

Habitat selection and demography of a nonmigratory woodland caribou population in Newfoundland

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Abstract: Several studies have shown that habitat selection and population limitation of woodland caribou (*Rangifer tarandus caribou*) is typically associated with the interaction among human-induced habitat alteration, wolf predation (*Canis lupus*), and the availability of alternative prey such as moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*). Although woodland caribou inhabiting Newfoundland have been exposed to moderate levels of timber harvesting, black bears (*Ursus americanus*), not wolves, are the principal large predator in this system, and moose represent the alternative large prey species. During a 4-year period of timber harvesting, we monitored the location and status of 24 adults and 46 calves to determine coarse-scale habitat selection and survival rates of a nonmigratory and demographically isolated woodland caribou herd in Newfoundland. We also estimated pregnancy and recruitment rates and determined potential causes of mortality. Habitat selection significantly varied among seasons but was consistent with the hypothesis that caribou avoid habitats where the likelihood of contact with a predator or alternative prey was high. Population growth rate ($r_s = -0.01 \pm 0.06$ (mean \pm 1SD)), calf recruitment (percentage of 10-month old calves = 13%), and adult survival rate (0.87) indicated that the population was stable. Mean pregnancy rate (96%), parturition date, and the lack of evidence for malnutrition in 22 carcasses suggested that the availability of quality forage is not a key factor limiting population growth. Although predation could not be linked to the death of adult caribou, black bears were responsible for 5 of 15 calf fatalities. This study suggests that black bears need to be considered more seriously as a factor influencing coarse-scale habitat selection and demography in woodland caribou herds.

Résumé : Plusieurs études ont démontré que le choix de l'habitat et le contrôle de la population chez des caribous des bois (*Rangifer tarandus caribou*) sont ordinairement associés aux interactions entre les modifications de l'habitat par les humains, la prédation exercée par les loups (*Canis lupus*) et la disponibilité de proies de rechange comme l'orignal (*Alces alces*) et le cerf de virginie (*Odocoileus virginianus*). Bien que les caribous des bois de Terre-Neuve aient déjà été exposés à la coupe modérée de bois, ce sont les ours noirs (*Ursus americanus*) et non les loups qui sont les principaux prédateurs de grande taille dans ce système et les orignaux servent de grandes proies de rechange. Au cours d'une période de coupe d'une durée de 4 ans, nous avons suivi et déterminé le statut de 24 adultes et 46 jeunes pour déterminer le choix de l'habitat à une échelle grossière et les taux de survie d'un troupeau de caribous des bois non migrants et isolés démographiquement à Terre-Neuve. Nous avons également estimé les taux de grossesse et de recrutement et examiné les causes possibles de la mortalité. Le choix de l'habitat varie significativement d'une saison à l'autre, mais se fait en accord avec l'hypothèse selon laquelle les caribous évitent les zones où la probabilité de rencontre avec un prédateur ou une proie de rechange est élevée. Le taux de croissance de la population ($r_s = -0,01 \pm 0,06$ (moyenne \pm 1 erreur type)) le recrutement des jeunes (le pourcentage de jeunes de 10 mois = 13 %) et le taux de survie des adultes (0,87) dénotent une population stable. Le taux moyen de grossesse (96 %), la date de la mise bas et l'absence de symptômes de malnutrition sur 22 carcasses indiquent que la disponibilité de brout de qualité n'est pas un facteur limitant de la croissance de cette population. Bien qu'il ait été impossible de relier la mort des caribous adultes à la prédation, les ours noirs ont été responsables de 5 des 15 cas de mortalité chez les jeunes. Cette étude indique que les ours noirs influencent le choix de l'habitat à une échelle grossière et la démographie des troupeaux de caribous des bois, et de ce fait ils doivent être pris en compte plus sérieusement.

[Traduit par la Rédaction]

Introduction

One ungulate species that appears particularly sensitive to large-scale changes in habitat associations is woodland cari-

bou (*Rangifer tarandus caribou*). Across North America, numerous studies have attributed the decline in local caribou populations to the effects of forestry operations and oil and gas exploration and extraction (Bergerud 1974; Edmonds

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1988; Cumming 1992; Bradshaw et al. 1997; Stuart-Smith et al. 1997). Predation, particularly from wolves (*Canis lupus*), is considered by some researchers to represent a key factor limiting woodland caribou populations, and coarse-scale habitat selection is thought to minimize predation risk (Bergerud and Elliot 1986; Seip 1992; Chubbs et al. 1993; Schaefer et al. 1999; Rettie and Messier 2000). Timber harvesting and oil and gas development generate early succession forest habitat that can lead to increased densities of moose (*Alces alces*) and white-tailed deer (*Odocoileus virginianus*) and, in turn, increased wolf density (Schwartz and Franzmann 1989). Black bears (*Ursus americanus*) also preferentially forage in regenerating forest stands and will prey on the calves of ungulates (Lindzey and Meslow 1977; Franzmann et al. 1980; Schwartz and Franzmann 1991; Samson and Huot 1998).

In such systems, even if the numerical response of wolves and bears is independent of prey density, the fragmentation of preferred caribou habitat (i.e., mature forest and associated bog-fen and heath complexes) by human-induced early succession habitat increases the likelihood of caribou exposure to predators. In addition, the direct (timber harvesting) or indirect (predator avoidance) loss of preferred foraging habitats has been shown to limit caribou daily movement rates and home-range size (James and Stuart-Smith 2000; Smith et al. 2000). This alteration in behaviour may result in increased competition for food and an associated decrease in adult survival, pregnancy, and recruitment rates (Thomas 1982; Skogland 1986).

There are currently 13 identifiable subpopulations of caribou on the island of Newfoundland, most of which exhibit some degree of seasonal range overlap, with one exception (Mahoney 2000). The Corner Brook Lakes (CBL) herd was first described by Grant (1902) as a race distinguishable from other populations on the island and has recently been identified as a separate and distinct herd (sensu Fuller and Keith 1981; Bergerud 1985). The CBL herd ranges over a 1000-km² area where timber harvesting has been ongoing since 1920. Absence of hunting, migratory movements, and immigration likely influence habitat use and demography of this population, but wolves, which were extirpated from Newfoundland around 1920, are not a factor here. Black bears and caribou, however, have coexisted on the island since the end of the Wisconsin ice age, and coyotes (*Canis latrans*) have been present since 1985 (Larivière and Crête 1993). Furthermore, lynx (*Lynx canadensis*) occur in the region and have been identified as predators on caribou calves in Newfoundland (Bergerud 1971; Mahoney et al. 1990). Moose were twice introduced around the turn of the century (circa 1878 and 1904, Pimlott 1953) and have successfully colonized the entire island, providing a high density of alternate prey for black bears (current estimate = 150 000; S. Mahoney, unpublished data).

The resource management goal for the CBL area is to provide sustainable forestry while maintaining a persistent caribou population. Therefore, the principal objective of this study was to determine which habitats were preferred and which were avoided by caribou within the CBL area during timber harvesting from 1994 to 1997. Another objective was to obtain estimates of demographic and population growth rates and the causes of mortality during this period. Our

results were then compared with other studies to better understand the interaction among human land-use practices, coarse-scale habitat selection, and mortality factors limiting population size in woodland caribou herds.

Materials and methods

Study area

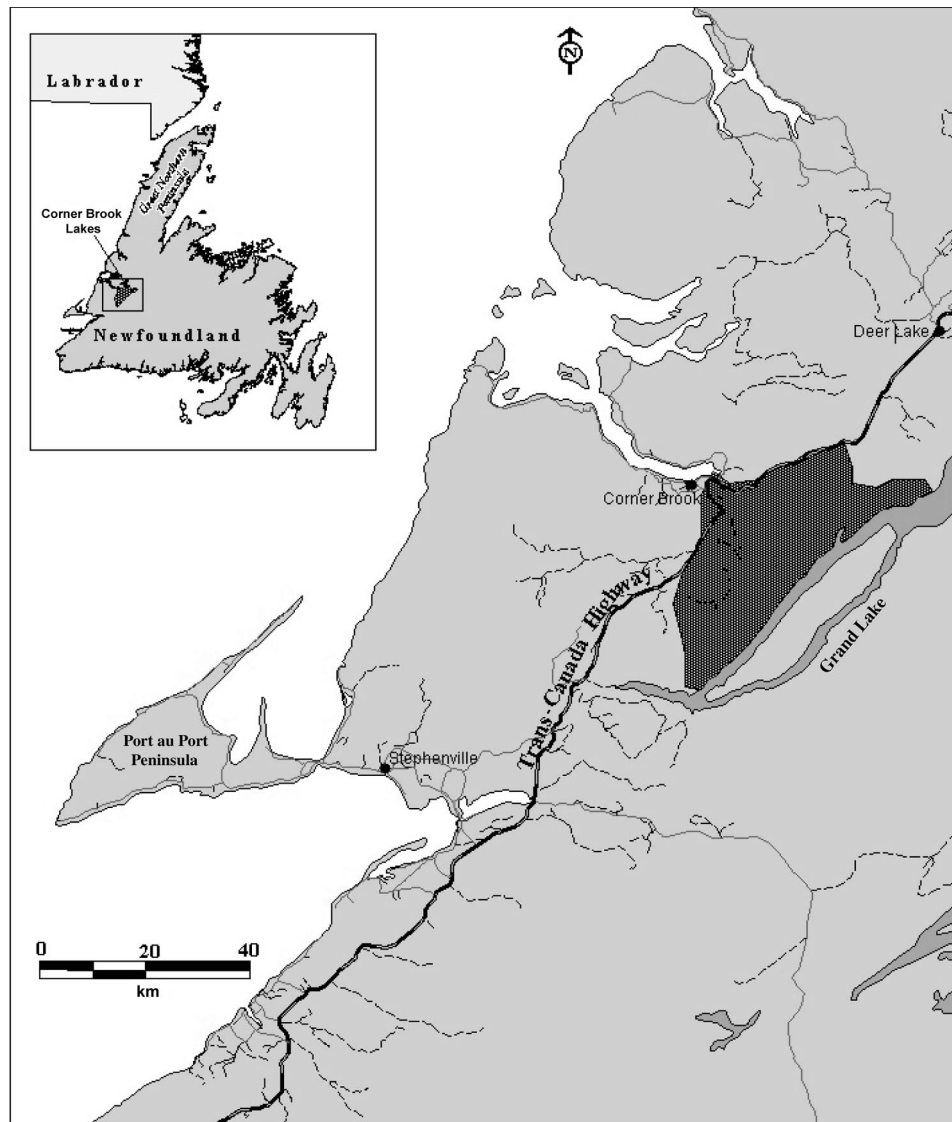
The study was conducted in the west central region of Newfoundland, which is bounded on the east and west by Grand Lake and the Trans-Canada Highway (Fig. 1). The area covers ~1016 km² and was defined by the outer perimeter of the home range of radio-collared individuals. The topography is rugged throughout, particularly in the northern area where a plateau, rising to 650 m, is divided by the steep-sided valleys (approaching 40° slopes) of Copper Lake, Valley of the Lakes, and Steady Brook Lake drainage basins. Bedrock underlying the plateau is primarily semi-pelitic schist and psammitic gneiss, the southern area consists of platformal sedimentary bedrock. The area is within the Central Uplands and West Coast climatic zones (Banfield 1983), which are characterized by mild summers and cool winters. Mean daily temperature ranged from -4 to -10°C in February and from 10 to 20°C in July. Snow fell primarily from December through April with annual accumulations >400 cm. Mean annual precipitation ranged from 1000 to 1250 mm.

Forest stands were dominated by balsam fir (*Abies balsamea*). Other major tree species included black spruce (*Picea mariana*), white spruce (*Picea glauca*), jack pine (*Pinus banksiana*), trembling aspen (*Populus tremuloides*), white birch (*Betula papyrifera*), and yellow birch (*Betula lutea*). Forest stand productivity (volume/ha) begins to decline after 80–100 years as trees become susceptible to insects (e.g., hemlock looper (*Lambdina fiscellaria*)) and wind. Approximately 37% of the study area consists of non-forested areas, including numerous patches of coniferous and deciduous scrub, extensive rock and heath barrens on the plateau and barren hilltops along the edge of Grand Lake. Rock and heath barrens consisted primarily of dwarf birch (*Betula glandulosa*), willow (*Salix* spp.), crowberry (*Empetrum nigrum*), cloudberry (*Rubus chamaemorus*), and raspberries (*Rubus idaeus*). There were numerous small (<0.5 km²) wetland and riparian areas, typically containing sedges (*Carex* and *Eriophorum* spp.), interspersed among barren and forested habitats.

Logging operations have been ongoing in the area since the early 1920s, and although clear cutting was and still is the prevailing harvesting technique, the method of transporting the wood has changed. Originally, horses hauled the logs to the nearest large stream or river, and logs drifted to the mill or to an access point on the railway. In the 1940s, tractors replaced horses and could be used year-round. After 1964, whole trees were dragged by skidders to a central "landing", cut to length, and loaded onto trucks for transport to the mill. The use of skidders and logging trucks has resulted in a network of roads in the study area.

Habitat delineation

Availability of habitats was based on the Newfoundland Forest Service inventory database. Seventeen habitats were

Fig. 1. Location of the Corner Brook Lakes study area in Newfoundland.

delineated (Table 1). F-20 habitat (0–20 year old balsam fir) represents harvested blocks since 1980, whereas F-40 to F-60 habitats (21–60 year old balsam fir) represents secondary-growth timber. F-80 (61–80 year old balsam fir) habitat represents early climax forest, whereas F-80+ (>80 year old balsam fir) is considered mature forest for balsam fir. F-80 and F-80+ habitats are associated with moderate–full canopy closure that determines the abundance of terrestrial and arboreal lichens (*Cladonia*, *Cetraria*, *Alectoria* spp.). The Mort habitat represents forest stands with >26% tree mortality and contains an abundance of terrestrial and arboreal lichens. The BNS (rock and heath barrens), Scrub (softwood and hardwood scrub), Bog (open bog and treed bog), and Water (ponds and lakes) habitats depict relatively open but undisturbed areas for caribou. Although the “Other” category accounts for only 0.01% of the study area, we did not pool this habitat with another one as it represents a unique composite of the landscape (i.e., small patches of virgin timber). The remaining habitats are related to human land-use practices (e.g., power line (PL) and road corridors), includ-

ing small stand remnants that are the result of harvesting or clearing activity and, subsequently, are typically adjacent to recently disturbed areas.

We digitized polygons for each of the 17 habitats using the program MAPINFO (version 5.5) and incorporated it into a geographic information system (GIS) database. During the study period, the database was updated each year to account for changes resulting from timber harvesting (including road construction) and other human land-use practices (e.g., clearing land for agriculture). Data on these human-related disturbances were grouped by year and not by exact date. Patch size was determined following the addition of 1997 disturbance data.

Animal capture

In March 1994 and June 1995, 24 adult caribou (17 female (F) : 7 male (M)) were captured by darting from a Bell 206L helicopter using xylazine hydrochloride (5 mg·kg body mass⁻¹). Animals were fitted with VHF radio collars (equipped with 24-h activity sensors; Lotek Engineering, Newmarket,

Table 1. Habitats available to woodland caribou (*Rangifer tarandus caribou*) in the Corner Brook Lakes study area, Newfoundland.

| Description | Habitat code ^a | Total area (km ²) | Proportional area | Median patch size (km ²) |
|-----------------------------|---------------------------|-------------------------------|-------------------|--------------------------------------|
| Balsam fir | | | | |
| 0–20 years old | F-20 | 73.6 | 0.0725 | 0.034 |
| 21–40 years old | F-40 | 60.8 | 0.0598 | 0.038 |
| 41–60 years old | F-60 | 218.9 | 0.2155 | 0.043 |
| 61–80 years old | F-80 | 146.6 | 0.1444 | 0.056 |
| >80 years old | F-80+ | 118.9 | 0.1171 | 0.050 |
| Mortality timber | Mort | 0.7 | 0.0007 | 0.006 |
| Rock and heath barrens | BNS | 59.0 | 0.0581 | 0.067 |
| Softwood and hardwood scrub | Scrub | 202.4 | 0.1992 | 0.023 |
| Open bog and treed bog | Bog | 35.6 | 0.0351 | 0.022 |
| Lakes and ponds | Water | 78.5 | 0.0773 | 0.004 |
| Agricultural land | AG | 3.4 | 0.0033 | 0.039 |
| Cleared land | CL | 3.3 | 0.0033 | 0.017 |
| Residential land | Res | 5.8 | 0.0057 | 0.021 |
| Roads | Road | 2.3 | 0.0023 | 0.216 |
| Power lines | PL | 4.7 | 0.0047 | 0.141 |
| Stand remnant | Rem | 0.9 | 0.0009 | 0.006 |
| Virgin timber | Other | 0.1 | 0.0001 | 0.012 |
| Total | — | 1015.6 | 1.00 | 0.034 |

^aHabitat codes correspond to those used in Fig. 3.

Ont.) and uniquely numbered plastic ear tags (Kane Veterinary Supplies, Cambridge, Ont.). An incisor tooth was extracted for aging (McEwen 1963) and body mass was recorded to the nearest 1 kg using a spring scale (model TD-5, John Chatillon & Sons, New York) suspended from the helicopter. Total body length, heart girth, shoulder height, and metatarsus length were measured to the nearest 1 mm (Dauphiné 1976).

During spring (late May to mid-June) of each year, calves (<3 days old) of radio-collared and non-radio-collared females were captured on the ground, ear-tagged, and fitted with flexible elastic VHF radio collars (with activity sensors). Forty-six calves (19 F : 27 M) were radio-collared during the spring in 1994 ($n = 9$), 1995 ($n = 11$), 1996 ($n = 10$), and 1997 ($n = 16$). Age (days) was estimated from the condition of the umbilicus and extent of hoof wear. Body mass and morphometric measurements were collected following the same protocol as for adults.

Location data and seasonal ranges

We defined four seasons based on calving period, plant phenology, and average monthly snowfall: spring (1 May – 30 June), summer (1 July – 30 September), autumn (1 October – 30 November), and winter (1 December – 30 April). Years refer to biological years or 12-month periods beginning on 1 May of each year. For example, a 1994 annual survival estimate contains data collected from 1 May 1994 to 30 April 1995.

Radio-collared animals were located using a Cessna 185 fixed-wing aircraft equipped with a Lotek receiver (model SRX_400) and two-directional H-antennae mounted on the wing struts. Flight altitude ranged from 150 to 300 m above ground level (agl). Locations (universal transverse mercator coordinates (UTMs)) were recorded using an on-board

global positioning system (GPS), and information on habitat and group size was collected. The UTM's were then overlaid on the GIS habitat database. For 1994–1997, monitoring flights during spring were conducted once per week until late May (precalving period), every 2 days until calves were collared (calving period), and then once per week until the end of June (postcalving period). During summer, autumn, and winter of all years, monitoring flights were conducted every 4–10 days. The exception was in 1997 when systematic aerial monitoring stopped at the end of spring. We obtained 1635 locations for adults (≥ 2 years of age; Hearn et al. 1990) and 573 locations for calves and yearlings from spring 1994 to spring 1997 (i.e., 13 potential season-year periods).

For adults only, we calculated 95% minimum convex polygons for each animal in each season-year period for which we had 10 or more locations (Rettie and Messier 2000) using the program HOME RANGE (Ackerman et al. 1990). The median number of radiolocation points per individual per season (i.e., seasonal range) was 16 (range = 10–45). We obtained enough locations to calculate 101 individual seasonal ranges (79 F : 22 M) across 10 of the 13 potential season-year periods. Because we restricted the estimation of seasonal range to ≥ 10 locations, no seasonal range estimates could be calculated for the summer and autumn of 1994 or the winter of 1996–1997.

Habitat-selection analysis

We assessed habitat selection of adult caribou at the coarse-scale or second-order level (Johnson 1980). At this scale of analysis (i.e., seasonal range selection of the population), the use of buffers around location data is not necessary (McClellan et al. 1998; Rettie and McLoughlin 1999), and the confidence in habitat-selection estimates is primarily related

to the number of individuals sampled from the population (Otis and White 1999). Our analysis was based on the method of Manly et al. (1993), which considers all H habitats in the study area as available and each seasonal range as the area used by an individual. For each individual seasonal range, the proportional habitat used (U_i) of each H habitat (H_i) was calculated as

$$U_i = \frac{\text{Area in seasonal range covered by } H_i}{\text{Total area of seasonal range}}$$

The proportional availability (A_i) for each habitat was calculated as

$$A_i = \frac{\text{Area in study area covered by } H_i}{\text{Total study area}}$$

For each individual seasonal range, the sums of U_i and of A_i each totaled 1.00. A set of resource selection indices (w_i ; Manly et al. 1993, pp. 40–41) for each individual seasonal range was then calculated as

$$w_i = \frac{U_i}{A_i}$$

and then standardized using the following equation:

$$b_i = \frac{w_i}{\sum_{i=1}^H w_i}$$

Standardized resource selection indices (b_i s) are insensitive to the inclusion of unused habitats that are defined as being available (Manly et al. 1993, p. 45). Thus, for each animal that had a seasonal range estimate, we had 17 b_i s based on the 17 available habitats in the study area (Table 1). For our analysis, the set of b_i s for each individual seasonal range represented the basic sample unit ($n = 101$ individual seasonal ranges).

The set of 17 b_i s for each individual seasonal range was then used to calculate 16 synthetic variables based on the difference between sequential pairs of b_i s (Arthur et al. 1996). Beginning with females, the synthetic variables were used in a multivariate analysis of variance (MANOVA) to determine the effect of reproductive status, season, and year on habitat selection. For the purpose of this analysis, reproductive status of females was classified as no calf produced, with calf, or lost calf. Females that had lost a calf between subsequent relocations were deemed to have lost it immediately after the previous location and were classified as “lost calf” for the rest of the year. Following the analysis of females, a similar MANOVA was conducted on females and males to examine the interactions among the response variables (synthetic variables) and the explanatory variables (sex, season, and year).

Post-hoc multiple comparison tests were performed using paired t tests on the rank of each resource selection index for each individual seasonal range. We used Holm’s modification of the Bonferroni approach to control the type I error rate using an α level of 0.10 for paired contrasts (Arthur et al. 1996).

Population estimation

In March 1994–1997, fixed width transects spaced 1 km apart and oriented in a north–south direction were surveyed for caribou using a Bell 206L helicopter at an altitude of 150 m agl. In March 1994, the survey was conducted 6 days after the last animal was collared. The survey crew included the pilot, navigator, and two rear-seat observers. Each observer scanned a 500 m wide strip, providing 100% coverage of the study area. The navigator recorded the number and composition (adult male, adult female, yearling, calf, non-classified) of each group and the presence of radio-collared individuals. Data on group composition was used only when the entire group could be classified. The habitat and location of each sighting was recorded on a 1 : 50 000 topographic map. All surveys, except in 1996, were conducted after a fresh snowfall and under good to ideal weather conditions. In 1996, because of poor snow conditions, the survey was carried out over patchy snow, 4 days after a fresh snowfall.

Annual estimates of population size (N) and associated 95% confidence intervals (CI) were based on the assumptions of the Lincoln–Petersen equation (Krebs 1989). Because we could accurately monitor the status of each radio-collared individual, the number of marked animals before each annual survey was known. We also determined the approximate 95% CI for the average four estimates as $N \pm 2 \times$ standard error (SE), following the equation of Rice and Harder (1977):

$$SE = \sqrt{\frac{1}{K(K-1)} \sum_{i=1}^k (N_i - \bar{N})^2}$$

where K is the number of estimates, N_i is the estimate for each year, and \bar{N} is the average for all 4 years.

Pregnancy and recruitment

During mid- to late May (precalving period) and until mid-June (calving period) of each year, radio-collared females were assessed for pregnancy. Observations were made from a helicopter, and pregnancy was determined visually by presence or absence of a calf-at-heel or presence or absence of a distended udder (Bergerud 1964). The standard deviation for combined annual pregnancy rate was calculated from the binomial distribution (Zar 1984).

Previous studies have estimated the recruitment rate of calves into a population at 9–12 months (Bergerud 1980; Fuller and Keith 1981; Rettie and Messier 1998). These estimates are based on the assumption that calves at this age are subject to similar mortality rates as yearlings and adults. We estimated recruitment rate from calf-to-cow ratios and calf percentages determined during our March aerial surveys (i.e., 10-month recruitment rate). The number of cows was adjusted to account for those adults that were not classified during surveys (mean = 24% of adults observed, range = 17–37%). Year-to-year variation in recruitment rate was examined using log-likelihood ratios. We calculated the standard deviation for combined annual recruitment rate (based on pooled data) from the binomial distribution (Zar 1984).

Survival and rate of increase

After detecting an inactive signal (mortality mode), the collar was retrieved and the area was searched to locate remains

and determine cause of death. Predation was recorded as the cause of death if the remains were disarticulated or crushed (Hearn et al. 1990) and if there were signs of a struggle and blood. If no external evidence was obvious and decomposition was minimal, a complete necropsy was performed in either the field or the lab. In all cases, remains were examined for evidence of malnutrition. A visual ranking (poor, moderate, or good) was assigned to the extent of fat deposition in the bone marrow (Seip 1992), and visceral and subdermal areas.

Survival estimates, with 95% CI, were calculated using the Mayfield (1975) method within the program MICRO-MORT (Heisey and Fuller 1985). Estimates were based on the assumption that all censored animals (slipped or malfunctioning radio collars, $n = 14$ of 70) were assumed to be alive at the end of the year or season, and date of death was the midpoint between detecting an inactive sensor and confirmation of mortality. The mean number of days between recording an inactive signal and inspection of the site was 31 days (range = 2–166 days, $n = 9$) for adults and 30 days (range = 0–112 days, $n = 27$) for calves. We generated annual survival probabilities, independently, for adult females, adult males, adults (pooled females and males), and calves. Survival estimates were constrained so that they did not exceed 1.00. The Z test for two independent proportions was used to compare survival estimates between years (Zar 1984, pp. 395–397). To minimize the type I error rate and maximize statistical power, we only compared minimum and maximum survival probabilities (i.e., estimates that provided maximum effect size) for adults (including yearlings) and calves, independently (Toft and Shea 1983). Average annual survival rates and variances were calculated using the geometric mean and associated 95% CI (= antilog (geometric mean \pm 1.96 SE (log value))).

Following the method used by Rettie and Messier (1998), we used our estimates of survival and recruitment rates (calf-to-cow ratio adjusted for nonclassified animals) to calculate Caughley's (1977) survival–fecundity rate of increase (r_s) based on the adult female (individuals >10 months of age) segment of the population. The sex ratio of calves during March surveys (0.43 F : 0.57 M, $n = 56$) did not differ significantly ($Z = 0.95$, $P > 0.20$), and therefore, we assumed that the sex ratio for 10-month old calves was 1:1. Rate of increase was calculated as

$$r_s = \ln (\text{female survival} + \text{female survival} \\ \times \text{recruitment} \times 0.5)$$

Beginning with the estimated annual mean and variance obtained for female survival and recruitment, we used Monte Carlo simulation to generate 1000 estimates of each variable. These estimates were then used to calculate the mean annual r_s (\pm 1 SD) for the population from 1994 to 1997.

Results

Habitat and home-range size

Secondary-growth timber (F-40 and F-60) constituted 26% of the study area, whereas recently harvested (F-20) and early climax stands (F-80) and mature timber (F-80+) comprised 7 and 26% of the study area, respectively (Table 1). Nondisturbed but relatively open habitats (bogs,

scrub, rock and heath barrens, ponds, and lakes) accounted for 38% of the landscape available to the CBL caribou population. Overall, median patch size was 0.034 km² and ranged from 0.006 km² (stand remnants and mortality timber) to 0.067 km² (rock and heath barrens) for nonlinear habitats (Table 1).

From 1982 through 1998, records indicated that an approximate area of 63 km² has been harvested (87% cut when this study was complete; Fig. 2). Annual cuts ranged from 5 to 890 ha and average harvest block size ranged from 2.5 to 11.8 ha. During this study, 27.6 km² of timber was harvested (8.9 km² in 1994, 5.5 km² in 1995, 5.9 km² in 1996, and 7.3 km² in 1997).

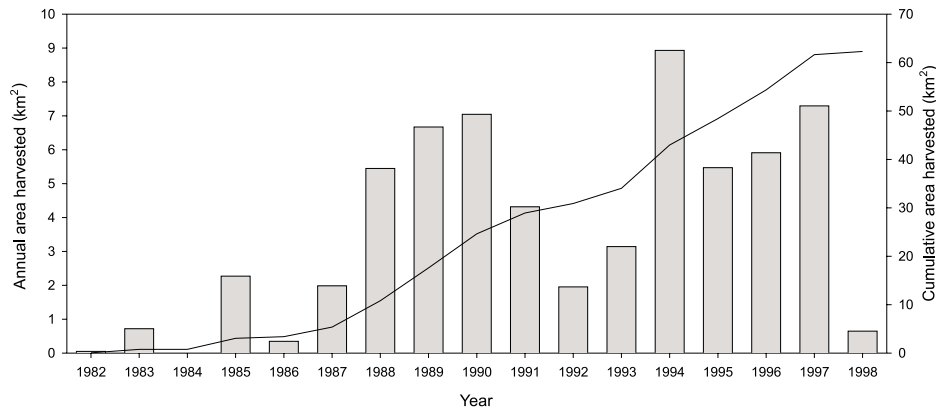
Individual home ranges of all radio-collared adults overlapped extensively in the study area. In addition, no radio-collared individuals (adults, yearlings, or calves) were recorded emigrating from the study area during the study. After pooling data across seasons and years, individual home-range size of female (89.8 ± 13.3 km² (mean \pm 1SE), $n = 17$) and male (84.0 ± 25.6 km², $n = 5$) adult caribou were not statistically different ($t = 0.20$, $df = 20$, $P > 0.50$). After pooling data for adults across years, analysis indicated that there was a significant trend in home-range size among seasons ($F_{[3,71]} = 2.75$, $P = 0.05$). For example, home-range size of adult caribou was greatest during autumn (43.6 ± 9.8 km², $n = 19$), followed by winter (40.7 ± 6.6 km², $n = 20$) and spring (33.2 ± 7.6 km², $n = 17$). During the summer, the area used by an individual (17.4 ± 2.7 km², $n = 19$) decreased by about 50% relative to other seasons.

Seasonal range selection

For adult females ($n = 79$ seasonal ranges), analysis of resource selection indices generated no significant two- or three-way interactions among reproductive status, season, and year (MANOVA, $F \leq 1.26$, $P \geq 0.17$). Habitat selection was also independent of each of these factors ($F < 0.98$, $P > 0.50$). Subsequent to pooling the set of resource selection indices for adult female and male caribou, we did not find any significant interactions among sex, season, and year ($F \leq 1.42$, $P \geq 0.06$). Habitat selection did not differ between females and males ($F_{[13,73]} = 1.16$, $P = 0.32$), and no year effects could be detected ($F_{[39,217]} = 0.79$, $P = 0.81$). However, habitat selection did vary statistically with season ($F_{[39,217]} = 1.54$, $P = 0.03$). Subsequently, we performed paired comparisons of the ranks of resource selection indices between each habitat within a season.

Standardized resource selection indices and paired contrasts indicated that adult caribou selected rock and heath barrens (BNS), virgin (Other), and mature forest stands (F-80+) significantly more than the other habitats available on the landscape during all seasons (Fig. 3). Although the selection index for mature forest stands changed marginally among seasons, the selection value for rock and heath barrens in winter was about half the value calculated during spring through autumn. In contrast, the value of virgin timber stands for caribou appeared to double in winter relative to the other seasons (Fig. 3).

Hardwood and softwood scrub habitat was relatively more preferred during spring, summer, and autumn than in winter (Fig. 3). In general, recently harvested stands (F-20) and habitats associated with continuous or frequent human dis-

Fig. 2. Annual (bars) and cumulative area (solid line) of timber harvested in the Corner Brook Lakes study area, 1982–1998.

turbance, such as agricultural, cleared, and residential land and roads, were utilized significantly less relative to other habitats during all seasons. Young (F-40), secondary-growth (F-60), and mortality timber were preferentially selected over the preceding habitats (e.g., agricultural land and roads) but were relatively avoided compared with highly selected habitats (e.g., barrens and mature forest). Bogs, early climax forest stands (F-80), and ponds and lakes represented habitats of intermediate selection value for caribou (Fig. 3). Selection indices suggested that early climax forest stands appeared more important to caribou in autumn and winter, whereas bog habitat was more valuable to caribou during summer and autumn.

Population size, adult sex ratio, and reproduction

During late-winter aerial surveys, the number of animals observed among years ranged from 95 to 236, and the fraction of individuals classified ranged from 63 to 83% (Table 2). Annual estimates of population size and associated 95% CI varied markedly and were largely dependent on the fraction of collared animals sighted. For example, the proportion of collared animals sighted each year was 38% (5/13) in 1994, 46% (6/13) in 1995, 8% (2/25) in 1996, and 12% (3/26) in 1997. For 1994–1997, mean population size of the CBL caribou herd was 584 animals or 0.6 caribou/km² (95% CI = 0.3–0.8 caribou/km²). However, it is recognized that there is a large degree of uncertainty associated with this population estimate. The sex ratio (M:F) of classified adult caribou also varied among years (Table 2). Overall, the mean sex ratio across years was approximately 0.8:1.0.

Aerial surveys during the precalving through the postcalving periods indicated that parturition date ranged from 24 May to 12 June. Monitoring of radio-collared females indicated that pregnancy rate for this population was high in each of the 4 years of this study (Table 2). No radio-collared yearling females ($n = 2$) were observed to be pregnant. Overall pregnancy rate of radio-collared adult females during the study was $96 \pm 3\%$ ($n = 46$). During calving, individual females isolated themselves from other caribou and 75–80% calved in early climax and mature timber. After 2–4 days, radio-collared females were recorded moving from closed timber stands to the barrens, where they would form small groups of two to three cow–calf pairs. Some females were also observed to calve in extensive scrub habitats, interspersed with patches of bog and barrens.

Calf recruitment and timing and causes of mortality

Calf recruitment to 10 months of age varied significantly among years ($G = 54.61$, $df = 3$, $P < 0.01$) and was associated with the proportion of calves observed (Table 3). The March calf-to-cow ratio in 1996 was markedly higher, whereas recruitment in 1994 was lower compared with 1995 or 1997. Overall, the recruitment of calves into the CBL population during the study was 0.24 ± 0.02 (mean \pm 1SD), and the average percent calves observed was 13%.

Although our data on caribou mortality is sparse, some trends are worth noting. None of the seven natural deaths of adults showed evidence of depredation or malnutrition. Two animals died during each of spring, autumn, and winter, and one adult died in summer. Of the 15 calves that died, 8 deaths occurred during the spring within 2 weeks of parturition (mean number of days between recording an inactive signal and site inspection = 7; range = 2–14). Two calves died in summer, three died in autumn, and two died during winter. Five of the eight spring fatalities showed evidence of bear depredation, and the cause of the remaining three deaths could not be verified. For the remaining seven deaths, three were associated with infections, three died of unknown causes, and one was killed illegally. None of the calves showed evidence of malnutrition.

Survival and rate of increase

Although we had limited data for estimating adult male survival rates, annual survival probabilities for adult female and male caribou appeared to be similar (Table 4). After pooling data for adults, we could detect no statistical difference in annual survival rates between 1994–1995 and 1995–1996 ($Z = 1.54$, $P = 0.12$). Mean annual survival probability for adult caribou in the CBL population during the course of this study was 0.87.

Annual survival probabilities for calves appeared to vary among years (Table 4), but a comparison between 1994–1995 and 1996–1997 revealed no statistical difference ($Z = 1.18$, $P > 0.20$). Average annual survival rate of calves from 1994 to 1997 was 0.45.

Using our mean annual estimates (and associated variance) of calf recruitment to 10 months of age and adult female survival rate, we determined that the average survival–fecundity rate of increase (r_s) for the CBL population was -0.01 (SD = 0.06).

Fig. 3. Mean selection indices (b_i) and significant differences between paired contrasts for each of the 17 habitat types during spring (a), summer (b), autumn (c), and winter (d) for adult woodland caribou (*Rangifer tarandus caribou*) in the Corner Brook Lakes area, 1994–1997. Each row provides the mean selection value for a given habitat and whether it was significantly avoided (–) or preferred (+) relative to the habitat in each column. Habitat codes are defined in Table 1. n , number of seasonal ranges.

(a) $n = 29$

| b_i | AG | Bog | F-20 | F-40 | F-60 | F-80 | F-80+ | Mort | CL | BNS | Scrub | Rem | Road | PL | Res | Water | Other | |
|-------|------|-----|------|------|------|------|-------|------|----|-----|-------|-----|------|----|-----|-------|-------|---|
| AG | 0.00 | | - | | | - | - | - | | | - | - | | | | | - | - |
| Bog | 0.06 | + | | + | + | + | | - | + | + | - | | + | + | + | + | | |
| F-20 | 0.00 | | | | | | - | - | - | | - | - | | | | | | - |
| F-40 | 0.00 | | | | | | | | | | - | - | | | | | | - |
| F-60 | 0.01 | + | - | + | + | + | | - | - | + | - | - | + | + | | + | | - |
| F-80 | 0.03 | + | | + | + | + | | - | + | + | - | - | + | + | - | + | | |
| F-80+ | 0.18 | + | + | + | + | + | + | | + | + | | | + | + | + | + | + | - |
| Mort | 0.01 | | - | | | | | | | | - | - | | | | | | - |
| CL | 0.00 | | - | | | | | | | | - | - | | | | | | - |
| BNS | 0.28 | + | + | + | + | + | + | | + | + | | | + | + | + | + | + | + |
| Scrub | 0.11 | + | | + | + | + | + | | + | + | | | + | + | + | + | | - |
| Rem | 0.00 | | - | | | | | | | | - | - | | | | | | - |
| Road | 0.00 | | - | | | | | | | | - | - | | | | | | - |
| PL | 0.04 | | - | | | | + | - | | | - | - | | | | | | - |
| Res | 0.00 | | - | | | | | | | | - | - | | | | | | - |
| Water | 0.06 | + | | + | + | + | | - | + | + | - | | + | + | | + | | - |
| Other | 0.22 | + | | | | | | + | | + | - | + | + | + | | + | | - |

(b) $n = 25$

| b_i | AG | Bog | F-20 | F-40 | F-60 | F-80 | F-80+ | Mort | CL | BNS | Scrub | Rem | Road | PL | Res | Water | Other |
|-------|------|-----|------|------|------|------|-------|------|----|-----|-------|-----|------|----|-----|-------|-------|
| AG | 0.00 | | - | | | - | - | - | | | - | - | | | | | - |
| Bog | 0.09 | + | | + | + | + | | | + | + | | | + | + | + | + | |
| F-20 | 0.00 | | | | | | - | - | - | | - | - | | | | | - |
| F-40 | 0.00 | | | | | | | | | | - | - | | | | | - |
| F-60 | 0.02 | + | - | + | + | + | | - | + | + | - | - | + | + | | + | - |
| F-80 | 0.02 | + | | + | + | + | | - | + | + | - | - | + | + | - | + | - |
| F-80+ | 0.18 | + | | + | + | + | + | | + | + | | | + | + | + | + | + |
| Mort | 0.01 | | - | | | | | | | | - | - | | | | | - |
| CL | 0.00 | | - | | | | | | | | - | - | | | | | - |
| BNS | 0.29 | + | | + | + | + | + | | + | + | | | + | + | + | + | |
| Scrub | 0.13 | + | | + | + | + | + | | + | + | | | + | + | + | + | |
| Rem | 0.00 | | - | | | | | | | | - | - | | | | | - |
| Road | 0.00 | | - | | | | | | | | - | - | | | | | - |
| PL | 0.06 | | - | | | | + | - | | | - | - | | | | | - |
| Res | 0.00 | | - | | | | | | | | - | - | | | | | - |
| Water | 0.07 | + | | + | + | + | + | - | + | + | | | + | + | + | + | - |
| Other | 0.13 | | + | | | | + | - | | | - | | | | | | - |

Fig. 3 (concluded).

(c) n = 19

| b_i | AG | Bog | F-20 | F-40 | F-60 | F-80 | F-80+ | Mort | CL | BNS | Scrub | Rem | Road | PL | Res | Water | Other |
|-------|------|-----|------|------|------|------|-------|------|----|-----|-------|-----|------|----|-----|-------|-------|
| AG | 0.00 | | - | | | - | - | - | | | - | - | | | | | - |
| Bog | 0.08 | + | | + | + | | | | + | + | | | + | + | + | + | |
| F-20 | 0.01 | | - | | | - | - | - | | | - | - | | | | | - |
| F-40 | 0.01 | | | - | | - | - | - | | | - | - | | | | | - |
| F-60 | 0.04 | + | | + | + | | | | + | | - | | + | + | | + | |
| F-80 | 0.08 | + | | + | + | | | | + | + | | | + | + | + | + | |
| F-80+ | 0.16 | + | | + | + | + | | | + | + | | | + | + | + | + | + |
| Mort | 0.05 | | - | | | | - | | | | - | - | | | | | + |
| CL | 0.00 | | - | | | - | - | - | | | - | - | | | | | - |
| BNS | 0.21 | + | | + | + | | | | + | + | | | + | + | + | + | |
| Scrub | 0.10 | + | | + | + | + | | | + | + | | | + | + | + | + | + |
| Rem | 0.00 | | - | | | - | - | - | | | - | - | | | | | - |
| Road | 0.00 | | - | | | - | - | - | | | - | - | | | | | - |
| PL | 0.02 | | - | | | - | - | - | | | - | - | | | | | - |
| Res | 0.00 | | - | | | - | - | - | | | - | - | | | | | - |
| Water | 0.04 | + | | + | + | | | - | - | + | | | + | + | + | + | |
| Other | 0.19 | | | | | | | | | | | | | | | | |

(d) n = 28

| b_i | AG | Bog | F-20 | F-40 | F-60 | F-80 | F-80+ | Mort | CL | BNS | Scrub | Rem | Road | PL | Res | Water | Other |
|-------|------|-----|------|------|------|------|-------|------|----|-----|-------|-----|------|----|-----|-------|-------|
| AG | 0.00 | | - | | | - | - | - | | | - | - | | | | | - |
| Bog | 0.04 | + | | + | | | | | + | + | - | - | + | + | | + | |
| F-20 | 0.01 | + | | | | - | - | - | | | - | - | + | + | | + | |
| F-40 | 0.02 | | - | | | - | - | - | | | - | - | | | | | - |
| F-60 | 0.03 | + | | + | + | | | | + | + | | | + | + | - | + | |
| F-80 | 0.07 | + | | + | + | | | | + | + | | | + | + | + | + | |
| F-80+ | 0.12 | + | + | + | + | + | | | + | + | | | + | + | + | + | + |
| Mort | 0.01 | | - | | | - | - | | | | - | - | | | | | - |
| CL | 0.01 | | - | | | - | - | - | | | - | - | | | | | - |
| BNS | 0.13 | + | + | + | + | | | | + | + | | | + | + | + | + | + |
| Scrub | 0.05 | + | + | + | + | | | | + | + | | | + | + | + | + | |
| Rem | 0.00 | | - | | | - | - | - | | | - | - | | | | | - |
| Road | 0.00 | | - | | | - | - | - | | | - | - | | | | | - |
| PL | 0.05 | | | | | + | - | - | | | - | - | | | | | - |
| Res | 0.00 | | - | | | - | - | - | | | - | - | | | | | - |
| Water | 0.04 | + | | + | | | | - | + | + | - | | + | + | | + | |
| Other | 0.40 | + | | | | | | | + | + | | | + | + | | + | |

Table 2. Estimates of population size (95% confidence interval (CI)), adult sex ratio (males to 100 females), and pregnancy rate from late-winter surveys of the Corner Brook Lakes caribou herd, 1994–1997.

| Year | Population size | Males : | | | |
|-----------|----------------------------|----------------------|--------------------------|----------|----------|
| | | 100 females | Pregnancy | <i>n</i> | <i>m</i> |
| 1994 | 345 (182–748) | 80 | 0.89 (<i>n</i> = 9) | 158 | 100 |
| 1995 | 440 (239–917) | 75 | 0.93 (<i>n</i> = 14) | 236 | 184 |
| 1996 | 925 (374–2129) | 53 | 1.00 (<i>n</i> = 14) | 110 | 91 |
| 1997 | 624 (284–1425) | 97 | 1.00 (<i>n</i> = 9) | 95 | 76 |
| 1994–1997 | 584 (328–840) ^a | 76 ± 18 ^b | 0.96 ± 0.03 ^c | 599 | 451 |

Note: Pregnancy rate was determined from radio-collared females (*n* = number of collared females censused); *n*, number of animals observed during survey; *m*, number of animals classified.

^aArithmetic mean with 95% CI (see Methods).

^bArithmetic mean ± 1 standard deviation (SD).

^cBased on pooled data ± 1 SD (calculated from binomial distribution).

Table 3. Late-winter estimates of percentage of calves and calf-to-cow ratios for the Corner Brook Lakes caribou herd, 1994–1997.

| Year | Percentage of calves | Calf-to-cow ratio | <i>n</i> |
|-----------|-------------------------|--------------------------|----------|
| 1994 | 6.3 | 0.12 | 82 |
| 1995 | 11.0 | 0.22 | 120 |
| 1996 | 22.7 | 0.45 | 55 |
| 1997 | 11.6 | 0.26 | 43 |
| 1994–1997 | 12.9 ± 6.9 ^a | 0.24 ± 0.02 ^b | 300 |

Note: Percentage of calves was based on the total number of animals observed during the survey (i.e., *n* in Table 2); adjusted number of cows (*n*) = number of cows observed + (number of cows observed / total number of adults observed and sexed) × number of unsexed adults observed).

^aArithmetic mean ± 1 standard deviation (SD).

^bCalculations based on pooled data (± 1 SD calculated from binomial distribution).

Discussion

Coarse-scale habitat selection

Caribou inhabiting the CBL area exhibited strong habitat selection at the landscape scale, and we hypothesize that such coarse-scale selection is primarily associated with predator avoidance and foraging behaviour. For example, relative avoidance of recently harvested stands (F-20), early succession stands (F-40), and roads may represent a direct response to minimizing the risk of contact with predators, especially wolves (Bergerud and Page 1987; Bergerud et al. 1990; Seip 1992; James and Stuart-Smith 2000; Rettie and Messier 2000). Despite the relatively long absence of wolves from this system, female and male caribou avoided early seral stage habitats where the likelihood of contact with black bears (or wolves) and secondary prey (moose) would be high and the quantity of preferred food of caribou would be low. Likewise, the synergistic preference for mature forest stands, heath barrens, and scrub habitat provides individuals with food items that contain sufficient digestible energy and protein necessary for growth, reproduction, and over-winter survival (Rominger et al. 2000). For example, analysis of 62 fecal samples (Mahoney 2000) indicated that the primary forage for the CBL herd included lichens (*Cladonia*,

Alectoria, and *Cetraria* spp.), sedges (*Carex* spp.), and deciduous browse (*Salix* spp.), a diet similar to that of other woodland caribou populations (Cringan 1957; Bergerud 1972; Darby and Pruitt 1984). Use of early climax and mature timber stands by caribou also provides cover during winter storms and facilitates travel and foraging because of lower snow accumulation (Fuller and Keith 1981; Darby and Pruitt 1984; Rominger and Oldemeyer 1989).

Unlike similar studies in the boreal forests of northern Alberta and Saskatchewan (e.g., Stuart-Smith et al. 1997; Rettie and Messier 2000), we found significant seasonal variation in the relative use of preferred habitats by caribou in the CBL area. For example, after the calving (spring) and late-lactation period (summer), there was a decrease in the relative use of barrens and scrub habitat in autumn and particularly during winter. The selective value of bog habitat was highest during summer and autumn, whereas small patches of virgin timber appeared to have greater use during the calving period and winter. Such seasonal variation in habitat use by caribou in the CBL area may represent an adaptive behavioural response to temporal changes in forage quality and the seasonal presence of black bears relative to caribou inhabiting bog–fen complexes with continuous presence of wolves in the boreal forest of Alberta and Saskatchewan. In contrast, the lack of significant variation between sexes and years in the CBL herd is consistent with other studies on coarse-scale habitat selection in woodland caribou (Stuart-Smith et al. 1997; Rettie and Messier 2000). Seasonal variation in habitat selection between sexes has been reported in large migratory caribou herds (Russell et al. 1993), and this may be one of the fundamental differences in the ecology of migratory and nonmigratory ecotypes.

Similar to the results of Rettie and Messier (2000), we detected no significant effect of female reproductive status on coarse-scale habitat selection. However, because the number of females with “no calf” was quite small in this study and many females that had “lost a calf” likely were “with a calf” for at least 2 weeks after parturition, we likely had little statistical power to detect an effect during the spring (calving and postcalving periods). However, during the summer, autumn, and winter, we should have detected an effect if one existed. If the mobility of a calf is similar to that of an adult, once a calf has survived through spring, then our results suggest that parental behaviour may explain little variation in

Table 4. Annual survival rates of adult females (AF), adult males (AM), pooled adult females and males (Adults), and calves in the Corner Brook Lakes area.

| Year | AF | AM | Adults | Calves |
|-----------|-----------------------------------|----------------------------------|-----------------------------------|----------------------------------|
| 1994–1995 | 0.78 (0.56–1.00), <i>n</i> = 8.4 | 0.54 (0.16–1.00), <i>n</i> = 1.7 | 0.74 (0.52–1.00), <i>n</i> = 10.2 | 0.35 (0.11–1.00), <i>n</i> = 2.7 |
| 1995–1996 | 0.94 (0.83–1.00), <i>n</i> = 15.0 | 1.00 (1.00–1.00), <i>n</i> = 4.5 | 0.95 (0.87–1.00), <i>n</i> = 19.5 | 0.42 (0.18–0.98), <i>n</i> = 4.4 |
| 1996–1997 | 0.93 (0.81–1.00), <i>n</i> = 14.2 | 1.00 (1.00–1.00), <i>n</i> = 6.7 | 0.95 (0.87–1.00), <i>n</i> = 20.9 | 0.61 (0.35–1.00), <i>n</i> = 6.1 |
| 1994–1997 | 0.88 (0.78–0.99) | 0.81 (0.54–1.00) | 0.87 (0.74–1.00) | 0.45 (0.32–0.62) |

Note: 1994–1997 values represent the geometric mean with associated 95% CI (= antilog (geometric mean \pm 1.96 SE (log value))). Values in parentheses represent the 95% CI; *n*, number of animal years.

coarse-scale habitat selection for females of this herd during most of the year. However, calving site selection by solitary females was strongly biased towards mature timber, followed by bog and scrub habitats, and soon after parturition, females formed small groups of two to three female–calf pairs in the open barrens. These maternal behaviours are typical of woodland caribou and are hypothesized to decrease detection by predators (Fuller and Keith 1981; Brown and Theberge 1985; Bergerud et al. 1990).

Factors limiting population growth

Current estimates of adult survival, calf recruitment, and population growth rates indicate that the CBL population is stable. Mean annual survival rate of adults was 0.87, which is within the range considered typical for woodland caribou (87–93%; Bergerud 1980), and is consistent with that of nondeclining populations (Fancy et al. 1994). Annual late winter calf-to-cow ratio ranged from 0.12 to 0.45 (mean = 0.24), and the average percentage of calves was 13%. Bergerud (1974) suggested that caribou populations with 12–16% calves at 10–12 months of age are likely stable, which is supported by our estimate of population growth rate ($r_s = -0.01 \pm 0.06$ (mean \pm SD)).

Availability of quality food resources can be a key factor limiting reproduction and over-winter survival in cervid populations (Thomas 1982; Skogland 1986; Messier et al. 1988; Crête and Huot 1993). For adult females, poor body condition during summer and autumn is usually associated with reduced pregnancy rates (Dauphiné 1976; Cameron 1994) and can influence the quality and quantity of milk, which can affect the growth, nutritional condition, and subsequent survival of calves during winter. In addition, poor nutrition during winter can result in reduced parturition rate, lower birth mass of calves, or a delay in the time of birth (Reimers et al. 1983; Skogland 1983; Cameron et al. 1993). Pregnancy rate among collared females in the CBL herd (96%) was higher than the average (82%) for North American populations (Bergerud 1980) and similar to that reported for Saskatchewan by Rettie and Messier (1998). Visual inspection of dead adult females and males, and calves also provided no evidence of malnutrition. Although we have no estimate of abortion rate in this herd, the calving period was similar to that of other woodland caribou populations (Fuller and Keith 1981; Edmonds 1988; Stuart-Smith et al. 1997). These results suggest that the quantity of quality forage was sufficient to meet the nutritional requirements of reproduction in females of this population from spring through winter.

For adult male ungulates, mating behaviour is often associated with a decrease or cessation of food intake (Clutton-Brock et al. 1988). Therefore, winter survival is generally

dependent on energy reserves deposited before the rut and access to quality forage after the rut (Clutton-Brock et al. 1982; Dumont et al. 2000). These selection pressures can contribute to differences in survival between sexes and may be coupled with a female bias in adult sex ratio. For this study, the average annual proportion of adult males during the late-winter census was 43% (76 M : 100 F), which is higher than the mean sex ratio for North American populations (36% M; Bergerud 1980) and is likely related to the absence of legal hunting in this population. However, given that the sex ratio of 10-month old calves did not differ from unity, the female bias in adult sex ratio suggests that the natural mortality rate in males may be marginally higher than that of females in the CBL herd. This does not imply that food quality is directly affecting the survival of adult males but rather that the energetic costs incurred by males during mating may be more difficult to offset relative to reproduction in females, which may make males more vulnerable to other mortality agents (e.g., disease, temperature). We maintain that our results on female reproductive parameters (pregnancy rate, time of parturition) and the lack of evidence for malnutrition in a sample of 22 dead animals indicates that the quantity of quality forage is not a key factor limiting the growth rate of this herd. However, the potential for food accessibility to limit ungulate population growth still exists, especially during years of heavy snowfall or hard-packed snow conditions (Fancy and White 1987; Ballard et al. 1991; Modafferi and Becker 1997). Similarly, overharvesting of preferred autumn and winter foraging habitats (i.e., forested stands greater than 60 years of age) would decrease food availability and have the potential to adversely affect reproduction and over-winter survival rate in this population.

In this study, black bears were verified in the death of 5 of 15 calves (33%), and all individuals were killed within 2 weeks of parturition. Three other calves died during the first 6 weeks after birth, but the exact cause of death could not be determined. Although wolves are currently not present in this system, black bears are common in the study area. Black bears and brown bears (*Ursus arctos*) have been shown to be an important source of mortality on moose and caribou calves in Newfoundland and other regions of North America, particularly in spring and summer (Franzmann et al. 1980; Mahoney et al. 1990; Ballard et al. 1991; Schwartz and Franzmann 1991). Without knowledge of the density of black bears in the CBL area, any link to the strength of predation from black bears on this caribou herd is tenuous. However, some discussion is warranted here.

Caribou in the CBL area demonstrated an avoidance of disturbed and early succession forested habitats. In environments where bear density is high and caribou calving areas

become limited or adjacent to preferred bear and moose habitat, black bear predation could have a strong effect on population growth in a woodland caribou herd. This may be especially true in the CBL population, which exhibits little seasonal movement and is demographically isolated. For example, timber harvesting and associated early succession habitat can lead to increased moose numbers and preferred forage areas for black bears (Franzmann and Schwartz 1985; Albright and Keith 1987; Samson and Huot 1998). Rettie and Messier (2000) predicted that in environments where the seasonal ranges of nonmigratory caribou herds and a secondary prey species (like moose) become less separated, predation (especially by wolves) will cause caribou populations to persist at low numbers. Studies have also shown that caribou populations not exposed to predation can reach or exceed densities greater than 2.0 individuals/km² (Ferguson et al. 1988; Heard and Ouellet 1994), and the density of the CBL herd (0.6 individuals/km²) is within the predicted range (<1 individual/km²) of predator limitation by wolves (Bergerud 1980). However, the ability of black bears to depress caribou population size to such a level remains to be determined. Nevertheless, the frequency of successful kills (functional response; Messier 1991) by black bears may be similar to that of wolves when calves are relatively young (i.e., within 6–8 weeks after birth). Both demographic and habitat selection patterns may be affected by bears, and the implications can be especially important in systems where both wolves and bears are present (*sensu* Messier 1994).

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