take the Avocet, symbol of the Royal Society for the Protection of Birds (RSPB) and for much of what is positive in British conservation, as an example. The author found that this bird bred along much of the east coast of England, but had been essentially reduced to occasional visitors by the time of his study period. The Second World War forced the closure of the English east coast to the public and by 1947 eight or so pairs of Avocets returned. Efforts by the RSPB to protect the breeding areas have been successful and this species now numbers several hundred pairs and has recolonised a significant portion of its earlier range.

I found this pattern of early abundance, 18th century loss and 20th century recovery, to be typical of many species. Several species of seabirds, ducks, gulls, passerines and even some raptors have made advances. The data for Corncrake, a small land rail, tell a very different story. In this atlas they are shown as common through almost all of Britain and Ireland. I have never even heard a Corncrake because I have not visited their final remnant sanctu-

ary in the Hebrides and Ireland. This story is sadly true of several other species such as Wryneck, Lesser Spotted Woodpecker, Woodlark, Sand Martin (or Bank Swallow) and Nightingale to name a few. There is even one species that I did not know was a British nesting bird, Pallas's Sandgrouse; it essentially died out in 1909.

Informative and necessary, though less interesting from a non-resident's viewpoint, are the detailed delineation of the county system, then and now, and a description of the data sources. The reasons for the changes in populations, both up and down, are covered in a chapter describing the late 19th century environment. This is such fascinating reading for anyone, I think the author should publish it as a separate paper so that it reaches a wider audience. The author looks at a variety of factors from the number of horses, through climate change to agricultural use. Not surprisingly the use of land for agriculture dominates the discussion. The area under agriculture peaked in the 1920s and has been slowly decreasing, with most of the loss going into urban growth. There has also been a slight rise in woodland acreage, most of which had disappeared in pre-Roman times. Changes in the law, a fivefold decline in gamekeepers and the loss of hedgerows are all carefully analyzed and incorporated in this thought-provoking chapter.

This is not so much a book to read as to enjoy. I keep wondering about this species and that, and then looking them up to compare with my own experience. I am amused by the old names (Snowflake for Snow Bunting, Fern Owl for Nightjar) and captivated by the engravings. I also recognize that this is an important contribution to the conservation of birds. The better we understand our past actions and the changes they brought on, the more informed will be our decision on what to do in the future. The inherent conservation and management messages apply to more than just a few islands off the coast of Europe.

ROY JOHN

754 Woodpark Road S.W., Calgary, Alberta T2W ZS4

Messages from an Owl

By Max R. Terman. 1996. Princeton University Press, Princeton, New Jersey. 217 pp., illus. U.S. \$24.95.

For those who have come to know them intimately, owls are the most fascinating of all birds. Max Terman, a professor of biology at Tabor College in Kansas, rescued a four-week-old fledgling owl, deserted and starving. He kept it for a-while as a pet, but the time came when he had to let Stripey go into the wild. Terman's case was different from anyone before him; he attached a radio transmitter to the owl

before he let it go. The first two transmitters, weighing 5 g each, were applied in turn to the tibio-tarsus, and the subsequent 19 g transmitters were attached by a backpack harness. Each time the radio battery went dead Terman was able to catch the owl and apply a new radio — on twelve occasions. As a result, this owl was followed off and on for six years.

Terman had a burning question: would Stripey be imprinted to humans? The answer, unlike that for a nestling raised from one or two weeks of age: only

partially. Finding the answer is the focus of this book. Stripey eventually learned to hunt, but by trial and error, somewhat haltingly. Terman's offering of food brought the owl back whenever it was hungry. Unquestionably Stripey would have died on any one of a number of occasions in the first two years without supplementary feeding, and did not become fully independent until about four years of age.

Terman tries hard to avoid being anthropomorphic, but at times he breaks his own rule and can not help speculating how the owl felt when it was retrapped or approached closely. Stripey, because of its hooting pattern, thought to be a male during its first four years, consorted with another owl for the first time when nearly three years old, mated at four years without location of a nest or young, and laid eggs and raised two young for two years in succession, when nearly five and six years of age. Only in these last two years did Terman learn she was a female.

In understandable terms, beamed at neophyte birders or members of the general public who have a special interest in owls, Terman teaches his reader about the Great Horned Owl, the consummate predator. He uses his owl as an example to illustrate principles of ecology, ornithology and animal behavior in general and of Great Horned Owls in particular. For example, he discusses courtship, prey, learning from experience, niche, reproductive fitness, size of the nesting territory and the hunting range (the latter is larger), and functions of the white bib and the feather tufts that are called horns. He tells of the remarkable vocal repertoire, which includes "short barks, chuckles, laughs, whistles, screeches, and screams," in addition to the expected hoots.

We learn also of Terman's life, his wife's adeptness in fastening radio harnesses on owls, his adopted twin daughters, his love for golf and golf courses, and his interest in the Bible. Each of 26 short chapters is preceded by an apt quotation, six by biologists, five from the Bible, the rest by poets, authors, philosophers, and a psychologist.

Terman's interest in animal behavior, his previous experience and his available equipment, together

qualified him for this study. It could not have been carried out with a wild owl, because numerous recaptures to replace failing batteries would have been impossible. Terman's previous studies in mammalogy meant that he had on hand numerous small mammal traps with which to catch it food.

Sixty-seven black-and-white photographs, some of suboptimal quality, add to the interest. There is a helpful, eight-page chronology, 1 1/2 pages of suggestions for further reading, and an index.

I have a few criticisms of this otherwise well-written and thoughtful book. Since he tells of the events chronologically, there is inevitably some repetition. His interpretation of mortality statistics is quite wrong (he says that only 1% of owls are still alive by four years of age). He tells us that young owls should not be raised as pets, since when released, because of imprinting, they approach too closely to humans and may be shot. Even more likely, I would suggest, they will starve to death. He fails to explain that the Canadian "jerkin" from Manitoba, shown to him at the Sutton Avian Research Center in Oklahoma, was a male gyrfalcon.

Because this is a popular book, he does not cite references for some of his most interesting statements. Where, for instance, did he get the important piece of information that it takes a force of 13 000 g or nearly 30 pounds to break the self-locking grip of a Great Horned Owl's talons? I wish Terman had discussed more than two (of a dozen or more) theories to explain reversed sexual dimorphism in most raptors; the females, unlike most other birds, being much larger than the males.

This book is something of a sequel to the several-times-reprinted classic, *One Man's Owl* by Bernd Heinrich. Anyone who has enjoyed Heinrich's book will also appreciate this one, which has the added advantage of information from radio-telemetry.

C. STUART HOUSTON

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The Wood Duck and the Mandarin: The Northern Wood Ducks

Lawton L. Shurtleff and Christopher Savage. 1996. University of California Press, Berkeley. 232 pp., 260 colour photographs, 8 maps. U.S. \$34.95.

Lawton Shurtleff purchased the 800-hectare Indian Meadow ranch in Sonoma County, California, in 1968. He constructed a lake and in 1970 two Wood Duck pairs occupied nest boxes. He added twenty ponds and another hundred nest boxes, and the Wood Duck population increased. In 1972, a pair of Mandarin ducks arrived, escapees from a wild

bird collection only 30 km distant. Shurtleff, now 78, has encouraged both species in his property replete with redwoods and oaks. This book, filled with outstanding colour photographs, depicts the seasonal activities of the two most beautiful of the world's duck species. History and conservation are well covered, based on the research of Henry M. Reeves.

The Wood Duck has two completely separate ranges, the largest in eastern North America, west to the eastern edge of Saskatchewan, and the other in

southern British Columbia and the three Pacific states. Wood Duck numbers reached perilously low levels near the turn of the century. The passage of the Migratory Bird Treaty Act in 1918, low bag limits through the 1930s, and post-war building of more than 100 000 nest boxes, have all contributed to the recovery of this attractive duck. Nevertheless, about 95% still nest in natural tree hollows and snags. According to Shurtleff, Minnesota now has the greatest population of any state.

Co-author Christopher Savage has studied the Mandarin in his native Great Britain and in eastern Asia, where it holds an important place in art and literature. Sadly, due to hunting and continuing habitat loss, the Mandarin is a threatened species. Prime habitat in the forests of Ussuriland, the eastern tongue of Siberia that extends down along the Sea of Japan to Vladivostok, are being clear-cut at a frightening rate; each year fewer snags are left for nesting in old-growth forest. Few Mandarins have survived the human pressures in eastern China. Only in Japan is it reasonably well protected.

Shurtleff quotes Aldo Leopold's "stern note of caution" that attempted introduction of species to different continents results most often in failure. Yet

the Mandarin's best hope for longterm survival may be in Britain. Early in this century local groupings of 300 Mandarins were kept by the Duke of Bedford at Woburn Abbey, Bedfordshire, soon followed by another group belonging to the famous ornithologist, Lord Grey of Fallodon, in Northumberland. Nevertheless, the current wild population of these exotics derives mainly from the 45 given in 1931 by the famous waterfowl biologist, Jean Delacour, to Alfred Ezra for his estate in Surrey. The Mandarin was admitted officially to the British and Irish List in 1971; there are now between seven and thirteen thousand birds in the wild. Throughout Britain, as elsewhere, they use natural tree cavities and man-made nest boxes, and the clutch size of fourteen is larger than in their normal haunts.

This book is beautifully produced, well-written, and contains seven helpful pages of instructions for building and caring for duck nest boxes. It would be a tasteful addition to the coffee table of any duck hunter, waterfowl biologist, or wildlife photographer.

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Ontario Birds: A Field Guide to 125 Common Birds of Ontario

Chris Fisher. 1996. Lone Pine Publishing, Edmonton. 159 pp., illus. \$17.95

Upon first opening this book, one is met with a well-organized series of bird descriptions. Each page is set aside for one species, complete with an illustration, general description, and fact listing for each. The fact listing includes identification tips, nesting and feeding details, and miscellaneous notes. A useful chart at the bottom of each page gives the reader an instantaneous impression of abundance and seasonal distribution with a highlighted area outlining the breeding period.

The author brings out many interesting facts that many experienced birders will find new. This is somewhat of an accomplishment as the book is directed at beginners. Environmental issues (past and present, failures and successes) as they relate to several species are addressed.

The newest name revisions are used (e.g., Baltimore Oriole) and a particularly interesting feature is that the author translates the long scientific names for many of the species. The author's sense of humour comes out successfully many times through the book.

What is it though, that compels people to misname their books? Ontario Birds is misnamed as it unapologetically only treats the 125 common birds of southern Ontario (or is it 126 species as is contradictorily stated in the introduction). As such, three

species (American Tree Sparrow, Pine Grosbeak, and White-winged Crossbill) are listed as nonbreeders, even though they are known to nest in Ontario (albeit north of the Golden Horseshoe).

Approximately half of each page is allotted to a general description of each bird. However, for several species (e.g., Broad-winged Hawk, Virginia Rail, Common Tern) this text lends itself more towards a description of the broader taxonomic group, not the individual species. Perhaps there should have been a page devoted to each group as well as individual species accounts.

The order in which the birds are presented is akin to the Audubon style rather than the more conventional taxonomic style. This was done as an aid to the beginning birders. As such, "ground feeders" are all together (grouse, doves, lark) as are aerial feeders (nightjars, chimney swift, kingfisher (?)) but interestingly, not swallows). "Colourful songbirds" is another category with obvious omissions. Scarlet Tanager and Rose-breasted Grosbeak are there, but not Eastern Meadowlark or Baltimore Oriole (which are placed in their taxonomic grouping of blackbirds). Behaviours of the birds are often eloquently described, "Like a taut bowstring, the heron tenses before it fires" and "like large swallows, Black Terns dip and spin... as though to defy the laws of flight that restrict most other birds." However, referring to the courship dance of a Goldeneye as being

“Nature’s most entertaining slapstick routine” is disrespectful to the ritual and the birds.

Two artists did the vast majority of the illustrations (three others contributed 19 of the illustrations), most of which are good, some extremely nice. There are a few cases in which salient features outlined in the text cannot be seen in the drawings, and a few have outright errors (the purple head on the Common Goldeneye comes to mind).

Text and illustration should work together to help people identify a bird. As such, comparing radically differently shaped birds to get a feel for size is not useful. For instance, the author tells us that Whip-poor-wills are robin-sized. I don’t find this useful because the two birds are radically different in shape. Saying that the meadowlark is robin-sized will be useful to beginners. Taking this one step for the worse, the author refers to several birds as being smaller or larger than a hawk. Which hawk?

The final section of the book outlines a seasonal

approach to birding and supplies many useful tips on equipment and getting started in this hobby. The different types of optics and their uses are introduced quite well. The reader will also find the standard bird diagram in this section, with markers pointing out the pertinent topographic features. Unfortunately, this diagram is poorly labelled — “primary feathers” points to secondary feathers while “secondary feathers” points to greater coverts. The markers for “breast, flank and, belly” point to three neighbouring spots which cannot give a novice an understanding of these *regions*.

This book has a lot of potential. I would not recommend this book in its current state, though a second edition, properly edited (and titled) would be a joy for any southern Ontario birder to own.

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Landscape Approaches in Mammalian Ecology and Conservation

Edited by William Z. Lidicker Jr. 1995. University of Minnesota Press. Minneapolis. ix + 215 pp., illus. U.S. \$35.95.

The association between wildlife and habitat typically has been studied and interpreted at two scales, the regional (or continental) and the stand (or individual) scale. Regional scale associations relate animal and plant distributions over very large areas, such as from the equator to the Arctic, or from the boreal forest biome to the temperate forest. However, the predominant scale of study in wildlife ecology has been at what is often termed the stand scale; locations of individuals are related to immediate surroundings of vegetative cover, to the amount of food, proximity to water, or other parameters, then averaged and compared to the amount of that habitat available in the area. In the mid-1980s, the role of the landscape emerged as a valid and distinct scale in which wildlife distributions could be related to much larger processes. For example, adjacent populations are known to act as sources and sinks within a larger “metapopulation”, replenishing or receiving individuals from neighbouring populations, dependent, in part, on the barriers and conduits existing within the landscape. This book, *Landscape Approaches in Mammalian Ecology and Conservation* is one of the best compilations to date of the landscape influence on mammals.

The book, organized into nine chapters, is written by a series of noted authors on landscape ecology and mammalogy, selected principally from their involvement in a 1991 international conference in Australia. And although the authors discuss ideas and projects

from numerous regions (i.e., Canada, United States, Australia, and several European countries) and species (microtine rodents, weasels, marsupials, and marten) the similarity in the interpretations of how animals respond at this scale gives an indication of the coalescence of the landscape concept.

The first of three parts outlines the concept, its development, and its potential application to wildlife science and conservation. Most of the book is dedicated to the second part where five chapters provide the data and evidence for theories on how patch heterogeneity and configuration influences animal movement, and how the effect of predation varies by prey density in patches adjacent to the one they utilize. The chapter on weasels and rodents in Norway is particularly worthwhile because the 10-year data set provides the longer period necessary for understanding the dynamics of population change. The third part of the book presents two experimental manipulations of rodent populations in fragmented and patchy landscapes. As shown in these papers, one advantage of working on small rodents can be the increased opportunity for controlling the design and heterogeneity of their landscape.

There are only a few significant drawbacks to the book worth mentioning. The book’s size is one. At only 213 small-sized pages, the reader is left hoping for more information. Similarly, the book focuses on small-sized species, and species generally not at the top of that landscape’s trophic hierarchy. As such, this book does not provide much information on the landscape-level relationships of large carnivores and their prey. Nevertheless, because of the quality of the

papers within, and the strong compilation of ideas in one source, I recommend this book to any ecologist or wildlife manager who wishes to learn more about mammals at a landscape level, particularly those concerned with larger-scale processes.

GRAHAM J. FORBES

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Ruddy Ducks and Other Stiffetails: Their Behavior and Biology

P. A. Johnsgard and Montserrat Carbonell. 1996. *Animal Natural History Series*. University of Oklahoma Press, Norman. xiv + 291 pp., illus. U.S.\$ 49.95.

This book is the first in what looks to be a promising series of books based on animal natural history from University of Oklahoma Press. Johnsgard is a veteran author of more than 30 books, while Carbonell is a recent doctoral graduate whose thesis was based on stiffetails. Together, they have assembled a trove of information on the Oxyurini, the stiff-tail ducks. Ironically, Montserrat claims that we know rather little about these birds. While there appears to be room for quite a bit more work on these birds, the vast amount of information in this book cannot be referred to as "rather little".

The book is divided into two main parts. The first takes a comparative approach to overview the biology of the stiffetails. Evolution, taxonomy, morphology, behaviour, and reproduction are covered both to compare species within the Oxyurini and, less frequently, to other ducks as well. Twelve figures and 19 tables summarize several aspects of the biology of these birds. The colour photographs are clustered in this section as well; they are all good, though most of them appear to be of birds in captivity. As such, they are not aesthetically pleasing shots, but they adequately illustrate the appearance of each species.

The second section devotes one chapter to each of the eight species covered. I had feared that this was simply to be a reformatting of the material in the first section, and to some extent that is true, but the detail is actually much greater. Full descriptions are given for each bird, including measurements and all of the plumages (where known). Interestingly, molting sequences for these plumages are given elsewhere in the species' account, a choice which I found odd. Identification tips are given for birds in the hand and in the field.

The habitat preferences and range for each bird are covered, but by far, most of each species account is devoted to behaviour. There are figures (redrawn from cine film sequences) that illustrate often complex behaviours such as sousing and other courtship rituals. Nesting and parental behaviour make up the balance of these sections. No aspect of the known biology of these birds appears to have been left out.

The book is dominated (though not overtly so) by research done on the North American Ruddy Duck (*Oxyura jamaicensis*). This bias undoubtedly arises from several factors including population size (it is the most abundant of the stiffetails) and distribution (present over much of western North America and introduced into Europe, both of which are major centers of research relative to the distribution of other stiffetails). The bias is taken to an unfortunate end in the section dealing with Comparative Biology — the segment entitled Pair Bonding describes behaviour only for the Ruddy Duck. A significant portion of the knowledge of the other species comes from work done at the Wildfowl Trust in England. Although these studies on captive, displaced birds lead to a better understanding of their biology, I do question the value of reporting egg laying dates and other phenological data for captive birds in England whose natural range is tropical South America or Africa.

This book is a very good synthesis of information on the stiffetails and would be suitable reading for both naturalists and professional ornithologists. The authors have pulled together over 150 years of scientific research in a very enjoyable book.

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The Amphibians and Reptiles of the Yucatán Peninsula

By Julian C. Lee. 1996. Cornell University Press, Ithaca. xii + 500 pp., illus. + plates. Cloth. U.S. \$175.00.

Amphibians and reptiles captivate the imaginations of most people from early childhood, instilling fear in some, curiosity in most, but wonderment in all. In North America, the diversity of species is

greatest in Mexico. Although there are several summaries of the amphibians and reptiles for many Mexican States, few are lucid, and none approach the quality, completeness and excellence of this most recent contribution. In fact, very few herpetological faunal works on any region of the world equal this

masterpiece. First and foremost, Julian Lee's work is a guide to the 182 species on the "hitchhikers thumb" of Mexico, the Yucatán Peninsula. The vast majority of the book is concerned only with this. It is lavishly illustrated with 189 drawings and 187 colour photographs of species, plus 188 detailed dot range maps, and more - much more.

Simple descriptions and lists often leave one wondering about environmental associations of the various species. Unlike many, this book provides a succinct summary of the region's environment, including physiography, climate and vegetation. Lee provides an overview of the major habitats of amphibians and reptiles, complete with colour photographs, and he notes key species restricted to each region. For the herpetological historian, his review of explorations and the taxonomic chronicle will be an indispensable reference for individuals interested in the biological exploration of Mexico.

Most of the book concerns detailed descriptions and identification keys to the amphibians and reptiles of the Yucatán Peninsula of Mexico. The keys, provided both in Spanish and English, are taxon-specific and are distributed throughout the book. For the peninsular amphibians, Lee provides keys to tadpoles, as well as for adult frogs. One criticism of the book is that from the Family-level keys, one must search through the book to find the generic keys, and finally seek out the species keys. There is no cross referencing of pages allowing one to work efficiently either forward, or backwards if the need arises, as is often the case in practice.

The species accounts contain the majority of information. For each species, there is a list of name synonymies. Common names are given in American, Mexican, Belizean, and Maya. The cultural sensitivi-

ty is an uncommon welcome addition. The species are described in sufficient detail to positively confirm their identification. Numerous figures and maps greatly assist in species identification. Within the discussion of species, similar species are noted along with the characteristics that separate them. The range of each species is both described and figured in a shaded map depicting all known locality records. Natural history notes are provided, including observations of behaviour, reproduction, food, and ecology. Lee also provides the etymology of each species name. He also comments on taxonomic problems, and provides a list of all known locality records and location of the voucher specimens.

The book ends with a wonderful review of ethnoherpetology — amphibians and reptiles in the secular, religious lives of the Maya, and with Maya Mythology. Just in case you are not familiar with herpetological terminology, Lee provides a glossary of terms. The literature cited is extensive.

Again, this book is destined to become a clear classic example on how state books should be produced. However, I was surprised that it was not a collaborative effort involving any one of many eminent Mexican biologists, and equally surprised that more of the book was not written in Spanish, as is typical of most more recent endeavours. And even though the book is one of the most outstanding herpetological monographs, its rather steep price will preclude purchase by many, especially those that may need it most, our Mexican colleagues.

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The Garter Snakes: Evolution and Ecology

By Douglas A. Rossman, Neil B. Ford, and Richard A. Seigel. 1996. University of Oklahoma Press, Norman. xx + 332 pp., illus. U.S. \$65.00.

Garter snakes are undoubtedly the best-studied group of snakes in North America, if not the world. The literature is enormous and deals with everything from descriptive taxonomy to sophisticated physiological investigations. These snakes have been the focus of numerous evolutionary studies, including molecular genetics, predator/prey investigations, courtship behaviour, dispersion and home range, and life history, among others. This wealth of knowledge is not surprising given their relative abundance, diurnal habits, typically gentle nature, and ease of maintenance in captivity. With 29 species, the garter snake genus *Thamnophis* is one of the most speciose North American assemblages of snakes. Surprisingly, this is the first summary of

the incredible wealth of knowledge in almost half a century.

Three recognized experts of garter snake biology have collaborated to produce a valuable compendium of the state of knowledge, intended for both the lay person and the professional. Given that many a child has garter snakes as their first reptilian pets, the goal of popularizing the vast wealth of technical information is admirable. The first three chapters consist of an authoritative summary of taxonomy and phylogenetic hypotheses, a list of species and subspecies name changes, and valuable keys to the species and subspecies. The review will form a valuable resource for taxonomists, if not a necessary reference. Several new taxonomic arrangements are given in the book, along with an apology for not simultaneously providing the usual justification.

Chapter 4 is a general overview of ecological data and conservation efforts. Much of the data are summarized in tabular form which will greatly facilitate the retrieval of information. Tables on reproductive ecology, diet, densities, and age and size at sexual maturity are particularly valuable. Chapter 5 summarizes variation in several behavioral attributes and Chapter 6 provides a guide to the care and maintenance of garter snakes for laboratory-based investigations. More than half of the book is devoted to species accounts, which include species-specific information on taxonomic history, identification, subspecies composition and distribution, description, and a summary of life history and ecology. Most species are illustrated by excellent colour photographs.

As a compendium, a quick check of the literature shows shortfalls. For example, garter snake distributions in the Chihuahuan Desert of Mexico are missing the distributional records from the authoritative work in this region (Morafka, 1977, *Biogeographica* Vol. 9), and the well-known, invaluable reference volumes to the Mexican herpetological literature by Smith and Smith are missing. Several prior referrals of *Thamnophis validus* as "*Nerodia valida*" are missing making the synonymy for this species incomplete; other examples also occur. Although these deficiencies exist, the consequences are minor, except for the systematist interested in taxonomic history.

Although this book will serve as a valuable resource, it falls short in achieving one goal; evolution is missing. In order to evaluate evolutionary trends in behaviour and ecology, a defensible genealogical hypothesis is required, and none exists. The authors do not present their own evolutionary

hypothesis but rather non-critically summarize older morphological and more recent molecular work. The most recent molecular hypothesis falls short owing to invalid methods of data analysis (presence/absence coding of alleles) and extensive missing data (sequence analysis). Although a wealth of behavioral and life history data are available in the book, these were not evaluated in light of opposing phylogenetic hypotheses to see if resolution of controversies could be made. Thus, the anticipated synthesis is missing. The three major sections of the book largely stand independent of one another. And, finally, the taxonomy has not been viewed in terms of more recent advances in species concepts - advances that allow diagnosable, allopatric populations to be considered as species. For example, *Thamnophis validus celaeno* is isolated on the southern tip of the Baja California, Mexico peninsula whereas all other subspecies occur on the mainland. The Baja California population is diagnosable and clearly not interbreeding freely with mainland conspecifics; it could be recognized as a species and likely so without protest from colleagues. In other cases, such isolated populations have been recognized.

In spite of these minor shortcomings, the book will serve as both an inspiration and starting point for future research. Its highly-readable text will be enjoyed by the curious, serious amateur and academic alike.

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Foundations of Animal Behavior: Classic Papers with Commentaries

Lynne D. Houck and Lee C. Drickamer. 1996. The University of Chicago Press, Chicago, xvi + 843 pp., illus. Cloth U.S. \$95; Paper U.S. \$34.95.

Two signs can indicate that a scientific discipline has reached maturity. One is international recognition, and the other is a tendency to look back at the path taken to get there. Both signs are exhibited by ethology, the study of animal behaviour. Recognition came in 1973, when the Nobel Prize in Physiology and Medicine was awarded to Karl von Frisch, Konrad Lorenz, and Niko Tinbergen, for their founding contribution to ethology. This surprised the world because it was the first time that this prize was awarded to field biologists (to this day, it remains the only time). As to the historical perspective, it has been provided in book form by Gordon M. Burghardt (*Foundations of comparative ethology*, Van Nostrand Reinhold, New York) and Donald A.

Dewsbury (*Studying animal behaviour: autobiographies of the founders*, University of Chicago Press, Chicago) in 1985. Now comes this new, and equally valuable, collection of classic papers.

The contributions were chosen by the two editors and a board of six active researchers whose expertise covered a broad cross-section of subdisciplines. In all, 44 papers were retained. Most of the papers (39) date from the three decades that preceded the awarding of that famous Nobel Prize. An exception to this rule is the first part of the volume, where four book excerpts from before 1925 illustrate the historical origins of ethology. There follows five more parts, each of which contains 7-9 articles grouped under the following banners: (1) goals and methods of ethology; (2) the development of behaviour, including learning and genetic bases; (3) neuronal and hormonal mechanisms; (4) unusual sensory capabilities,

some of which allow exceptional feats of orientation and communication; and (5) the evolution and adaptive significance of behaviour. The chosen articles strike a good balance between conceptual and empirical contributions, as well as between European and North American researchers. Fittingly, each of the three Nobel winners is represented.

Each of the six parts is preceded by an enlightening commentary, 10–15 pages long, that places the chosen contributions in the historical context of the subdiscipline. These commentaries also enabled their authors to cite and comment upon other significant papers which did not make the final cut, for lack of space and not for lack of wanting.

Each paper is reproduced as it appeared in its original book or journal. From a historical point of view, this is a nice touch. Unfortunately, for those papers that were originally published on a larger page format than that of the book (16 × 23 cm), it also means a reduction in font size. In some cases, the let-

ters become no taller than 1 mm. People with weak eyes, beware.

In their preface, the editors point out that this collection of articles will be useful to students and teachers of ethology because it will take them beyond the dry textbook facts and give them a chance to imagine the excitement and wonder experienced by the founders. Students will benefit in other ways: all royalties from the sale of the book will be donated to the Animal Behavior Society to create student research awards. And I would suggest that established researchers can benefit too: in this book they will find a source of renewed inspiration as well as examples, for them to follow, of the high standards that have made ethology a reputable scientific discipline.

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Peterson Flash Guides: Backyard Birds, Atlantic Coastal Birds, Pacific Coastal Birds, Hawks, Eastern Trailside Birds, Western Trailside Birds

By Roger Tory Peterson. 1996. Houghton Mifflin Company, New York. A series of six laminated folding charts with colour illustrations on 24 panels, 11.5 × 21.75 cm. U.S. \$7.95 or Can \$10.95 each.

This series of “guides” is presented as “a revolutionary new tool for identifying birds. Unfolding in a flash, they show, at a glance, all the birds of a particular type (hawks, for example) or place (coast, mountains, or backyard).” This claim is partly true because each flash guide depicts only approximately fifty to 100 species for the various groups or areas. The typical illustrations of the time-honoured Peterson field guides are used to depict most of the selected species. A short text accompanies each illustration and gives a few details about the species. A series of symbols accompanies the text and shows the season when the species can be seen, in what ecoregion it occurs, and its feeding preferences. It means that the reader has to learn the meaning of the eighteen symbols used throughout the series before taking full advantage of the information they contain. Dimensions are given in inches only [perhaps, the flash guides are intended for the USA market only although the price in Canadian currency appears on the back panel!!].

The quality of the illustrations is generally excellent particularly those previously used in the original guides. The text is easy to read but the information it conveys is so bland that the reader cannot expect to learn much about birds. Each flash guide contains twelve plastic laminated folding panels, much like a road map.

After having examined and looked at the “flash guides” for sometime, I have yet to find an answer to the question that I raised when I first saw them: “What for”? The only use I can see for this type of guide is for a person interested in birds but with little knowledge or desire to learn more about them than what is given on the panels. The flash guides may be intended for use in the field by those who have a general interest in birds and a limited knowledge or by school children who are initiated to the beauty of birds.

The public may find these guides useful but it is doubtful considering their price. The price of the series is very high and only a selected number of species are treated. One can get for approximately the same cost, or less, the two volumes of the Peterson eastern and western field guides to the birds of North America that have much more to offer and are easier to use. These guides have become classic references and continue, for good reasons, to be popular among naturalists and bird watchers, even beginners, because of their quality and the information they provide, particularly on identification. They are a much better all around value than this “revolutionary new tool.” I therefore can recommend the acquisition of traditional guides to the birds, either the Peterson series or any of the other excellent ones that are now on the market, instead of the flash guides. Any of these traditional guides are a better value.

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Amphibians of Oregon, Washington, and British Columbia: A Field Identification Guide

By C. C. Corkaran and C. Thomas. 1996. Lone Pine Publishing, Edmonton, Alberta. 173 pp. Illus. \$21.95; U.S. \$16.00.

This useful volume may be the most profusely illustrated guide to amphibians produced to date anywhere. It covers two northwestern states and one adjacent province, all bordering the Pacific in North America. Earlier guides which include the same area in a larger coverage (Nussbaum et al. 1983; Stebbins 1985) or parts of it (Cook 1984; Green and Campbell 1984) are now more than a decade old and in some cases (e.g., Cook 1984) out-of-print.

The superb colour photographs which dominate virtually every page depict live salamanders and frogs with many ages and poses for each species not just of adults, as normally illustrated in guides, but also of the more rarely included larvae and eggs. There are also many useful black-and-white diagrams of critical characters, including those in detailed pictorial keys to eggs, larvae, and adults which cover 23 pages near the end of the book. Numerous habitat photographs in colour are also included. Although the distribution maps are based on the latest available records from state and provincial data files, sources rapidly increasing in comprehensiveness from continuing surveys and environmental studies, they are disappointing in that they show only broad areas of occurrence, not localities. And beware: because only Washington and Oregon are mapped in the United States, and British Columbia protrudes east of both, the maps for the Tailed Toad, *Ascaphus truei*, and the Coeur d'Alene Salamander, *Plethodon [vandykei] idahoensis* appear to show greatly disjunct distributions in the eastern portion of the British Columbia far beyond any records visible in the United States only because no localities are included for Idaho or Montana as these states are extra-limital to the text.

Although classification is not a primary focus of this book, some conflicting taxonomic contentions are noted for included forms, such the species (as given here) or subspecies status for the forms of *Plethodon vandykei*, the use of *Scaphiopus* or *Spea* for western spadefoot toads, and the anticipation of David Green's split of *Rana pretiosa* (subsequently published as Green et al. 1997). Original describers and date are included for all names, but surprisingly

the name *Dicamptodon tenebrosus* is credited to Good 1989 who brought it out of the *D. ensatus* synonymy, rather than to Baird and Girard 1852 who actually originated it.

The detail on identification allows the authors to discourage (disparage?) collecting, even the taking of voucher specimens. Unfortunately, though emotionally commendable, this approach will render identifications in difficult taxa unverifiable and therefore useless for valid documentation. As a source of life history and habitat summaries and descriptions of eggs, larvae, and metamorphosed individuals, the book is exceptionally strong and shows the field experience of the authors to particularly good advantage. For these accounts and the illustrations, this book should be on the shelf or in the pack of any naturalist in the area.

The Canadian Heritage Department is acknowledged for their help in subsidizing the Canadian publisher of this book, though the authors and substantial portions of the text are American. By a strange turn of fate, Canadian Heritage is also the federal department responsible for The Canadian Museum of Nature which cut (among other fields) all research staff in vertebrates except fish over four years ago and thus abandoned its support for many original projects then active that emphasized the fauna of this country, including Canadian books on amphibians and reptiles.

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Snakes in Question: The Smithsonian Answer Book

By Carl H. Ernst and George R. Zug. 1996. Smithsonian Institution Press, Washington and London. xvii + 203 pp., illus. Cloth U.S.\$49; paper U.S. \$24.95.

This is the second volume in the Smithsonian Answer Book series (the first was on Sharks) designed

to capitalize on groups which markedly arouse public curiosity. The choice here is excellent: snakes are numerous (2600 species; 2800 taxa if subspecies are included), occur the world over, often evoke strong reactions of loathing or fascination, and ignorance and

misinformation about them stubbornly persists. Because of the latter, far too often they fall victim of the "snake reaction syndrome" [grab and wield the hoe, question later] wherever encountered by humans. Moreover, in common with other reptiles, new research on them rapidly makes previous texts outdated. Newly described species and new facts about others accelerate as the world inventory of nature races against the seemingly imminent obliteration of much world diversity as a consequence of ever-expanding human numbers and resource consumption.

The question-and-answer format is divided into: 1. Snake Facts [definition, build, breathing, movement, senses, food, enemies, reproduction, etc.]; 2. Folk Tales [falsehoods, supernatural powers, tales, etc.]; 3. Giant Snakes: Big and Biggest [qualifications - 3 meters or more total length; pythons, boas, ratsnakes, king cobra, taipans, bushmaster, mamba, others]; 4. Snakebite [differences and numbers, distribution, antivenom, etc.]; 5. Snakes and Us [why important, why snakes are present in houses and how to get rid of them, snakes as pets, how to become a snake specialist, what remains to be learned]. These topics are encompassed in 92 questions, split equally between major and minor ones, and 11 accounts of individual or groups of species that represent the largest kinds. Five appendices follow the text: 1. Classification of snakes; 2. Pygmies to giants: Body sizes of selected species of snakes; 3. Slower than they seem: Locomotion speeds of selected snakes and other animals; 4. Snake offspring: The many and the few; 5. Herpetological organizations [disappointingly, only three U.S. based international and seven selected U.S. regional societies are listed]. There is a glossary [155 terms: adaptation to yolk sac], a general biography, a subject bibliography [by sections and questions], a taxonomic index, and a subject index. Sixty-four colour photographs of individual snakes by a variety of photographers (individually acknowledged) are arranged in 24 plates on 8 pages inserted together between pages 46 and 47. Additional illustrations are by Molly Dwyer Griffin. In the text, 72 figures (diagrams, sketches, and photographs) and 8 tables are scattered throughout. Not surprisingly, the majority appear in the initial section which covers 73 of the 154 pages of text.

The question/answer format serves well; even when it unabashedly talks down to the reader, the

intrinsic fascination of the topic and up-to-datedness of the information dominates. Examples of the latter abound. The vertebrate classification included shows birds as reptiles without qualification or reservation (Figure 1.1, page 2). The discussion of Jacobson's organ mentions that the forks of the tongue are not inserted in its cavities when the tongue is withdrawn into the mouth as was long believed. Instead, traces of scent the tongue has picked up from the air are now known to be placed on a pad on the floor of the mouth and this is elevated and pressed against the pits of Jacobson's organ (page 20). *Liochlorophis* is recognized as the generic name for the snake formerly called *Ophedryx vernalis*, and its common name is now given as two words not three [Smooth Greensnake] (Appendix 4, page 169) [the genus *Ophedryx* now contains only the eastern U.S. *O. aestivis*, the Rough Greensnake].

The writers have impeccable qualifications not only to create this synthesis of the most interesting questions one might ask about snakes but also to present the most up-to-date answers. Carl Ernst, professor of biology at George Mason University, Fairfax, Virginia, has been senior co-author of *Turtles of the United States* (1972, revised 1992 to include Canada) [the latter reviewed by D. Seburn. 1995. *Canadian Field-Naturalist* 109(4): 490], *Turtles of the World* (1989) [reviewed by P. T. Gregory. 1991. *Canadian Field-Naturalist* 105(1): 131-132.], *Snakes of eastern North America* [reviewed by Ross MacCulloch. 1991. *Canadian Field-Naturalist* 105(1): 129.] and *Venomous Reptiles of North America* (1992); George Zug is curator of herpetology at the National Museum of Natural History (United States of America) and most recently author of *Herpetology: An Introductory Biology of Amphibians and Reptiles* (1993) [reviewed by F. R. Cook. 1995. *Canadian Field-Naturalist* 109(4): 483-485].

The present book could earn a justly prominent place on any natural history reference shelf. Only the price is regrettable, it is steep, especially for a brief popular reference in hard cover, but worth it for the convenience and updating offered.

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Opossums, Shrews, and Moles of British Columbia

By David W. Nagorsen. 1996. Royal British Columbia Museum Handbook. University of British Columbia Press, Vancouver, in collaboration with the Royal British Columbia Museum. 169 pp., illus. \$24.95.

For those of us interested in the insectivores, and in particular the shrews, of North America, this book

provides a welcome addition to the bookshelf. It is the second volume in a series of handbooks designed to update *The Mammals of British Columbia* by Cowan and Guiguet (1965), which is out of print.

Nagorsen's book is coarsely divided into five sections. The first two give an account of the general

biology of opossums and insectivores; the next two sections provide a species checklist and keys to identification; and the last section includes species accounts.

The first two sections give a nice introduction to those characteristics that make opossums, shrews, and moles unique and interesting subjects of study. The author's enthusiasm for the shrews and moles is evident here in his description of insectivore natural history. Further, this introductory material provides all the basic information needed by the novice to use the keys and species accounts provided later.

Keys are provided to identify insectivores based on whole specimens or skulls, which taken together provide a robust tool for identifying some of the more problematic forms of the region. Well-done line drawings illustrate diagnostic characters, and diagrams provide instructions on how measurements should be correctly taken.

A species account is given for each of the opossum, nine species of shrew, and three species of mole that inhabit British Columbia. Each account provides a description, natural history account, and notes on the range, taxonomy, and conservation status of these species in the region. I appreciated that, along with the mean, the author provided a range and sample size for all body measurements. The skull diagrams were small (a ca 5.5-by-8-cm window enclosed top, bottom, and side views) but illustrative. Black-and-white line drawings of whole specimens accurately depicted each species but provided little help in discriminating among species.

Throughout the book, Nagorsen emphasizes the biogeography of this diverse region. Several maps describing the geographical features of British Columbia are given, including a full-color, fold-out map of the Biogeoclimatic Zones of British Columbia, as determined by the Ministry of Forests. Also, each species account is accompanied by a dot map, representing all known locality records for British Columbia. These features combine to impress the reader with the importance of the lower Fraser River valley, an area undergoing rapid urban growth, to the diversity of insectivores in British Columbia.

I was impressed by the author's successful attempt to address both the working mammalogist and layperson by taking advantage of the primary literature while avoiding jargon. Each sub-section of the book and species account ends with a list of 5–10 important references. Where it was necessary to use obscure terms, the author defined them in the text. Also, a glossary of germane terms is given at the back of the book.

I strongly recommend *Opossums, Shrews and Moles of British Columbia* by Nagorsen to anyone interested in these groups. It provides an excellent guide to the species found in this region and a useful reference to anyone working with insectivores.

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Amphibian Biology, Volume 1: The Integument

Edited by Harold Heatwole and George T. Barthalmus. 1994. Surrey Beatty & Sons PTY Limited, Chipping

Norton, New South Wales, Australia. Pages i-xi + 1-418, illus.

Amphibian Biology, Volume 2: Social Behaviour

Edited by Harold Heatwole and Brian K. Sullivan. 1995. Surrey Beatty & Sons PTY Limited, Chipping Norton, New South Wales, Australia. Pages i-xi + 419-710, illus.

Of the conventional major groupings of living vertebrate animals — mammals, birds + reptiles (no longer as distinct as we once thought), amphibians and "fish" (a catch-all term for several classes as distinctive as tetrapod ones), the amphibians have had the lowest public profile. Their members — frogs, salamanders, caecilians — are commonly perceived as of marginal direct economic value to humans. As well, amphibians are generally unattractively moist and sometimes slippery: featherless, hairless, scaleless. They are frequently associated with low, wet, insect-infested areas where the their major group

(frogs) are raucously vocal about sex in the spring. In the first half of the 1990s, when rumours spread of a world amphibian decline which might forewarn us of imminent environmental deterioration, amphibians achieved a brief pulse of news value. However, this faded as the probable causes often proved intractable and varied, and the natural population fluctuations wide. World-wide monitoring studies continue, but must largely sustain themselves, once again under-prioritized and consequently underfunded.

Often overlooked by non-biologists is that, because of their naked skins (and shell-less eggs), amphibians have had an important historic role for teaching and research in anatomy, physiology, and embryology, and, because of their courting aggregations (noisy or not), have increasingly contributed to

our knowledge of mate selection and speciation. Reptile research has been well served by the multi-authored syntheses provided by *Biology of the Reptilia* edited by Carl Gans and colleagues (16 volumes, 1969-1988; Academic Press and Alan R. Liss, Inc., both of New York), but that for amphibians has been less so. Over 65 years ago, G. K. Noble single-handedly produced *The Biology of the Amphibia* (1931, McGraw-Hill, later reprinted by Dover) which remained the primary reference until W. E. Duellman and Linda Trueb coauthored *Biology of Amphibians* (1986, McGraw-Hill Book Company). Other texts have reviewed selected aspects: *Physiology of the Amphibia* published by Academic Press, Volume 1 (1964) edited by J. A. Moore, 2 (1974) and 3 (1976) edited by B. Lofts. Single volumes of note have been *Frog Neurobiology, a handbook* by R. Llinas and R. Precht (1976, Springer-Verlag, Berlin); *The Reproductive Biology of Amphibians* edited by D. H. Taylor and S. J. Guttman (1977, Plenum Press, New York); and *Environmental Physiology of the Amphibians* edited by M. E. Feder and W. Burggren (1992, University of Chicago Press, Chicago).

It is now timely to have an amphibian reference series in the scope of the Gans reptile volumes. Five are planned to date and a measure of the scientific community support is given by senior editor Heatwole in the introduction to the initial volume where he writes that of 64 potential authors contacted for contributions to the series only three begged off, pleading overwork. In keeping with skin and courting being remarkable aspects of amphibians, the first two volumes of the series emphasize these topics.

Volume one, *The Integument*, contains 11 chapters by 17 contributors from the United States (9), Israel (4) and Australia, Italy, United Kingdom, and Germany (1 each). The chapters (and authors) are: The Structure of the Integument (Harold Fox), Ontogenesis of Amphibian Epidermis (Michael R. Warburg, Dina Lewinson, and Mira Rosenberg), Pigmentation (Sally Frost-Mason, Randall Morrison, and Kenneth Mason), Biophysics of Ion Exchange across Amphibian Skin (Uri Katz and Wolfram Nagel), The Role of Cutaneous Acid-Base-Electrolyte Exchange in Extracellular pH Regulation (Daniel F. Stiffler), Effects of Skin Circulation on Water Exchange (Robert H. Parsons), Cardiovascular Regulation of Cutaneous Gas Exchange (Gary M. Malvin), Effects of Unstirred Layers on Cutaneous Gas Exchange (David T. Booth), Bioactive Secretions of the Amphibian Integument (Vittorio Erspamer), Role of Skin in Reproduction and Behaviour (Lynne D. Houck and David M. Sever), and Biological Roles of Amphibian Skin Secretions (George T. Barthalmus). The volume is fittingly dedicated to Dr. Vittorio Erspamer, who at age 82, delivered a manuscript within a year accord-

ing to the opening tribute by George T. Barthalmus. This is published as an 173-page chapter which constitutes 41% of the volume.

Volume two, *Social Behaviour*, contains 7 chapters by 17 contributors, 15 from the United States, and one each from Spain and England. The chapters (and authors) are: Intersexual Selection and Alternative Mating Behaviour (Tim R. Halliday and Miguel Tejedo), Female Choice and Mating System Structure (Brian K. Sullivan, Michael J. Ryan, and Paul A. Verrell), Parental Care (Martha L. Crump), Aggregation and Kin Recognition (Andrew R. Blaustein and Susan C. Walls), Interspecific Interactions and Species Recognition (H. Carl Gerhardt and Joshua J. Schwartz), Aggression and Territoriality by Salamanders and a Comparison with the Territorial Behaviour of Frogs (Alicia Mathis, Robert G. Jaeger, W. Hubert Keen, Peter K. Ducey, Susan C. Walls, and Bryant W. Buchanan), and Field Studies of Steroid Hormones and Male Reproductive Behaviour in Amphibians (Lynne D. Houck and Sarah K. Woodley). The volume is dedicated to Dr. Kentwood Wells whose classic paper "The Social Behaviour of Anuran Amphibians" appeared in the journal *Animal Behaviour* in 1977 and has influenced nearly every worker in studying behavioural ecology of frogs since, according to the opening tribute by H. Carl Gerhardt and Joshua J. Schultz.

The two volumes are large (12 × 8.5 inches), and profusely illustrated with black-and-white photographs and a sprinkling of plates in volume one of living amphibians which show their often spectacular colours. But make no mistake, despite the coffee-table format and colour, the text is technical reference material, rich in data, and these volumes are not for a single reading session. For topic-dipping, however, they are a treat. Even if the price is too steep, or the information too dense, for your home bookshelf, urge your local institution or library to purchase these for their reference section, and consult them often.

Proofing is occasionally sloppy, as early as the misspelling of co-editor's credit for the Dedication to the first volume. The authors (and reviewers and editors as well, apparently) of the series were not always alert to current systematic nomenclature. In Volume 1, for example, in summarizing Twitty's classical studies with western North American newts (page 64) the generic name *Triturus* used in the original publications is retained without reference to the transfer of these newts to *Taricha* in the 1950s. They are also indexed as *Triturus*, though *Taricha* also appears in the index as a separate entry for later references. This may reinforce the long-standing conviction of some systematists that some physiologists, so precise with their own detailed terminology, are often careless or out-of-date with the

names meant to serve to identify the whole organism used in their studies. It is particularly unfortunate as Twitty was an exception himself to this impression, his nomenclature was correct for the time it was published, and he even once recognized and described a new species from the material he used that is still valid.

In progress for the series are Volume three, a review of sensory perception including the ability to detect magnetic and electric fields, Volume four covering paleontology, and Volume five on osteology.

If the other volumes being planned for embryology, endocrinology, biomechanics, ecology, populations, taxonomy, life histories, digestion, circulation, anatomy, cell biology, and biogeography are all realized this series could surpass the earlier reptile series in total volumes.

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Handbook of the Birds of the World, Volume 3: Hoatzin to Auks

Edited by Josep del Hoyo, Andrew Elliot and Jordi Sargatal. 1996. Lynx Edicions, Barcelona. 821 pp., illus. U.S. \$175.

Good books are often the most difficult to review and this is one that every birder will prize. *Birds of the World: Volume 3* is the latest large, glossy, and expensive addition to the 12-volume project to document the world's bird species. Like previous editions it is well written, lavishly illustrated and covers some of the world's most intriguing birds. What more can I say?

This volume covers thirty groups of birds. The major ones are cranes, rails, bustards, shorebirds, gulls, and auks. Many of the minor groups contain only one or two species that have been a problem to classify. Hoatzin, for example, is a bizarre creature that has some un-birdlike features and it is an intriguing species with which to start the book. The photographs of Hoatzin are, like many in the book, marvellous. Each family, whether it has one or many members, is described in detail. Some people may have difficulty with the sections on Systematics as they are replete with technical terms and many will find this demanding reading. The remaining text on habitat, habits, breeding, conservation, and other family characteristics is less scholarly and will likely be more pertinent to the average birder.

The family section is followed by a field-guide style coverage of each species. This provides the same type of information as the family segment, but for the individual species. A range map gives the world-wide distribution for summer, winter, and permanent residency. One component of these species accounts I found enlightening was the remarks headed "Status and Conservation."

The illustrations in the species accounts are for adults in summer plumage only. Where there is a difference between sexes or sub-species then the alternative plumage characteristics are also shown. For most birds this is reasonable, but I did have a problem with the birds that are more often seen in winter than in breeding plumage. For example, Purple Sandpipers and Dovekie occur in the north and Asian Dowitcher in the south mostly in their

winter plumage. All birds are shown standing, making important details seen in flight, difficult to discern. The distinguishing tail pattern of the recently split Belcher's and Olrog's gull is a case in point.

In drawing up the list of species, the authors have used the finest division criteria. This means that controversial splits, like Thayer's Gull, are included as a separate species. The author's rationale is that from a population point it does not matter if they are eventually lumped; their data are still valid. I noted that they had split the Bush-hen into Plain Bush-hen (Philippines) and Red-tailed Bush-hen (Australia and other Pacific islands). This split was missed by the latest Australian field guide (Simpson and Day 1966) published earlier this year.

One thing this type of book brings is a world perspective. A bird that few of us see regularly and very rarely in anything but small numbers is the Dovekie; world population eight to 18 million. Compare this to a bird I have recently seen in huge numbers, the Sandhill Crane; world population over half a million. I recently added two birds to my life list. The first, Long-tailed Jaeger has been a jinx bird for years. I was always on the wrong boat on the wrong day in the wrong year! I never thought of it as a rarity, just that I was unlucky. The other bird, Ross' Gull, I have always considered a true rarity, needing dedicated effort rather than a change in luck, to see. Both these species have similar world populations!

Looking at the world distribution maps raises a point I have wondered about several times. *Vanellus* Lapwings occur throughout the world, except the polar regions and North America. A typical *Vanellid* is large, colourful and entertaining. All the 23 living species seem happy to use farmland, pasture, airports, lawns or other human enclaves. It is a pity we missed out! We also do not have a bustard, but we do have turkeys.

Reviewers feel an obligation to find errors, it somehow seems to justify their existence. By looking hard, I can see some minor points that merit a mention. As with previous editions, some information is out of date. For example, the Whooping

Crane statistic for the "current" population is about 20% low (*see* Jones 1996). The French names used are the European version and, in some cases, the North American French name is different. Francophones will have little problem recognizing the species concerned, however. Some photographs do not carry the common name of the species shown. The range maps, because of their size (the world is shown in a 5 cm by 3.5 cm box) can often be difficult to interpret. Despite this problem I believe I can detect some minor errors, like the incomplete range of the Sandhill Crane. The historical records for Corn Crake in Australia and the recent North American occurrences of the Common Crane are missed. It has been some years since I saw a bustard and the plates show birds that are longer and more slender than I recall. The artist has lost the solid chunky appearance of these impressive birds. All these I feel are trivial points compared to the huge quantity of valid information in the book.

There are two items that cause me a little more concern. Recently, at a school presentation my data on Whooping Crane heights were challenged by a young lad. These cranes were as high as his eye, and he had the references to prove it. The height I had quoted was too high and this book make a similar error. The second and more important problem is the illustration of some terns. As I read the book, I

would try to identify the birds illustrated before reading the identifying captions. I had difficulties with the terns. The Caspian Tern, for example, is depicted as paler and with more of a sandy overtone than I have seen in the field. The difference in leg lengths of Common and Arctic terns are far more noticeable than depicted. Indeed, many tern illustrations are not up to the same standard as the those of other birds.

From the insightful foreword, written from an artist's perspective by Robert Bateman, to the minutiae of subspecies, this book is an amazing contribution to bird literature. It will be a major reference for years to come and is a wonderful purchase for anyone who can afford it. There are nine more volumes planned so we can anticipate more pleasure to come. The next volume will likely include that most spectacular of bird families, the parrots. I can hardly wait!

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Birds of Kenya and Northern Tanzania

By Dale A. Zimmerman, Donald A. Turner, and David J. Pearson. 1996. Princeton University Press, Princeton, New Jersey. 740 pp. illus. U.S. \$65.

For years birding in Kenya has been a matter of wild excitement at the abundance of riches tempered by constant frustration with the inadequacy of the guides. No longer: this superb book brings East Africa into the world of late 20th century field guides. The Kenyan avifauna is indeed a rich one: this work covers all 1080 species definitely recorded there, plus 34 additional ones from northern Tanzania, enabling areas of the Serengeti and other regularly-visited areas in that country to be adequately covered as well. Hence it includes 90% of Tanzanian species and 85% of those in Uganda.

The guide has a lengthy and valuable introduction, followed by 124 plates (three devoted to Tanzanian species), then 401 pages of species accounts, and concluding with appendices listing Tanzanian and Ugandan species not covered, a gazetteer, bibliography, and indices to both English and scientific names. If all this sounds thorough, it is characteristic of the rest of the book.

The introduction not only provides the usual explanatory sections on the format of the book, but has useful information on climate and vegetation zones, the latter illustrated by 38 photographs of typical habitats.

There is an excellent and very well-illustrated section on terminology with a good glossary; the authors recognize that users will be familiar with either North American or European plumage terminologies, and sensibly give both.

The length of the species accounts varies, but each has the usual descriptive sections, with diagnostic features italicised, followed by information on voice, similar species (with differences briefly summarized), habits, and a quite thorough summary of status and distribution, including the ranges of different races as relevant, and usually complemented by a small range map.

The plates are crowded but not cluttered, and in most cases the illustrations are satisfyingly large, with all Kenyan species shown, and alternative poses and plumage variations given as appropriate. The nine species of *Mirafra* lark, for example, have 26 birds shown (and you'll need them all!). Most of the plates are by Zimmerman, but a number are by Ian Willis and Douglas Pratt. Facing pages give a capsule description of habitat and identification features for each species.

So this is one of those delightful books where the reviewer has to work to find fault! All this thoroughness does have a downside, however: this is a formidable piece of equipment. At 4 1/4 pounds, and about 18 × 25 × 4 cms, hardcover, you'll not slip

this field guide neatly into your backpocket! Given the paucity of other field reference material, opting for thoroughness rather than brevity was probably a wise choice, especially as much East African birding is necessarily either from or close to a vehicle.

There are a few minor weaknesses. Some of the illustrations in my copy are quite dark. This is most noticeable on Plate 61, where some of Africa's most brilliant birds appear positively dingy, and the Lilac-breasted Roller has become dull green, but from an identification standpoint the doves on Plates 48 and 49 may be more troublesome. Conversely the glossy starlings on Plate 77 really do not usually look as vivid as the plate implies, but highly iridescent species are hard to portray, and the plate does at least include a qualification.

Two sources of continuing frustration which are really out of the authors' control have to do with nomenclature and with more difficult species. Kenyan

ornithology has not yet achieved the refinements in the identification of difficult groups that have been developed over the years in Europe and North America. Hence, although there are now illustrations of all the *Cisticola* warblers and all the female-plumaged weavers, actually identifying the birds will still often be problematical. On nomenclature, the authors have adopted a careful and conservative approach, which is understandable and probably correct. Nevertheless, this still means that African birds continue to labour under at least three different sets of English names, and I suppose now will always do so.

None of this should detract from what is a wonderful achievement. This splendid book is a "must" for anyone visiting East Africa, and a valuable reference for the continent as a whole.

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The Wind Masters: The Lives of North American Birds of Prey

By Pete Dunne. Illustrated by David Sibley. 1995. Houghton Mifflin Company, Boston, New York. xvi, 263 pp., illus. U.S. \$22.95.

Diurnal raptors, commonly known as birds of prey, have fascinated naturalists, bird watchers, casual observers, and the general public for a long time because of the mysterious aspects of their life history and behaviour, and sometimes also, because of their size, and the legends they have engendered. Much serious and well-documented information is available now to satisfy the curiosity of individuals who can spend the time in a library to consult scientific journals or the extensive syntheses and handbooks that have appeared in recent years on these birds. However, many of these references are not always readily available and are often labourious to read for the non-initiated. This is not the case with the present book which will contribute to fill an important gap in the dissemination of information on diurnal raptors.

In spite of conservation efforts in North America, raptors continue to be threatened by human activity and a reference combining good literary qualities and sound facts could contribute immensely to disperse a deep appreciation for these birds. This book is a fine combination of these essential qualities.

The author has written in a lively and elegant fashion short stories about thirty-three species of North American raptors. His selection of species provides an

excellent cross section of the diversity of this group because falcons, hawks, kites, the osprey, eagles, New World vultures, and the California Condor become the main performers of his accounts.

Information on the distribution is given as well as details and descriptions on the ecology, behaviour, and general life history of each species, always in a vivid and absorbing style which should appeal to a majority of readers. The information supplied is general in most instances but accurate and current. I found few minor inaccuracies, the most serious being mistaking Fred Sibley for Dr. Charles G. Sibley [page 100] who, with associate John Ahlquist, has given avian taxonomy a new vigour with his innovative classification of the birds of the world.

The black-and-white line drawings by David Sibley are very attractive and pleasant. The artist was successful in giving an impression of life and movement to most of them. They are among the best illustrations of this type that I have seen.

I have no hesitation in recommending this small book to naturalists, nature lovers, bird watchers, general readers, and even ornithologists. Almost every account constitutes a little drama that retains the attention of the reader to the last line.

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Shrikes (Laniidae) of the World: Biology and Conservation

Edited by Reuven Yosef and Fred E. Lohrer. 1995. Proceedings of the Western Foundation of Vertebrate Zoology, Volume 6, Number 1. 439 Calle San Pablo, Camarillo, California 93012. 343 pp. paper.

These are the proceedings of the First International Shrike Symposium, held in January 1993 in Florida. The purpose of this symposium was to focus attention on the decline of shrike populations worldwide. Additional objectives were to review current research and establish research priorities, assess the global status of shrikes (the 30 species in the genera *Lanius*, *Corvinella*, and *Eurocephalus*), establish a world working group, and develop conservation guidelines. The proceedings consist of some 60 papers, including some not given at the symposium itself, plus appendices giving distribution maps and common names (in ten languages). There is an extensive "literature cited" section but no index.

The papers are grouped into eight parts. After general comments and four papers on evolution, systematics, and biogeography, the largest block – roughly a third of the total – discuss population status and trends. These are followed by shorter sections on foraging ecology and habitat selection, reproductive ecology, captive breeding and techniques, and conservation and management. The symposium concluded with a paper offering conclusions and recommendations.

The papers vary greatly in length and scope, and what emerges is a portrait of a group of small predators with some intriguing questions about their biology. These include behaviours that make them vulnerable to larger predators, naturally low densities that may make intraspecific communication difficult, a range of different mating systems, and a distinctive habit of impaling prey. All these topics offer opportunities for investigation, but the main

thrust of the seminar was on shrikes as threatened species, and it is to this area that most of the papers were directed.

All those shrike species that have been studied are indeed in trouble. As might be expected, the picture is reasonably clear for the five species that occur in North America and Europe, but with virtually no information for many of the African and Asian ones. The reasons for the declines are more ambiguous: there is correlation with modern intensive agriculture, but just why this is so is not clear, and research is only beginning to probe the dynamics of shrike behaviour. There is an abundance of possible causes, and it is probable that there are many factors working together. Conditions outside the breeding season emerge as being critical in some cases, with loss of habitat, the elimination of large insects due to pesticide use, and cold winters all possible contributing factors.

Four papers (two of them Canadian) discuss conservation strategies: this contrasts with the 25 that identify the scope of the declines. Clearly the struggle to save the shrikes has barely begun, and their future still looks bleak. But there are things that can be done already, some as seemingly simple as increasing the number of perches in otherwise suitable habitat.

This symposium set a positive note: it represented an important step in trying to save these birds. The proceedings are certainly not a popularised treatment of the subject, but are required reading for anyone involved with shrikes and their recovery programmes, and are also an excellent compendium of current information on these interesting species.

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A Birder's Guide to Trinidad and Tobago

By William L. Murphy. 2nd Edition. 1995. Peregrine Enterprises, 1011 Ann Street, Parkersburg, West Virginia 26101. vi + 160 pp. illus. U.S. \$15.95.

This is a revision of the author's 1986 book, updating the text where appropriate, with some additional material, a more readable typeface, and a new cover. The photos appear to be unchanged from the first edition, but the maps (a weakness in the earlier edition) have been redrawn and in some cases wholly revised, and are now much improved.

The first 44 pages of the book are devoted to an outline of the islands, with a broad range of useful information for the potential visitor. In many ways Trinidad and Tobago provide the birder with an ideal

introduction to neotropical birds. Murphy recognizes this and deals thoroughly with the things such a newcomer to the tropics might need to know. This is also one of the sections where there has been major updating, as there are many newcomers providing services to birders and the islands are no longer as safe as they once were. Murphy deals in detail with these aspects, and hence the book is an excellent source of up-to-date information on places to stay, services to use, and areas of concern, as well as on the main birding locales.

The next 66 pages provide detailed directions to 21 birding localities (four more than in the earlier edition). The number of locations may seem small,

but they do indeed include all the best-known places on the islands. In this section large blocks of text are unchanged from the first edition, but the changes that have been made are important ones, and there are improvements in layout and style. The directions given are generally satisfactory, and enhanced by the new maps.

One specific area that could be improved is in the account of Port-of-Spain sewage lagoons. The author says in the section on safety that he would not venture there without an armed guard, but he does not make any reference to this in the glowing account taken unchanged from the 1986 edition. Readers, alas, tend to skip introductory sections.

The book concludes with a miscellany of information including a very useful listing of "target" species, a list of accidentals and 13 pages of seasonal bar charts. As the abundance of fewer than 30% of the species varies over the course of the year I wonder if this latter section could not be significantly simplified and shortened, but the three sections together form a valuable complement to this authoritative guide.

The rather "chatty" approach used in the first edition is retained, but does not detract unduly from the

information given. My reaction to the first edition was that it was rather too enthusiastic and "gung-ho", and if anything the revision is more so. However, this is a matter of personal taste. On a more serious level, I had hoped that the new edition might deal in some detail with the large seasonal variations that exist. There are local movements, feeding patterns that are influenced by flowering periods, and variations in accessibility due to the rains. For example, Asa Wright is a very different place in November than it is in February with the Immortelles in bloom. Even some of the birds are different. Such information would strengthen a future revision.

These criticisms aside, Murphy has produced an excellent introduction to birding in Trinidad and Tobago. It will be useful to anyone planning a birding trip there, whether alone or with a group, and his revisions are significant enough to encourage the more seasoned visitor to acquire a copy of the new edition.

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Female Control: Sexual Selection by Cryptic Female Choice

By W. G. Eberhard. 1996. Princeton University Press, Princeton, New Jersey. 501 pp., illus. Cloth. U.S.\$85; paper U.S.\$29.95.

This is another solid brick in the building of our understanding of organic evolution. It is a book in the series of monographs in behaviour and ecology edited by John R. Krebs and Tim Clutton-Brock. Both are world leaders in this field. Two fundamentals of life are to live and to have offspring. The first is natural selection and the second sexual selection. A major theme of the book is that sexual selection boils down to the competition between eggs for sperm and sperm for eggs so that the successful individual organism perpetuates its genetic material through subsequent generations. Cryptic female choice is a powerful influence on the outcome of sexual selection.

I salute Eberhard for a huge amount of work and a generally clear, accurate account of cryptic female choice. He writes, "This is a neglected aspect of sexual selection: female processes that affect male reproductive success and occur after the male has succeeded in coupling his genitalia with those of a female." A conventional view of reproduction is that once a male has inseminated a fertile female his progeny is assured. Eberhard says not so, and documents more than 30 ways inseminated females may determine what egg and sperm fuse, and if at all. For example, in the Dunnock (*Prunella modularis*) a

sparrow-like bird of Europe, the female may eject the sperm of one male when her cloaca is pecked by another. English Sparrows (*Passer domesticus*) may behave similarly. The phenomenon of cryptic female choice is a general process found in a wide variety of taxa composed of invertebrates (especially arthropods) and vertebrates including humans.

Eberhard writes that he has not provided final proof that cryptic female choice is a common, important evolutionary phenomenon. But he warns students of reproductive physiology, behaviour, morphology, and evolution that they may be missing many new and far reaching opportunities if they ignore the concept in their explanations and hypotheses. Among the many payoffs from understanding cryptic female choice are restoring the balance between the sexes in the outcome of reproduction, explaining hitherto puzzling behaviour (e.g., post-copulatory courtship) and physiology such as the varied form and chemistry of sperm and seminal fluids. Needless to say, improved understanding of reproduction has great practical application to agriculture and human health.

Naturalists will find this book rewarding for new insights into the incredible world of nature. The closer we look the more wonders are revealed. For naturalists also interested in general theory the work is an eye-opener to what is involved in reproduction and evolution. In developing his arguments Eberhard

sets his topic within related theory so we get a useful primer in current thinking on courtship, animal morphology, sexual selection, and organic evolution.

I read this book because I wonder about the courtship and reproductive behaviour of grouse (and humans!). Some are more or less monogamous and the male helps the female with their young (e.g., ptarmigan, *Lagopus* spp.). Others seem promiscuous and males and females live virtually separate lives (e.g., Blue Grouse, *Dendragapus obscurus*, and Ruffed Grouse, *Bonasa umbellus*). According to Eberhard, promiscuous females (and males) should show more mechanisms related to cryptic choice than those that are monogamous. While research is certainly needed, female grouse seem alike in reproductive anatomy and physiology. However, males and females of monogamous species are more alike externally than those of promiscuous species. This suggests that sexual selection is working at the overt level of behaviour and morphology, rather than by cryptic or internal female choice.

Red Fox: The Catlike Canine

By J. David Henry. 1996. Smithsonian Institution Press, Washington, D.C. 174 pp., illus. U.S. \$15.95.

Very few extensive, yet detailed studies of animal behavior have been conducted, particularly on species as elusive as carnivores. J. Henry David, a boreal ecologist, has dedicated years of his life to understanding aspects of behavioral ecology and social organization of the red fox. Originally published in 1986, *Red fox: The catlike canine* is now in its second edition, back by popular demand. With this new edition comes a new preface that summarizes recent advances in fox ecology since the original printing. The preface was written with two goals: (1) "to summarize some new research findings of fox biology from the past decade" and (2) "to share some reflections and convictions concerning field studies of free-ranging mammals". In this preface, Henry briefly describes canid phylogeny, foxes as carriers of rabies, social organization and resource dispersion, ecology of select threatened or endangered foxes, and reestablishment of extirpated foxes. This revised edition is also enhanced by several color plates depicting this fascinating mammal.

The main part of the book contains eight chapters including a brief philosophical introduction to conducting field studies using behavioral observation, an introduction to conducting field studies using behavioral observation, an introduction to the life history of the red fox, the life of a pup from birth to fall dispersal, diet and hunting strategies for various types of prey, evolutionary strategies for foraging for small mammals, caching behavior, scent-marking behavior, and a concluding chapter summarizing examples which emphasize the importance of incorporating observa-

Perhaps Eberhard's thinking is biased by his emphasis on invertebrates, particularly arthropods. Among his many hundreds of references relatively few deal with vertebrates, particularly birds and mammals. Perhaps evolution comes about differently in different groups and this is a theme that might be explored. What might this mean to human reproduction?

While the book convinces me that cryptic female choice occurs, I could not find outcomes. What are the results of cryptic female choice? What are females choosing and why? How does this relate to their survival and the long term perpetuation of their traits? These are tough questions and require detailed long-term studies by penetrating minds. Best wishes to Eberhard and may he show how cryptic female choice makes a fundamental difference in organic evolution.

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tions of animal behavior as a part of science. These chapters evolved from the author's personal observations and notes from a field study conducted, at least initially, in Prince Albert National Park, Saskatchewan.

Henry possesses the uncanny ability to combine unprecedented observations of fox behavior with rigorous science. He has undoubtedly logged more hours observing red foxes than any other individual, past or present. One must appreciate the innumerable hours required to witness a single instance of a red fox stalking a grasshopper or caching a shrew; Henry has recorded hundreds of these occurrences. When appropriate, the author who admirably states the limitations of these observations in the context of the scientific method, but does not dismiss or diminish their importance. Unique observations into the life of this handsome carnivore are presented in a way that peaks one's curiosity, and stimulates thought and discussion as to their evolutionary significance.

I consider *Red fox: The catlike canine* an exemplary work which aids in defining the "art" often stated but rarely attained in wildlife science. This book will appeal to a broad audience, including naturalists, ethologists, wildlife biologists, and anyone attune with observing nature. I trust this contribution will inspire others to expand on Henry's work and parallel this endeavor with other species.

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A Birder's Guide to Florida

By Bill Pranty. 1996. American Birding Association, Inc. P.O. Box 6599, Colorado Springs, Colorado 80934. xii + 388 pp., illus U.S. \$18.95.

This is a fourth edition of the late James A. Lane's guide which for over two decades has been an essential tool for birding in Florida. It is wholly rewritten, and features all the innovations in format and binding that have become trademarks of the current ABA/Lane series of birding guides. It seems a little sacrilegious to say that it is much better than its venerable predecessor, but it is. It also fills a real need, as the rapid development in the state together with the disastrous hurricanes of recent years have combined to make earlier editions seriously out-of-date.

This is more than just an update with all the places that have vanished removed. There are many new localities given. A measure of this more extensive coverage is that the core "finding" section of the new edition occupies 222 pages — more than the entire length of Lane's original guide.

A lengthy introduction includes useful sections on Florida habitats, weather, birding hazards and ethics, and a calendar of birding activity. The finding part of the guide then follows the pattern set by earlier editions, dividing the State into five regions, and covering key sites in each. Directions are concise and point-to-point mileages are given at each step. All the sections have accompanying maps which are clear and easy to follow, representing a major improvement from the often cluttered and sometimes ambiguous maps in the original Lane guide.

Although Lane's entertaining idiosyncratic touches are now gone, the author offers many of those useful insights that can be so important for a visitor: for example, under Tallahassee, we are told at one point both that it is acceptable to park on the street, and to be sure to depart the area in the same way you entered, as it is easy to get lost. Trivia, perhaps, but important trivia to a stranger, particularly when they include occasional warnings of safety hazards for some places.

The book concludes with some 100 pages devoted to Florida specialties, lists of exotic birds and other fauna, and bar-graphs of occurrence of all bird species known to occur in the State. The graphs retain the earlier format, with a line reflecting overall abundance in each of the five regions, followed by a bar showing monthly status for the State as a whole. This is a concise way of presenting a great deal of data, but at times it can leave one wondering about

the actual status of a species at a particular time and place; however, it is difficult to offer a reasonable alternative, and the charts are easier to read than formerly, and often have useful notes appended.

The ring binding is now standard format with the ABA/Lane guides. There is a sturdy wire ring binding, and the rear cover is extended to fold over the front of the book and is titled: presumably one is supposed to place the book on a shelf with the rings to the rear and the titled fold-over exposed as the book's 'back'. One either likes this approach a lot or hates it, as I have heard both kinds of comment. Personally I think it's a good idea, especially as it allows for an excellent full-colour map on the inside back cover, and the end of the cover can act as a bookmark. Finding guides are not intended to be examples of great bookbinding art, and this is eminently functional. The one downside is that the book is rather loose, and I wonder about its durability; however, conventionally bound finding guides have plenty of problems in that regard too.

I failed to discover any errors or misprints, and indeed any criticisms are minor. Weight and bulk are always factors in such guides, and I thought rather a lot of space was devoted to side issues of one kind or another. If I want historical details, for example, I'll look them up somewhere else.

One feature I always find troublesome with Lane's indices is perpetuated here: geographical features are grouped by kind rather than indexed individually; for example, one finds Collier-Seminole State Park under State Parks. This might be seen as good practice, but in practice the visitor is often simply referred (by locals) to Collier-Seminole, or Collier-Seminole park. To find it in the book one then has to wade through an array of references to Parks and other public lands (eight categories for State and six National). This is made even more confusing by occasional references to the title: Ocean Pond appears under Ocean, Eco Pond under Pond. Perhaps the author would consider changing this approach in future editions.

There certainly will be a demand for future editions. The above niggling aside, this is an excellent book, and a fitting continuation to a fine tradition. Don't go to Florida without it!

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Atlas of the Distribution of Fish within the Canadian Tributaries of Western Lake Superior

Edited by W. T. Momot and S. A. Stephenson. Occasional Paper #19. Centre for Northern Studies, Lakehead University. 1996. 383 pp., illus. \$30.

As the title indicates this book contains a minimum of text, six tables and a large number of maps. The introduction states the purpose of the Atlas is to accurately document what is reliably known of the distribution of fish in the Thunder Bay Region of Ontario in 1993. Future records of fish distribution in this area can be compared with this baseline and inferences made about the reasons for any new records or changes in distribution. The 1993 distribution is discussed briefly in terms of post-glacial dispersal routes of fish into the region and deliberate and accidental introductions.

For each species there is a pen and ink sketch and these are generally well done. This is followed by a

few sentences describing the ecology and importance of the species and maps based on the Ontario Ministry of Natural Resources Watershed Division Map 23WD showing sites of collection.

The Atlas is wire bound, printed on good paper and achieves its stated purpose. For the Thunder Bay area it is clearly the best and most-up-to-date of information on fish distribution. It will mainly be of interest to residents of this part of Ontario and biologists with an interest in detailed information on post-glacial dispersal of fishes into this rather dynamic aquatic region of the continent.

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Pleistocene Amphibians and Reptiles in North America

By J. Alan Holman. 1995. Oxford University Press, New York. 243 pages. Hardcover. U.S.\$65.00.

When, a few years ago, a frog skeleton was revealed in a clay concretion dating from the post-glacial Champlain Sea in the Ottawa River valley, there was little debate on who to send it to for identification: J. Alan Holman was the obvious first choice (Holman et al. 1997). A glance at the bibliography of this book shows why: no less than 59 entries (largely reports or interpretations of Pleistocene fossil herpetofaunas) have Holman as senior author; in 46 of these he is sole author. The 65-year-old specialist's first cited publication here was on a Florida cave in 1958; in ever-widening ripples this was followed by sites to the west, east and north. By 1962, he was publishing on Texas sites, 1965 on Missouri, 1966 on Illinois, 1967 on Georgia, 1970 New Mexico, 1971 on Kansas, 1975 on Michigan, 1977 on Maryland and South Dakota, 1982 West Virginia, and 1986 Ohio. By 1989 his publications included a site in England. The present book not only effectively synthesizes this lifetime of analyses from his own studies but also incorporates the previous and contemporary results of others. It is, therefore, an essential reference and springboard for the continuing research needed to enhance our understanding of the Pleistocene.

A two-page introduction to the Pleistocene opens the book. Following are sections: (2) The Pleistocene in North America, (3) The North American Herpetofauna: Late Cretaceous Through Pliocene, (4) A Bestiary [by family of extant and fossil taxa], (5) Identification of North American Pleistocene Herpetological Fossils, (6) Pleistocene Herpetofaunas in North America [170 sites listed], (7) Herpetological

Population Adjustments during the North American Pleistocene, and (8) Extinction Patterns in North American Pleistocene Herpetofaunas. A two-page Epilogue concludes the text. It is followed by References, Index, Site Index, and Taxonomic Index.

The text carries a sobering message. The Pleistocene is generally regarded as ending 10 000 years ago with the withdrawal of the last great glaciation, the Wisconsin, in progress, to be succeeded by the so-called "Holocene" or "Present". But has it really ended? Four major Pleistocene glaciations are classically recognized, but there may actually have been many more of lesser extent. The climatic deterioration leading to the first is dated at 1.9 million years ago. The Wisconsin lasted 100 000 years and was preceded by a 10 000 year interglacial, the Sangamonian. The cause(s) of glaciations are still not completely understood and we might actually be only at the end of one interglacial, on the verge of another glacial advance. The timing is disquietingly right.

A point well made is that many consider amphibians and reptiles, because they are partially or wholly terrestrial ectotherms (dependant on the external environment for most of their body temperature), to be especially sensitive indicators of climate. However, despite radical climatic fluctuations in the last 65 million years, many presently existing families were present at the end of the Cretaceous, many current genera in the Miocene, and still-existing species dominated the Pliocene. No families, no genera, and only 12 described species of amphibians and reptiles disappeared in the Pleistocene in contrast to mammals which lost 8 families, 46 genera, and 191 species, and birds which lost 2 families and

19 genera. But present herpetofaunas (groupings of species) did not exist intact through the Pleistocene. Their now-member species did not move synchronously together in response to climatic change and glaciations as units, but sometimes responded individually. This is shown by mixtures of species in some fossil localities which are considered strange by present associations and do not allow the tracking of community shifts.

There is information here for all naturalists interested in the history of faunas on this continent, and

essential reference material for any zoogeographer. It should be widely used by both groups.

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Reference

Holman, J.A., C.R. Harington, and R.J. Mott. 1997. Skeleton of a leopard frog (*Rana pipiens*) from Champlain Sea deposits (ca. 10000 BP) near Eardley, Quebec. *Canadian Journal of Earth Sciences* 34(8): 1150–1155.

BOTANY

Forest Plants of Central Ontario

By Brenda Chambers, Karen Legasy, and Cathy V. Bentley. 1996. Lone Pine Publishing, Edmonton. 448 pp., illus. \$24.95.

How does one write a field guide to plants for non-botanists? The aristocratic precision of the dichotomous key, with its perigynia beakless, its rootstocks loosely caespitose and its leaves pinnately dissected, may bring a warm glow of aesthetic pleasure to the avid botanist, but it frequently is as impenetrable to the casual plant observer as the hieroglyphics of quantum mechanics.

The *Forest Plants of Central Ontario*, a handy field guide to the flora of the northern part of the Great Lakes St Lawrence Forest Region, does a particularly good job for many groups of plants in guiding the would-be plant identifier without resorting to dichotomous keys. In addition to herbs, the authors ambitiously cover trees, shrubs, grasses, sedges and rushes, ferns and their allies, mosses and liverworts, and even lichens.

Each species is allotted an entire page. The common name is given in English and French along with the scientific name. A colour photo illustrates the plant and usually the flower. For the trees, the authors have thoughtfully provided a photo of the leaves against the bark. The text is divided into six sections: general (height and basic description), leaves, flowers (including approximate dates), fruits, habitat and notes. The notes often provide an expla-

nation of the scientific name, traditional uses of the plant or comments on similar species. Many species also have a brief note on what types of wildlife eat them. There is also always a scaled black-and-white line drawing of the plant, often with close-ups of certain structures such as the flowers.

For the herbs, a series of charts guide the reader to the potential genera. Flower colour (the weakest link in the chain) is the first step. Then the reader selects one of eight possible paths based on the number of petals, or the flower arrangement (e.g. in a dense head, or tubular). Then there is a choice of four different leaf structures: opposite, alternate, basal or compound. This often narrows the choice down to only one or two genera. In total, about 150 species of flowers are covered. Unfortunately not all of the other groups have such elegant guides. There is no key whatsoever for the 30 species of trees and the almost 90 species of shrubs are simply arranged into six types of leaf structure.

The book is sturdily bound and conveniently sized for carrying in a knapsack for a day's hike. Of course it won't have every plant encountered, but with roughly 400 species it is a painless introduction to the flora of central Ontario.

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Plants of the Western Boreal Forest and Aspen Parkland

By Derek Johnson, Linda Kershaw, Andy MacKinnon, and Jim Pojar. 1995. Lone Pine Publishing, Edmonton, Alberta. 392 pp., illus. \$24.95, U.S. \$19.95.

This is a wonderful book which, unlike most floras which are designed to treat the plants of a political region or regions, covers the common plants of the North American boreal forest and aspen parkland

from roughly longitude 92°W, west to northeastern British Columbia and Alaska. Its layout is not in the taxonomic sequence with keys as found in normal floras, but is colour coded to readily separate trees, shrubs, wildflowers (including some introduced weedy species), parasitic-saprophytic and carnivorous plants, aquatics, grasses and grass-like plants

such as sedges and rushes, ferns and fern allies, mosses and liverworts, and lichens.

A brief introduction describes this guide book and how to use it, the region and variation within it, the physical environments of climate, physiography, geology, soils, and geological history. Also included here are descriptions of the vegetation including the various forest types, wetlands, parklands, localized grasslands, and disturbed situations. Of particular interest is the relationship of plants and the native people, the impact of European immigration on the region, and the use of plants as food and medication.

Easily-used keys are provided in most of the sections and in many cases these are supplemented with fine line drawings which depict plant parts described in the adjacent key. Roughly half a page is devoted to each species found in a section. Here

are colour photographs and occasionally line drawings, common and scientific names, general descriptions plus description of leaves, flowers, fruits, habitats, and ranges. Of particular interest are the notes which include further descriptive comments but especially uses not only modern but also those of native people such as food, medicinal, cultivation display, warnings of poisonous properties, and historical information.

A glossary, references and an index to common and scientific names complete the work.

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Mountain Plants of the Pacific Northwest: A Field Guide to Washington, Western British Columbia, and Southeastern Alaska

By R. J. Taylor and G. W. Douglas. 1995. Mountain Press Publishing Company, Missoula. 437 pp., illus., U.S. \$20.

Mountain Plants is anchored by mostly excellent colour photos of some 400 species of Pacific northwest vascular plants, each accompanied by a brief species description as well as mention of similar species, site ecology, and distribution. Where the photos don't do the trick on their own (notable with the treatment of graminoides), excellent pen and ink sketches fill in. These sketches are also employed very successfully to introduce groups of plants and to explain technical characteristics.

The species treatment section is preceded by a functional introduction which describes the various vegetation zones found within the geographic area covered by the guide. This would have been clearer had the authors' not followed the unfortunately-common fashion of treating common names entirely in lower case letters. Without prior knowledge, for example, the reader cannot know if "mountain hemlock" refers to hemlock trees that are found on mountains or to *Tsuga mertensiana*, a species of conifer.

The success of the book as a field guide is reduced to some degree by the limited information provided in the brief descriptions. More bothersome, however, is the awkward arrangement of the species treatments. Species are assigned to one of four major groups (ferns and fern allies, trees, forbs and shrubs, and graminoids) and are then arranged alphabetically within these groups by family common name. (Are you still with me?) Even that curious arrangement is

not consistently followed. The Heath Family, for example, is followed by the Crowberry Family then the Honeysuckle Family. Rather than try to figure this all out, I suspect most readers will flee to the index. The latter, fortunately, is comprehensive and easy to use... so long as you have some idea of the species you are looking for.

The print employed in *Mountain Plants* is clear and readable. There seems to be relatively few typographical slips or factual errors in the text and these are not major. The worst I came across was that the "Key to identifying Ferns and Fern Allies" does not actually include any fern allies. Similarly, the overall representation of floristic variation of the region seems good. As a quillwort fan, however, I must take exception to Isoetaceae being the only major pteridophyte family not to be included, despite the occurrence of half a dozen *Isoetes* species within the guide's range. Although several pages on my copy were somewhat blurred, the book is well bound and is printed on glossy, high quality paper that presents the illustrations to full advantage.

All in all, this is a fine guide and is a worthwhile floristic reference for field botanists interested in the flora of British Columbia and the adjacent U.S. Pacific northwest. Its low price makes this profusely and colourfully illustrated guide an especially good value.

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The Book of Swamp and Bog: Trees, Shrubs, and Wildflowers of Eastern Freshwater Wetlands

By John Eastman. 1995. Stackpole Books, Mechanicsburg, Pennsylvania. 237 pp., illus. paper. U.S. \$16.95.

Most field guides are limited to identification. For the naturalist who wants ecology rather than taxonomy, John Eastman has written a delightful compilation of the natural history of wetland plants. Amateurs and professionals studying wetlands will find this book a readable and useful reference for the north-central and northeastern United States and adjoining regions of Canada. *Swamp and Bog* profiles 75 genera or species of woody and nonwoody vascular plants (ferns and horsetails are treated in single sections), as well as green algae, blue-green algae, stoneworts, and sphagnum. Taxon accounts are arranged alphabetically by common name, each occupying 1–4 pages of text, most accounts with at least one drawing. Accounts cover identification (very brief), common names, related taxa, habitat, life history, pollination, plant and animal associates, galls, pathology, and human uses. The Introduction argues for wetland conservation. There is a 4-page glossary but no index. The 14 x 21 x 1.8 cm size fits only the largest pocket, and a sturdy binding does not allow the book to lie flat.

Swamp and Bog entertained and informed me about Joe-Pye-weeds as butterfly plants, bur-reeds as deer food, cotton-grass tussocks (“a sort of pot-bound growth form without the pot”), bird feeding on cattail moth caterpillars, and the occurrence of mound-building ants with tamarack and poison sumac. I appreciated the discussions of insects visit flowers or feed on other plant parts; non-aquatic insects in wetlands sorely need ecological study.

References are not cited in *Swamp and Bog*, limiting its use as a source book for wetland science. Eastman has drawn on a wide range of literature as well as his own field work, and I was frustrated that I could not confirm or extend many intriguing statements. At least two direct quotations, on pages 93 and 154, are not attributed.

There are errors and unwarranted generalizations, of which I mention a few. “Plectoptera” (page 2)

should be Ephemeroptera, and “microplasma” (page 61) mycoplasma. Cattails (page 41) are intolerant of extended drying but do not require “relatively stable water levels” (they thrive in East Coast marshes with a mean tidal range of 1 m). Assessments of relative abundance may be Midwest-biased; *Eupatorium perfoliatum* is not the most common wetland *Eupatorium*, and *Cornus amomum* is more common than *C. stolonifera* (= *sericea*), in New York and southern New England. Statements about purple loosestrife (page 110) are narrow: There are important lepidopteran and coleopteran foliage feeders in New York in addition to *Eudryas unio*, several bird species nest and forage regularly in loosestrife, and I have seen many muskrat lodges constructed partly or entirely of loosestrife stems. I am not aware of a need for, or attempt at, biological control of loosestrife in Europe, although Cornell University and government agencies are introducing several European beetles to the northern U.S. for this purpose. Mention of a single species (page 154) slights the insect fauna of *Phragmites*. The claim that the highly carnivorous American Bittern and other herons eat *Cyperus* (page 131) is unusual and begs for documentation.

I found Amelia Hansen’s drawings generally helpful and pleasing. They range from starkly informative (moth damage to water-lily leaves), to charming (a troop of floating water-smartweed inflorescences), to mysterious (muskrat trails through an algal mat). Some are too dark (e.g., purple loosestrife spike and willow cabbage gall).

Despite its shortcomings, I recommend *Swamp and Bog* to anyone who is more than a casual visitor to wetlands. I hope the author and publisher will correct errors and add endnotes with literature references and observation details (e.g., how often and where?) in a revised edition.

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ENVIRONMENT

Population Dynamics in Ecological Space and Time

Edited by Olin E. Rhodes, Jr., Ronald K. Chesser, and Michael H. Smith. 1996. University of Chicago Press, Chicago. viii + 388 pp., illus. Cloth U.S. \$50; Paper U.S. \$17.95.

The product of a symposium held at the Savannah River Ecology Laboratory (SREL) in

1993, this exceptional book draws together 10 review papers linked to the theme of population dynamics in both space and time. It is planned to be the first in a series of books resulting from symposia at the SREL on different aspects of environmental science.

Chapters are grouped under four parts. In Part 1, Population Models, there are papers on metapopulation ecology and source-sink habitats. Three chapters in Part 2 make up Population Responses in Space and Time: multistage life cycles, overlapping generations, and migration (with emphasis on birds). Genetic Organization in Space and Time, Part 3, focuses on plant dispersal, gene conservation and the genetics of bacteria. The final part, Population Perturbations in Space and Time, provides reviews of ecotoxicology and a landscape ecology approach to biodiversity conservation.

The quality of all the chapters is high, with each of the papers peer reviewed before publication. Some of the papers delve into mathematics, especially Ilkka Hanski's chapter on metapopulation dynamics and Henry Wilbur's exhilarating attempt to apply chaos theory to multistage life cycles. Often the more mathematically oriented papers are among the most innovative in the volume.

Despite the wide field the editors have selected there is a great deal of cross-referencing of papers — a result of the fact that these papers are the product of a symposium, rather than just loosely related review papers. Nonetheless, it seems unlikely most readers would be interested in all the papers.

In addition to the scientific rigour of each paper is the added focus on conservation ecology. By linking together spatial and temporal aspects the editors clearly illustrate how conservation is not merely a three-dimensional (spatial) challenge but is really four dimensional and must be approached with greater sophistication. Three examples highlight a few of the conceptual issues that must be addressed.

In Search of Nature

By Edward O. Wilson. 1996. Island Press, Washington D.C. x + 214 pp., illus. U.S. \$19.95.

Few ecologists have the reputation of E.O. Wilson. Even fewer have his talent for conveying complex ideas about nature to a general readership and have won two Pulitzer Prizes.

This latest slim volume collects together twelve previously published essays and book chapters that date from 1975-1993. They are from diverse sources, ranging from the *New York Times Magazine* to *Sociobiology and Sociology*, a special monograph in *Revue internationale de sociologie*. The content is equally diverse but the topics are not unexpected if one has read Wilson before — ants, sociobiology, and conservation.

The essays are grouped into three parts: Animal Nature, Human Nature; The Patterns of Nature; and Nature's Abundance. Part one moves from

Ilkka Hanski offers the disturbing possibility that an entire metapopulation can be functionally extinct because of habitat fragmentation. The component populations will even appear relatively healthy. His theory has many implications for interpreting regional faunal collapses, such as many amphibian declines. A number of de-stabilized metapopulations could be eliminated by a wide-scale environmental event (such as a drought) that otherwise would not have been catastrophic.

Ronald Pulliam explores issues in source-sink habitats. Often individuals are forced into less optimum habitat for a variety of reasons, such as population pressure. Sometimes, however, environments appear to be good (source) habitat but really are sinks, or traps. Unfortunately, often human modified environments are really traps. Consider how an old-growth woodlot fragment attracts deep woods nesting birds yet their nests are highly likely to fall victim to edge predators.

The editors of the volume tackle aspects of gene conservation in one paper. Most captive breeding programs avoid inbreeding at any cost to ensure maximum genetic variation and yet some inbreeding can be necessary to preserve polymorphisms. As so often is the case, a little knowledge may be a dangerous thing.

An exciting graduate seminar course could be framed around this volume. In fact, I expect its insights, theories and models will inspire a number of graduate theses. I look forward to future volumes in the series.

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natural history to sociobiology, part two dwells mainly on sociobiology and the final part focuses on conservation. Individually, almost all of these essays are intriguing and thought-provoking. Wilson's fascination with snakes is exquisitely captured in "The Serpent." "The Little Things That Run the World," which first appeared in the journal *Conservation Biology* is a wonderful apologia for invertebrates.

Unfortunately, when read consecutively many of the essays suffer from repetition of theme and sometimes even content. For example, two essays discuss the fact that people are far more likely to develop phobias of natural things (snakes or spiders) than they are of modern dangers such as guns or knives. Not only is the point repeated but Wilson uses virtually the same examples in both cases. In addition, because the essays were originally written

for very different audiences the style shifts from colloquial to formal from one essay to the next. Nonetheless, read individually these essays represent some of the fascinating ideas of one of the century's great thinkers.

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Ecological Morphology

Edited by Peter C. Wainwright and Stephen M. Reilly (eds). 1994. The University of Chicago Press, Chicago. 36pp., illus. cloth U.S. \$65; paper U.S. \$24.95.

This book deals with ecomorphology, which is the capacity of the form of body parts (or whole bodies) to determine the ecological role of organisms. Is this a book for Naturalists? Yes and no. In the Introduction, the editors tell the reader that their target audience is "graduate students and others who are developing research programs in [ecological morphology]." Most of the chapters are written to reflect a large body of prior knowledge by the reader. However, in the Preface, the editors "hope that this book can introduce beginners to the major concepts and approaches in ecological morphology." After having read the book, it becomes clear that the editors must be defining "beginner" as someone who has a sound understanding of biology with at least some knowledge of physics and higher mathematics.

Having said that, almost anyone who decides to tackle this book should get something interesting from it. The book is divided into two major parts, concepts of ecomorphology and case studies. It is the latter component where naturalists will likely spend time reading about topics as diverse as habitat use by mosquitoes and locomotion in reptiles. Norberg's chapter on the wing shapes of bats will be particularly reminiscent to anyone who has marvelled at the diversity in the shapes of birds' wings.

The book's title does not expressly state that the contents are zoologically centred, but that is the case. There are a few dispersed examples that use plants, and Denny's chapter on the wave-swept environment contains the most. I would still recommend reading Denny's own book on the topic, *Biology and the Mechanics of the Wave-Swept Environment* (Princeton), for a more thorough treatment of the topic.

Did the editors meet their goals? They certainly drew together in this volume a number of papers that surveyed the major concepts in ecomorphology and they did provide a number of well-written case studies that illustrated the recent use of these concepts. Their third goal was to show the value of the integrative approach to studying biological systems; i.e., one shouldn't study simply morphology or ecology, but always look at the two to get the bigger picture. Most morphological studies actually do address the pertinent ecological issues, though the reverse is certainly not true. This is likely due to the fact that morphology dictates ecology; only Lamarkists would report the opposite. The editors have done a fine job in illustrating the relationship between morphology and ecology.

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Conservation of Great Plains Ecosystems: Current Science, Future Options

Edited by S. R. Johnson and Aziz Bouzاهر. 1995. Ecology, economy and environment: Volume 5. Kluwer Academic Publishers, Dordrecht. (Hingham, Massachusetts) 434 pp., illus. U.S. \$192.

On 7-9 April 1993 the symposium *Conservation of Great Plains Ecosystems: Current Science, Future Options* was held in Kansas City, Missouri. This symposium was the basis for this collection of papers. The intent of the symposium was "to help define the new Great Plains regional environmental initiative." The symposium was sponsored by a large number of partners including federal agencies in the United States, Canada and Mexico.

The book is organized into eight sections with the following headings: Defining and Valuing

Ecosystems of the Great Plains, Community and Economic Resources, Climate and Biological Resources, Land Resources, Water Resources, Energy and Mineral Resources, Agriculture in the Great Plains, and Environmental Management Initiatives. As the section headings indicate, an attempt is made to be comprehensive. A great deal of detail is supplied for the diversity and texture of ecosystems, species and cultures. Most of the information is American in origin, because as one contributor put it "information north of the border is lacking". The detail provided gives insight to how fragile the Great Plains ecosystem is.

With the detail comes a number of thought provoking questions as well as disturbing trends. The

contributors identify past, present, and future challenges for the region. Challenges which will require creative solutions that are responsive to the Great Plains environment.

Despite the technical style of writing the editors have carefully crafted a very readable collection of papers on a region often ignored in Canada. The

book should be of interest to researchers, managers, and policy makers of the Great Plains. A book which will prove to be a often used reference.

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Restoring Nature's Place: A Guide to Naturalizing Ontario Parks and Greenspace

By Jean-Marc Daigle and Donna Havinga. 1996. Ecological Outlook Consulting. 226 pp., illus. \$49. *Distributed by:* The Earth and Spirit Centre, P.O. Box 93, 270 Main Street, Schomberg, Ontario L0G 1T0 e-mail: eoutlook@ican.net.

Ecological restoration, habitat creation or enhancement, tree planting, and pond digging, are all becoming increasingly popular as people search for ways to actively undo the damage we have done to the land and to live more equitably with other species. *Restoring Nature's Place* is aimed at encouraging and guiding individuals or groups involved in these activities.

The book is divided into four main sections dealing in turn with social and environmental context, restoration itself, major ecosystems and people. In section one, the first chapter deals with why restoration is needed and why it is important, while the second chapter gives a thoughtful overview of community and ecosystem ecology. The second section details the process required in both landscape and site level restorations, with the clear message that a restoration should not be undertaken lightly. This is followed by more specific approaches to three ecosystem types, freshwater, forest, and meadow and tall grass prairie. Each chapter includes: choosing a model ecosystem and associated species for introduction. Planting and other techniques are evaluated. Long-term management needs are discussed. In addition there are lots of useful charts and tables with information specific to each ecosystem. The final two chapters, focussing on how to encourage (and handle) community participation in your project

and how to engage the minds, hearts, and spirits of participants, provide many useful suggestions and examples. The appendices include a guide to the habitat requirements of over 300 native plants. All of this results in a book with many useful resources for anyone undertaking a major restoration project. However, it also has several frustrating problems.

The text contains a disturbing number of typographical errors, misnumbered footnotes, missing references, unexplained abbreviations, crowded figures and unclear or missing figure captions. Not all the errors are superficial, as in one instance after correctly defining xeric as dry, they go on to state "Xeric communities usually refer to swamps".

These problems combine with an overuse of limp quotes, and a tendency to hyperbole in the beginning which sets a tone in sharp contrast with the careful and thorough approach to restoration the authors advocate. This is unfortunate because, although the remainder of the book contains detailed and practical information, the reader is left wondering what other errors have crept in.

The basic approach to restorations and the ecological concepts described are widely applicable; however, the book does focus on Ontario ecosystems, Ontario examples and Ontario sources of information and support and would therefore be less valuable to readers outside the province.

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Ecological Identity: Becoming a Reflective Environmentalist

By Mitchell Thomashow. 1996. Paperback edition MIT Press, Cambridge, Massachusetts. 205 pp., \$20.95.

Mitchell Thomashow teaches a course entitled *Patterns of Environmentalism* at Antioch New England Graduate School, where he uses the students' experience in their forming an identity of themselves as ecologists. The book is an outline of his course in environmental consciousness for graduate students exploring the development of ways of

environmental thinking in American history, and current American reflection on environmental issues. What is most interesting in the book is the range of environmental thinking and the attitudes which are considered. Beginning with the ascetical approaches of early environmentalists like Henry David Thoreau and John Muir, to the more modern philosophies of Rachel Carson and Edward O. Wilson, he shows a progression of humans reflecting on the world around them and conservationists battling with

developers. More importantly, he leads the reader to reflect on the tension between the need to preserve the natural world which we have around us now, and to consider the needs of our culture, for progress and innovation which impact on that same natural landscape. Thomashow identifies his students as people actively engaged in environmental issues, workers in the fields of waste clean-up, educators teaching children, and community groups, and people involved in conservation and political environmental activism. Their positions are widely dispersed over the spectrum of reflection on the environment, and he shows the reader that our positions too are widely dispersed. He presents arguments for and against conservationists, deep ecologists, industry advocates, farmers, and developers. Just as important however, there is an argument for the environmental attitude of each group named above, all of whom are sharers in environmental questions. There are no easy answers to the questions which Thomashow poses and much of his reflection comes from personal experience. One can see that he enjoys nature from a conservationist's viewpoint, and yet has to identify that he is much at fault in contributing to the waste and exploitation of the world which he enjoys.

Some interesting parts of the book deal with conflict resolution both in political activism and in individual encounters with people who are sharing the same recreational space. He shows the role that individualism plays in people making environmental

decisions, and the role of media in protecting its own interests. Certainly economic factors are explored, and the tension between exploitation and necessary development of lands and natural areas. Thinking as a conservationist, he leads his students to consider the consequences, then he brings other factors to their attention, and asks them to finally identify their position and suggest a course of action. Not only are guilt and outrage explored in his anecdotal style, but also responsible citizenship and some strategies of activism which his students have shared.

Thomashow's course is quite well defined on the basis of an adult learning style with the participants pooling their knowledge but drawing on classic and innovative strategies to solve their problems. A great deal of reflection in the book is directed to identifying the questions which need to be addressed by everyone interested in conservation in the United States and vicariously in our own situation. I found the book challenging and his anecdotes to ring true to my own experience. It is a book which I will be glad to recommend and to pass on to students of environment as well as people who struggle with their own ecological identities.

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Ontario's Old Growth: A Learner's Handbook

Mark M. Stabb. 1996. Canadian Nature Federation and Ancient Forest Exploration and Research, Ottawa. 47 pp., illus. \$7.

An Ancient Forest Atlas of the Lake Temagami Site Region (4E)

Peter Quinby, Thomas Lee, Caroline Schultz and Jennene Powers. 1996. Canadian Nature Federation and Ancient Forest Exploration and Research, Ottawa. 72 pp., illus. + map. \$10.

These two books published jointly by the Canadian Nature Federation and Ancient Forest Exploration and Research approach the subject of old growth forests in very different manners.

Mark Stabb's *Ontario's Old Growth*, is as its subtitle proclaims, a learner's handbook. A small book, profusely illustrated with line drawings, it introduces the subject of old growth forests at a very basic level. The entire book can be read in one sitting but is filled with solid bits of information, from how to determine decay class of logs, what kind of woodpecker formed that hole in a tree, and how to identify the species of dead fallen trees. This would be an excellent teaching aid for a senior elementary

or high school class. There is also a teacher's manual available.

An Ancient Forest Atlas of the Lake Temagami Site Region describes 23 old-growth forests in the Lake Temagami region of central Ontario. This region stretches east of Lake Superior to the Quebec border. The goal of the project was to identify extensive old growth stands as currently only 6% of the site region is protected. Each "ancient forest landscape" receives a two-page spread detailing currently protected areas, linkages to other landscapes, and logging history. Information is also provided on the tree species, headwaters of all rivers, surficial geology, and fire history. A small map identifies the location of the landscape within the site region. A folded map in the back pocket provides a more detailed overview of the site region. This book is a concise and valuable reference to the Lake Temagami area.

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Down Canyon: A Naturalist Explores the Colorado River through the Grand Canyon

By A. H. Zwinger. 1995. University of Arizona Press. viii + 318 pp., illus. Cloth U.S. \$35; paper U.S. \$16.95.

A tourist approached the author, after she completed an arduous climb from the bottom of Grand Canyon to the rim, with a question "Is there anything down there?" Zwinger's book provides an elegant answer to that inquiry. Based on many trips with scientists and naturalists through the Grand Canyon, Zwinger provides readers with delightful details about the richness of life there. She approaches it by dividing the book into the four seasons of the year. Three or four chapters are devoted to each season.

Zwinger covers the natural history, scenic grandeur, and scientific features of the canyon. Every detail from the smallest insects, birds, mammals, colorful flowers, to the complex geology is included. The human history, both of the prehistoric peoples and more recent visitors and settlers, is skillfully woven into each chapter.

I learned hundreds of interesting tidbits about canyon life. For example, trout there cannot be aged in the normal way because the water temperature is so consistent that there are no growth rings on the scales; members of the mustard family are toxic to most insects because they contain glucosinolates, the

substance that gives horseradish and mustard their bite; and the venom of the black widow spider is about fifteen times stronger than that of a rattlesnake. Changes wrought by man during construction of the Glen Canyon Dam are detailed, also.

Each chapter begins with a sketch by the author, followed on the facing page with a quote from an earlier traveler. Two detailed maps, from Lees Ferry (mile 0) to Pearce Ferry (mile 279.2), are most helpful in following the author's travels down the galloping Colorado River. More than 50 pages of notes are provided for those readers wishing to know more about the Grand Canyon.

The writing style is lucid, interesting, and poetic, but occasionally a bit florid. *Down Canyon* is an award-winning book. It won a Western States Book award in 1995.

At one time the author stated "... what the world didn't need was another book on Grand Canyon...." This book proves she was wrong. I highly recommend it if you have a strong interest in that region.

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Expanding Partnerships in Conservation

Edited by Jeffrey A. McNeely. 1995. Island Press, Washington, D.C. xvi + 302 pp., U.S. \$34.95.

As demonstrated by the autumn 1996 events in the Temagami region of Ontario, exploiters of a resource and people who wish to preserve an area may conceive they have little common interest. This book attempts to forestall such conflicts by fostering partnerships between stakeholders. In the view of most authors in this volume, the most important of these are formed with local people. Involvement of local individuals, groups, and communities may be difficult, but in the long term helps assure maintenance of protected areas.

This book contains revised papers from the IVth World Congress on National Parks and Protected Areas held 10–21 February 1992 in Caracas, Venezuela. The international array of authors describe conservation efforts around the globe from diverse backgrounds including industrial executives, fishery biologists, developers, a retired military officer, and several executives with various United Nations and non-governmental agencies.

The first chapter, by the editor, is a good introduction to the principles involved in building alliances. The following 31 chapters are divided into three sections: Principles of Partnerships, Partnerships with

Major Sectors, and Partnerships with Communities. A 12-page index gives a detailed listing by subject, geographical area, and author.

Unfortunately, the first two sections are disappointing, as many of the chapters are general overviews which offer an introduction to their topics, but lack examples or concepts. Chapters by Gary Machlis (on the role of social sciences), B. C. Y. Freezailah (on forestry), James Kapetsky and Devin Bartley (on fisheries), and Patrick Dugan and Edward Maltby (on maintaining natural areas for their role in the hydrological cycle) do not suffer this deficiency and are worthwhile reading.

The third section contains almost half the pages in the book and is comprised of eleven chapters written by participants in the meetings and negotiations that result in the formation of partnerships. These chapters give pragmatic approaches to and specific examples of creating local support for protected areas. Most of the cases come from areas of the world where dense populations exist immediately beside protected areas. Thus the examples may not have direct relevance to sparsely populated areas of Canada but the principles for fostering relationships are valid and useful whether in Canada or in an international forum.

Despite the weaknesses in the first two sections, this book is a valuable read. Its merit is to make clear that understanding politics, economics, human relations, and cultural values are as important as environmental information in achieving conservation goals. This is an important reminder for protected area managers, for students wishing to pursue a career in that field, and for people who act as "watchdogs" for protected areas. As well, politicians, developers, tourism operators, and other busi-

ness executives should read this book and realize there are a multitude of needs, interests, and ideas when defining value in natural systems. Creative approaches to exploiting, managing, and protecting areas begin with efforts to understand and accommodate these differences.

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The Song of the Dodo: Island Biogeography in an Age of Extinctions

By David Quammen. 1996. Scribner, New York. 702 pp., maps U.S. \$32.50; Can \$44.00.

Why the dodo? Because it lived on an island and was the first animal known to have been extirpated by man. Why the book? Because man is creating ecological "islands" of all kinds and scientific study of island biogeography has become important in preserving wildlife living in those islands. Islands are valuable in that they are an enclosed ecosystem, but the other side of the coin, of course, is that the native species are also vulnerable to inbreeding and imported disease or predators.

Song of the Dodo well deserves its best-seller rating. It is an in-depth study of the state of the art of island biogeography. The most complex theories are explained clearly and the book is unusually well crafted.

Islands include not only bodies of land surrounded by water, but bodies of land surrounded by development such as isolated forests and natural areas in pockets around towns and cities. In Madagascar, for instance, there are remnant forests separated by river valleys which have been developed. The forests contain small populations of threatened lemur species. These lemurs are becoming increasingly inbred because the separated populations will not migrate across the valley to other population and thus widen the genetic pool. The author visited many of the

important research areas such as Malaysia, South America, and Madagascar, and summarizes the current research and theories. Both Darwin and Wallace wrote papers on the subject, but of the two, Alfred Russel Wallace seems to have better realized the significance of islands in evolution and speciation. Wallace wrote a book called *Island Life* as long ago as 1880, and it was the first major compendium of island biogeography. A second major contribution is *The Theory of Island Biogeography* by Robert MacArthur and Edward O. Wilson (1967).

The research which has been done in South America on the area of forest required to preserve a balanced ecological system is particularly interesting if you apply it to the North American custom of preservation of inadequate small areas "reserved for wildlife". The findings of researchers as to what is an MVP (minimum viable population) of animals should cause concern, and disturb the complacency we feel when we read that a species has been "saved from extinction".

This is highly recommended reading for anyone working for, involved with, campaigning for, or studying the conservation of our world.

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Species Diversity in Ecological Communities: Historical and Geographical Perspectives

Edited by Robert E. Ricklefs and Dolph Schluter. 1993. University of Chicago Press, Chicago 416 pp., illus. cloth U.S. \$98; paper U.S. \$32.50.

Ricklefs and Schluter set out to broaden the concept of ecological communities by incorporating new types of data into community analysis. Only by considering large scale processes and history, they tell us, can the questions concerning the origin and maintenance of diversity patterns be addressed. As the title indicates, this volume includes papers that investigate the diversity of biological communities through the use of comparative, geographical, and

historical data. They review modern ideas about how local and mesoscale (regional) processes influence the numbers of coexisting species, present case studies of various regions and taxa, and suggest a new framework for research into biodiversity on expanded spatial and temporal scales.

The book is divided into four parts titled "Local Patterns and Processes," "Coexistence at the Mesoscale," "Regional Perspectives," and "Historical and Phylogenetic Perspectives." Ricklefs provides a well written introductory review of the theories relating to diversity and he and Schluter

provide a concise introduction to each section. The 30 chapters by 49 authors include discussions on diverse biota and regions; the reference section includes nearly 2000 entries.

Part one reviews how local abiotic processes, interactions between species, and chance result in a reduction of diversity. Tilman and Pacala review species richness theories and suggest methods to test them. Rosenzweig and Abramsky evaluate the possible explanations for the "hump-shaped" relationship between diversity and productivity, and find that no theory can explain it. Other topics include the environmental causes of trophospecies diversity, a look at community food webs (Yodzis), and environmental constraints on diversity (Underwood and Petraitis).

The second section examines the relationship between local diversity and regional processes from a mesoscale perspective. Holt classifies the regional processes that influence local species diversity patterns into five categories: source pool effects, life cycle requirements, source-sink population structure, habitat selection and metapopulation dynamics. Haydon, Radtkey, and Pianka use computer simulation to model experimental biogeography where ecology, history, and chance are controlled and evaluated as influences on species diversity. Hanksi, Kouki, and Halkka explore reasons why widely distributed species are usually more common locally.

Part three presents diverse case studies of geographical influences on community diversity. Chapter topics range greatly in biota and region with something of interest for everyone. Blondel and Vigne detail the historical account of the Mediterranean area and its biota including the influences of biogeography, geological events, glaciation, and human impact. Other topics in this section include: distribution of birds over a habitat gradient in Australia (Cody), diversity comparison of small mammals, birds, lizards, ants and termites of arid habitats, particularly Australia and North America (Morton), intercontinental comparison of insect herbivory on bracken fern (Lawton, Lewinson and Compton), parasitic communities of freshwater fish (Aho and Bush), planktonic community diversity

(McGowan and Walker), and diversity anomalies in mangrove vegetation (Latham and Ricklefs). The final chapter by Schluter and Ricklefs addresses the question of convergence and regional effects at the community level, applies their model to data from the literature, and suggests that convergence in species diversity is a common experience. The results indicate a strong habitat effect on local diversity (similar habitats have convergent diversity patterns).

The chapters in the fourth section use fossil records, systematics and phylogenetics to determine the influence of history and phylogeny on current species diversity. Two chapters describe the phytophagous insect communities using fossils (Cornell) and phylogenetics (Farrel and Mitter). These and subsequent chapters conclude that evolutionary history and biogeography are stronger influences on today's diversity patterns than local processes. Cadle and Greene use a phylogenetic approach to recount the influence of history on Neotropical snake assemblages. Latham and Ricklefs examine the temperate tree diversity in North America, Europe, and Asia. Van Valkenburg and Janis utilize the fossil record to analyze the large herbivorous mammal communities in North America.

Ricklefs and Schluter have expanded ecological community research to include historical and geographical perspectives, compiling varied and informative papers into a cohesive volume. A challenging book, it is well suited for graduate students and researchers, especially the abstract theoretical discussions in parts 1 and 2. The introductory chapter and prefaces to each section offer beginners the basic theories and background information on species diversity. Parts 3 and 4 offer concrete case studies based on the theoretical discussions in parts 1 and 2. Overall quality is excellent. Ricklefs and Schluter's innovative approach is both insightful and beneficial to the broadening of community ecology research.

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Forest Dreams, Forest Nightmares: The Paradox of Old Growth in the Inland West

By Nancy Langston. 1995. University of Washington Press, Seattle. 368 pp., illus. U.S. \$34.95.

The Blue Mountains lie between northeastern Oregon and southeastern Washington, on the old Oregon Trail, and the fate of its dense old growth forests is representative of what has happened in many of the forests of North America. This was never a particularly fertile region because of low rainfall and thin soil levels, but when the area was used by nomadic Indian tribes, the grazing, hunting,

and trapping resources were sustained. Cyclical fires cleared undergrowth and allowed Ponderosa Pine seeds to generate and larches to flourish. The forests thrived in volcanic ash soils but these soils eroded when eastern forest techniques were used. Trapping out the Beaver meant there were no Beaver dams to retain the meagre rainfall.

This detailed history is a tale of too much management and "improvement"; of well-intentioned efforts which made problems worse; of early 20th century

ignorance of the complex nature of forests and their basic biology. Once the diverse old growth forest was harvested, it was replaced by faster growing firs which are more susceptible to insect infestation, and now the new forest is not really profitable.

Permanent white settlements and their static cattle and sheep ranching operations in the valleys have decimated the fragile nutritious bunchgrasses, allowing cheatgrass to flourish. The Forest Services are in a quandary — the area cannot be returned to its original state and present biota is deteriorating. The

author proposes that a solution is to relinquish ideal efficiency and commodity production and substitute complexity, diversity, and uncertainty.

This is a tale of the effect of politics and greed on our most precious resources, a tale that is being repeated all over the globe. When are we really going to understand and act on what the scientists are telling us?

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Invasions of the Land: The Transitions of Organisms From Aquatic to Terrestrial Life

By M. S. Gordon and E. C. Olson. 1995. Columbia University Press, New York. x + 312 pp., illus. U.S. \$65.00.

Invasion of the land is a sophisticated and serious book about the establishment of terrestrial ecosystems on planet earth. It is the work of three established scientists who were colleagues (D. J. Chapman contributing a chapter) in the Department of Biology at the University of California (Los Angeles). They combined their talents to provide an up-to-date synthesis of the processes and events they believe occurred during colonization of the land by plants and animals. It is not a book designed for everyone. It will be most appreciated by readers with a background knowledge of plant life cycles and taxonomy, invertebrate systematics and ecology, physiology, and vertebrate paleontology. Although it is written by three authors, it does not suffer the faults of many multi-authored texts. The authors have created an integrated text using their own expertise to write specific chapters, basing their discussions on information provided at the outset on earth history, and contributing to the stated aims of the book.

Since much of the subject matter of this book relates to events which took place more than 300 million years ago, they can never be directly observed. To piece together the history of the colonization of the land requires evidence from many sources and sound deductive reasoning. It is in the assembling and weighing of the evidence, the consideration of alternate hypotheses, and the presentation and defense of the proposed scenarios that this book succeeds so well. Like a good detective story, it challenges the reader to think.

I found the chapter on Plant Transitions to Land especially well done and the analogy of the detec-

tive story fits perfectly the four footprints of the transition identified and discussed. Other chapters deal with Metazoan invasions of the land, considering arthropods, molluscs, annelids (leeches), and chordates, from the Cambrian to at least the Permian periods. The latter three groups are given special consideration in terms of their eco-physiology and the challenges they had to meet living in air. It is somewhat surprising how many of the characteristics required for success on land were already present in the aquatic ancestors of terrestrial groups and it is intriguing to realise how few features were lost and how few were added during the transition.

The book is not exhaustive but it does not claim to be. For example, it deliberately excludes insects and also excludes many vertebrate topics which are well described elsewhere. For these, and other topics the authors have excluded, there is an excellent and up-to-date bibliography.

The final summary and synthesis section of the book brings the contents to an appropriate end. Paleoenvironments were diverse and so were organisms. It is unreasonable to assume monophyletic origins for terrestrial groups of organisms nor is it likely that pathways can be followed because of the incomplete fossil record and the many false starts ending in extinctions.

This book is fascinating to read as well as being challenging and enlightening. I recommend it to anyone wishing to read or acquire an up-to-date, thought provoking, review of the conquest of the land.

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MISCELLANEOUS

The Ice-Age History of Alaskan National Parks

By Scott A. Elias. 1995. Smithsonian Institution Press, Washington, D.C. 150 pp.

The story of the north's Ice-Age climate, plants, and animals is unique. The great, unglaciated subcontinent Beringia, made up of most of Alaska, Yukon and Siberia, comprised a mosaic of environments including peat wetlands, glaciated uplands, and a startlingly productive arid grassland. This vast area, home to a strange and diverse fauna, was continuous land during glacial maxima. It was also in Beringia that humans first developed the technology to live in arctic climates and eventually colonized North America, arguably 13 000 to 24 000 or more years ago.

Elias skilfully presents the geology, past and present climate, and ancient life of four Alaskan national parks, and provides a compelling introduction to the prehistoric past.

The first third of the book introduces geological time, Alaskan geography and the locations of the state's national parks, Quaternary fossils and the sorts of evidence that scientists gain from studying the various fossil groups, and fossil preservation. These threads are woven together into a lively discussion of paleoecology, the understanding of ancient environments. Throughout this extensive and potentially very technical discussion, Elias always keeps in mind that he is writing for a general audience. The result is a readable and entertaining account.

The rest of the book interprets Denali National Park and Preserve, Bering Land Bridge National Preserve, Kenai Fjords National Park, and Glacier Bay National Park and Preserve. Accounts of these parks illustrate the Ice-Age story of Beringia and the glaciers at its edges and in its interior mountain ranges. Each park's ancient history builds an understanding of this broader story. Denali National Park and Preserve, which includes Mount McKinley,

North America's highest mountain, shows the mountain glaciers, periglacial steppe tundra, and mosaic of past and present ecosystems that lead us to a vision of full-glacial Beringia. Bering Land Bridge National Preserve, near the Bering Strait at the heart of the vanished subcontinent, gives us a view of the land that ancient hunters occupied in the Ice Age, moving eastward into a climate that may actually have been more harsh than the one they came from. The records at Kenai Fjords and Glacier Bay give us a dynamic look at the evolution of glaciers, and in both parks we can see the ongoing evolution of post-glacial ecosystems. This view is fascinating, because many of the changes that took place elsewhere more than 10 000 years ago are still underway at Kenai Fjords and Glacier Bay.

This is a very carefully prepared book. There are relatively few editorial oversights (for example, spelling variants "ostracodes" (page 15 and elsewhere) and "ostracods" (page 16 ff.)). I was unhappy with the presentation in only two places: Beringia is introduced on page 17 but not explained until page 54; and on page 18 it is erroneously stated that pre-Quaternary fossils are usually either impressions or mineral replacements lacking the original organic matter.

I recommend this book highly. Be sure to read it if you are planning to visit the north. If you are interested in the ancient past of any part of the Northern Hemisphere, you will find a great deal here that will interest you.

ADDITIONAL READING:

Guthrie, R. D. 1990. *Frozen Fauna of the Mammoth Steppe. The Story of Blue Babe.* University of Chicago Press. 323 pages.

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The Shape of Life: Genes, Development and the Evolution of Animal Form

by Rudolf A. Raff. 1996. University of Chicago Press, Chicago. xxiii + 520 pp. Paper \$29.95 U.S., cloth \$55.00 U.S.

This book tackles four topics which have, for decades, generated some of the most baffling prose in the English language, and (thanks to recent technical progress and the author's clear-mindedness) synthesises them into a coherent account of the origins and relatedness of animal taxa. Perhaps people who have worked on developmental genetics, embryology, relations of animal phyla, and the Cambrian radiation have thought they had a clear view of their sub-

jects, but they were never able to communicate these views to me, or to integrate them with the general neodarwinian body of evolutionary thought.

The binding of the paperback edition of this book is so stiff that one just glances past a smorgasbord of fascinating topics — edicarian fossils, monophyly of the pseudocoelomates, heterochrony, life histories of frogs and salamanders, echinoderm radial symmetry, cetacean origins, and a termite history of the world — because at first the book won't open flat enough to be read through. For such deep subjects Raff's style is light and breezy. Publications are cited

(unambiguously) only by authors' names, without dates, which somehow personalizes the references in the text. There may be errors in fields beyond my experience, but the only one I caught was a reference to all Choanichthyes (lobe-finned fish) as rhipisidians (page 162). One figure presents the generic names of its subjects only as initials ("H." and "R.,"; p 274). The figures are well drawn, but many are borrowed and some are not well integrated with the text.

The technical advances that have unified these fields are the world-wide search for Cambrian fossils, cladistic reasoning, biochemical phylogenies, and (especially) the discovery of homologous developmental genes shared by many phyla of animals. Raff isn't shy about the blindnesses and biases that have separated the disciplines he is synthesising. The implausible disdain of some cladists for fossils and non-dicotomous phylogenies is well known, as is the tendency for evolutionary biologists to treat developmental constraints as a "black box," which can be assumed to have any convenient properties.

Raff also affirms that the lack of apparent evolutionary connectedness in much developmental biology has not been due to a deep evolutionary programme that was beyond the ken of a naturalist. Many developmental biologists really have studied development as if it were independent of phylogeny. They treated their easily maintained laboratory

stocks of model organisms as mechanisms, rather than as samples of phyla, and have only begun to consider other taxa since the discovery of the homologous regulatory genes. I previously scorned the idea that biologists could take this point of view, but with Raff's assertion, as a developmental biologist, that this was the case, I apologize here to Drs Blackwelder and Garoian for that element of my negative review of *Handbook of Animal Diversity* (Schueler, 1989 [1990], *Canadian Field-Naturalist* 103(3):454).

Whatever the effect of this synthesis within individual fields, it has not produced a paradigm shift in evolutionary theory as a whole: Raff's conclusions about both phylogeny and development are so comfortably neodarwinian that there is no point in listing them. "Descent with modification by natural selection" has proceeded in all ages, and now that we begin to see their genetic bases, even the mysterious "laws of correlated development" have evolved much like any other characters. Give this delightful and important book to serious-minded young naturalists as an up-to-date introduction to zoology: for some of them it will be a cornerstone in their intellectual development.

FREDERICK W. SCHUELER

Biological Checklist of the Kemptville Creek Drainage Basin, RR#2, Oxford Station, Ontario K0G 1T0

Full House: The Spread of Excellence from Plato to Darwin

by Stephen Jay Gould. 1996. Harmony Books, New York. 244 pp.

Here's an exposition of what Stephen Jay Gould thinks people who don't understand statistics, progress, or evolution may think about these subjects, and how this differs from a quantitative naturalist's understanding of them. Along the way he provides some enlightening examples of how the shapes of distributions affect measures of central tendency, how aspects of the history of professionalized baseball parallel the post-Cambrian winnowing of animal phyla, and how tenaciously he clings to the notion that for most people evolutionary progress is defined as change that makes a member of any lineage more similar to a modern human person.

To read this book calmly, one must suppose that there are many people for whom it is a startling revelation that any ecosystem must be underpinned by masses of microbes, or that bacteria are the only life able to flourish in micropores in rocks, or that they themselves are assemblages of bacteria cohabiting in eucaryotic and other looser symbioses. To bolster his position that these people are a significant fraction of the population, Gould cites individuals who regard many of the most speciose and rapidly evolving

groups in the world as "unprogressive:" ants, teleosts, and arthropods in general. This book is not directed at those of us who respect social insects, flies, teleosts, rodents, grasses, and composite herbs as successful lineages who are, like hominids, pushing into new evolutionary territory. Is it better to accept the definition of the former group of people of "progress" and show that it doesn't occur, or to teach them to appreciate that progress is whatever improves a lineage's Darwinian fitness? Gould chooses the former course.

Yet "progress" in understanding the living world has always consisted of taking as much as possible the point of view of the creatures studied. Predarwinian philosophers may have defined organic progress by arbitrary external criteria, but once descent with modification by natural selection is the engine that forms the world, "progress" must be whatever makes a lineage more fit for its immediate environment. By this definition all "ordinary" natural selection (excluding genetic feedback loops that lead to population extinction or events in disastrously fluctuating environments) is progressive. "Progress" in human endeavours means doing whatever you do "better" by your own internal criteria, so

why should anybody consider rock-inhabiting bacteria less progressive than hypothetical spiritualized giraffes?

The analysis of professional baseball batting averages (undefined by Gould: "the average effectiveness of... batting, figured by dividing the number of safe hits by the number of times at bat;" Guralink, D. B., *Editor*. 1980. *Websters New World Dictionary*, 2nd college edition, Simon & Schuster, page 120), repeats the message Gould has been making for years in his columns in *Natural History* magazine: that 40% batting averages are not a "thing" that disappeared in 1941, but the tail of a distribution whose variance has declined with time. Here the message is re-enforced by documented declines in the variance of statistics that measure other aspects of the game.

In several instances Gould doesn't present much of a case for serious alternatives to his ideas. Geerat Vermeij's conclusion that progressive, escalated change of many kinds is pervasive (1987. *Evolution and Escalation: An Ecological History of Life*. Princeton University Press) isn't cited or considered. The final chapter of the book takes on the uncited ideas of D. D. Dutton (1995. *Darwin's Dangerous Idea*. Simon & Schuster, New York. 586 pages), with Gould emphasising the non-Mendelian characteristics of intellectual progress.

Gould concludes that there are no trends in evolution because changes in populations of lineages are random, but statistical randomness doesn't necessarily mean that events have no cause, merely that the

data may not have been viewed in terms of appropriately causal hypotheses. If there has been "no progress" what are we to say of the post-Miocene adaptation of all boreal and polar lineages to winter cold: hibernation, freeze tolerance, super-cooling, and migration? How far back did the ancestors of lineages of slugs have reduced shells compared with other snails? Would it have been "progress" if these lineages were seen, retrospectively, to have consistently reduced their shells when compared with other snails? Most living things have always been morphologically simple bacteria, but the "no progress" scenario implies that bacteria quickly elaborated their full complement of biochemical abilities, and then just coasted along, shuffling pre-existing adaptations to fit into new environments.

If the reader is prepared to avert his eyes from the shredding of the straw man of anthropocentrically defined evolutionary progress, and prepared to stomach a certain amount of "transendent" baseball talk, this is a great read and an interesting book: S. J. Gould warts and all: well-read, parenthetical, entertaining, and with a proper willingness to use the methods of multivariate morphometrics to understand the world.

FREDERICK W. SCHUELER

Biological Checklist of the Kemptville Creek Drainage Basin, RR#2, Oxford Station, Ontario K0G 1T0

American Museum of Natural History: 125 Years of Expedition and Discovery

By Lyle Rexer and Rachel Klein. 1995. Harry N. Adams, Inc., New York, Publishers in association with the American Museum of Natural History. 256 pages, illus.

The backbone of analysis and dissemination of data and theory on world biodiversity, even before this trendy term was coined, are the natural history museums. Most of these, in common with art museums, are said to date from the Ashmolean Museum formed in 1686, which served as a model for the British Museum established in 1753, the Musée National de l'Histoire Naturelle in 1793, and some 50 European museums in the early 1800s. These museums were created for public view of collections of real objects. At their best, they are staffed by dedicated and determined experts who study these objects and publish both detailed analysis for specialists and readable summaries for the public and thus contribute substantially to human knowledge and education. At their worst, they purvey nothing except what the early American master showman and huckster, P. T. Barnum, is credited with believing the public craves, amusement.

Quite possibly the most successful of the best that a museum can be, and the largest natural science museum on earth, is the American Museum of Natural History (AMNH), established in 1869 in New York. It succeeded where at least three predecessors had failed: a small museum of the Tammany Society was opened in 1790; a disparate private collection known as the American Museum purchased in 1792 by Charles Wilson Peale and moved to Philadelphia; and Delacourt's Cabinet of Natural History opened in 1804.

The AMNH founder, Albert S. Bickmore, had studied under the legendary Louis Agassiz who built the Museum of Comparative Zoology at Harvard University. Bickmore believed in museums as an educational force and pioneered the use of lantern slides for lectures, but also saw that museums should be institutions promoting original research. As such they do not directly create wealth but use it, and thus must have the interest of the rich and generous for existence and prosperity. He saw New York in the 1800s as an ideal location because of its concentration of wealthy potential benefactors. J. P. Morgan

was an early member on the AMNH Board of Trustees, apparently believing (like some other wealthy Americans of the time who contributed to developing major museums; Marshall Field in Chicago and Andrew Carnegie in Pittsburgh), that large commercial enterprises sanction knowledge of the world. The presence of committed benefactors allowed the AMNH museum to prosper through to the depression of the 1930s. From the 1940s on, federal government support became increasingly important to the adequate funding of research.

The AMNH began its existence by purchasing major collections then available in Europe but soon was propelled by dynamic staff into its own pioneering research and exhibits covering the world. The results set standards for all museums. It took the pioneering start on dioramas at the British Museum and created classic exhibits of life in context. These initiatives are portrayed in this book, following an introductory chapter on the founding of the museum, in nine chapters that cover major expeditions focused on the North Pacific, the Gobi, the Arctic and Antarctic Poles, Africa, Early Americans, South America, the South Pacific, Dinosaur and Mammal Paleontology. All are described and pictured in fascinating overviews of pioneering work by legendary staff members such as George Gaylord Simpson, Roy Chapman Andrews, Barnum Brown and many others. The book concludes with a chapter on the continuing search for knowledge in biodiversity and evolution and the modern techniques of molecular analysis in which the AMNH, like any other dynamic biology museum, is playing an important part now.

Although not mentioned in the book, some Canadian naturalists will realize that a portion of the roots of our own National Museum (now "Canadian Museum of Nature") lie in the AMNH. Our museum's development in the first half of this century (Collins 1928; Russell 1961; Zaslow 1975) was partly due to staff trained at the AMNH, partly to competition with the AMNH. This, in turn, influenced provincial museums across this country. The Canadian Arctic Expedition 1913-1916 was sponsored by the federal government because the AMNH had shown interest in further expeditions in the area. R. M. Anderson, a staff member of the AMNH from 1908 to 1912, was made chief of the Southern

Scientific Party of the expedition and appointed to the staff of the Victoria Memorial Museum (the early name for what was to be christened the National Museum of Canada in 1927) of the Geological Survey of Canada. He stayed as mammalogist until his retirement in 1946 (Soper 1962). The success of AMNH explorations for dinosaur fossils in Alberta by Barnum Brown led to the realization that Canada should be collecting its own and the hiring of the Charles H. Sternberg and his sons from Kansas in 1912. One son, Charles M., stayed with the Geological Survey and National Museum, retiring in 1950 but remaining for years after as an active research associate in paleontology (Russell 1982). Ornithologist Percy A. Taverner visited the AMNH at the beginning of his National Museum career, 1911-1942 (Cranmer-Byng 1996). There he observed their procedures and later picked taxidermist Clyde L. Patch for the National Museum staff. Patch built its first habitat groups during a career that spanned 1913-1952 (Lloyd 1954).

This book is a fitting celebration of a major world institution in "coffee-table" format. It includes 248 illustrations of exhibits and field sites, including 90 plates and 10 maps of expedition routes. It is equally worth reading by those interested in the development of museums or in vicarious exploration and discovery.

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Evolution Extended: Biological Debates on the Meaning of Life

Edited by C. Barlow. 1995. The MIT Press, Cambridge, Massachusetts xi + 333 pp., illus. U.S. \$17.95

Although evolution is a widely accepted theoretical concept, we as scientists have not yet succeeded in providing a working definition whereby the scientific community understands one another when we

speak of evolution. Each discipline has its own working definition that has been cast within the framework of that science's existing paradigm and differs from those of other disciplines. These subtle differences have, and continue to be contentious, providing the impetus for some of the greatest histor-

ical and modern philosophical debates on evolution. It is these differences of opinion that Barlow endeavors to illustrate in the first part of the book entitled "Is evolution going anywhere".

The central theme of the first two chapters focuses on the relationship between progress and evolution. Julian Huxley's exceedingly anthropocentric viewpoint that human behavior and intelligence are signs of progress, and therefore more evolved, contrasts sharply with those of Francisco J. Ayala and Edward O. Wilson. Ayala considers progress to be a value-laden judgment that cannot be defined biologically, while Wilson eloquently illustrates that progress implies a goal and that evolution has no goal, therefore evolution has nothing to do with goals or progress. Ayala and Wilson do nevertheless agree that evolution is a directional process, progressing from simple to more complex.

George G. Simpson also takes exception to Huxley's viewpoint and defines progress as an increasing awareness and perception in the environment and the ability to react accordingly. Evolution may not necessarily be accompanied by progress nor is it characterized by progress. Simpson believes that evolution is not a linear process, but rather, one that branches with the rate and direction being highly variable. Chapter 2 closes with excerpts from David M. Raup's *Extinction: bad genes or bad luck?*, leaving the reader to reconcile whether evolution is a directional or simply random process.

Part two entitled "Tools and metaphors of evolutionary processes" includes three chapters that address evolutionary processes. Whether Barlow intended it or not, she indirectly addresses a theme central to the philosophy of science. That is, the impact of societal values, public opinion, and the existing scientific paradigm on the way that science is conducted and manner in which these ideas are presented. Chapter 3 opens with a number of lengthy excerpts from the *Origin of the Species* to illustrate Darwin's metaphorical writing style and the manner in which he presented his ideas on natural selection and competition. Fortunately Darwin's ideas on evolution were not perceived as being heretical, even though they challenged the very essence of creation and authority of the church. Had the church not been so intertwined with politics and society, the theory of evolution might have gained popularity much earlier than the late 19th century. Excerpts from Richard Dawkins' *The Blind Watchmaker* provide good examples of contemporary writing style and the continued use of metaphors to illustrate the parallels between natural selection and competition and an arms race. For those of us who remember the cold war (this unfortunately dates us) it is an appropriate metaphor, but for those who were too young or not born during this period of history, the metaphor loses its familiarity and significance.

Integrative processes in evolution are presented in chapter 4. Gregory Bateson, François Jacob, Lynn Margulis, Mark McMenamin, and Peter A. Corning expound on the notion that multicellular organisms are merely components of a system operating in dynamic equilibrium with the other components. Jacob equates evolution to a "tinkerer" who produces a product out of existing material, with no clear plan as to what the end product is. Based on this model, we can see how convergent evolution may have occurred. Corning adds an anthropocentric twist to this idea by considering it to be some form of co-operative behavior. However, is this really co-operation or some form of parasitism that we do not yet understand? Corning takes the discussion one step further by introducing the reader to the concept of sociobiology and a number of other social theories. This adds a new dimension of confusion to the evolutionary theme of the book, but beautifully illustrates the degree to which evolutionary theories are value laden.

Behavior and evolutionary stability, in light of the 2nd law of thermodynamics are the central themes of chapter 5 "Ratchets, Uroboros, and the Role of Initiative". Passages from Jacob Bronowski's *Ascent of Man* illustrate the progression from simple to more complex organisms without their breakdown into component elements, a process which he calls "stratified stability". Stuart Kauffman's Newtonian viewpoint on evolution portrays simple and complex systems that exhibit order spontaneously while co-existing with natural selection under some type of driving force.

Part three entitled "Embracing the Cosmos" launches the reader into the realm where biological evolution and the human condition are juxtaposed. Pierre Teilhard de Chardin, Thomas Berry, and Julian Huxley's endeavor to justify the human condition as a part of the evolutionary process and illustrate the philosophical and moral dilemma some scientists are faced with when they attempt to reconcile their innermost personal thoughts, beliefs, and values with the scientific knowledge they possess.

In my opinion this is the most challenging chapter to read, for it addresses some of the most philosophically demanding questions that we as scientists are being asked to provide answers to. Should science and religion come together to formulate a single belief system? How does religion, which is based on faith fit in with the scientific process where hypotheses are testable and falsifiable? How ingrained are society's values in the scientific process? Is humanity really the pinnacle of evolution? Is humanity the custodian of evolution?

That the scientific process and religion are two separate, mutually exclusive concepts is the focus of chapter 7 "Banishing Cosmic Meaning". Criticisms of Chardin's unified view of science and humanity are presented in excerpts from the works of Peter Medewar and Jacques Monod. Medewar's considers

Chardin's work to be misleading and *The Phenomenon of Man* to be nothing but nonsense and tedious metaphysical conceits. Monad, although not as harsh as Medewar, denounces Chardin's work as being sloppy and lacking imagination. Monad himself attempts to explain the problem of science and religion and concludes that, though science dominates and permeates modern society, many people still retain ancient belief systems that are inherently anti-science in their philosophy. Society as a whole is faced with a moral dilemma. While science can unequivocally demonstrate that humanity is destroying this planet, the old value systems still determine our reaction and approach to solving problems. Often, the solution is morally unacceptable and the problem continues (e.g., population growth). Society tends to use or turn against science depending on the circumstance.

In Chapter 8, "Beyond the Binary", Barlow attempts to temper the two previously diametrically opposed viewpoints with comments by Mary Midgley, Stanley Salthe, and Theodosius Dobzhansky and introduces the Gaian/humanist view. The essence of this chapter focuses on the question that all of us have thought of at some point. Why are we here?

Part four "Evolution and Religion" begins with the chapter entitled "Evolution as Religion". Comments by Edward O. Wilson, Julian Huxley, Alister Hardy, and John C. Greene illustrate points of view that are scientific, anti-scientific, humanistic, and somewhere in between. Humanity is unable to comprehend the meaning of life and our purpose on this planet, seemingly without a unifying theory. Man has used his intellectual ability to answer some of these questions,

but there is still much that we do not know or understand, and that is where we presently find ourselves - in the unknown. Some continue to search for the answers, even though there may not be any, while others prefer to wait and criticize.

The final two chapters, "Responding to Creationism" and "Science into Myth" address the science versus creationism debate. Barlow presents an excellent historical overview of both sides of the debate, the conviction of the proponents of each side, and the chasm that continues to erode at the very fabric of our society and educational system. Will this problem ever be resolved? I doubt it. To do so requires one system of beliefs and values at the expense of humanity's cultural diversity and identity. Governments and cultures have been attempting (and still continue) to unify humanity into a single collective for thousands of years. The result of these activities has been bloodshed and genocide.

Barlow has meticulously constructed a concordance of ideas that span more than one hundred years of scientific history into a cohesive, thought provoking, and insightful view of what we know about evolution, but more importantly, what we don't know. If you are looking for answers to the meaning of life, you won't find them here. What is presented here is a variety of viewpoints, some you'll like, others you won't. The answers, if there are any, lie in the mind of the individual.

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