Factors influencing variation in site fidelity of woodland caribou (*Rangifer tarandus caribou*) in southeastern British Columbia

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Abstract: Where predation is a major limiting factor, it has been postulated that woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) reduce movements to minimize contact with predators and exhibit fidelity to seasonal ranges. We examined fidelity behaviour within season and among years of woodland caribou based on locations of 65 radio-collared individuals in British Columbia, Canada. We used average linear distances between all possible pairs of radiolocations of individuals to assess fidelity. Among-year interlocation distances were similar to within-season interlocation distances during summer, indicating that caribou did not shift their distribution during seasons when they were most vulnerable to predation. Among-year interlocation distances were significantly greater than within-season interlocation distances during both early winter and late winter, indicating that individual caribou shifted their distribution among winters. The amount that an individual's distribution shifted among winters varied among and within individuals over different years. During early winter this behavioural plasticity was correlated with snow accumulation, with individuals having greater interlocation distances in years with high snow accumulation. Our results indicate that site fidelity outside the calving season is unlikely solely influenced by predator avoidance. We suggest that seasonal shifts in the importance of limiting factors vary from predation in summer to food in winter.

Résumé : On a avancé que, lorsque la prédation est un facteur limitant important pour les caribous des bois (*Rangifer tarandus caribou* (Gmelin, 1788)), ceux-ci réduisent leurs déplacements afin de minimiser les contacts avec les prédateurs et montrent une fidélité à leurs aires de répartition saisonnières. Nous avons évalué le comportement de fidélité au cours des saisons et d'une année à l'autre chez le caribou des bois en étudiant les positions de 65 individus munis de colliers radio en Colombie-Britannique, Canada. Les distances linéaires moyennes entre toutes les paires possibles de positions radio individuelles ont servi à mesurer la fidélité. Les distances entre les positions au cours des années sont semblables à celles observées au cours de la saison d'été, ce qui indique que les caribous ne changent pas leur répartition durant les saisons où ils sont le plus vulnérables à la prédation. Les distances entre les positions au cours des années sont significativement plus grandes que celles observées au cours du début et de la fin de l'hiver, ce qui indique que les caribous changent leur répartition d'un hiver à l'autre. L'importance du changement de répartition individuelle au cours des différents hivers varie d'un individu à l'autre et d'une année à l'autre chez un même individu. Au début de l'hiver, cette plasticité comportementale est en corrélation avec l'accumulation de la neige; les distances entre les positions sont en effet plus grandes les années où il y a une forte accumulation de neige. Nos résultats indiquent qu'il est peu probable que la fidélité au site en dehors de la saison de mise bas soit influencée seulement par l'évitement des prédateurs. Nous croyons qu'il y a des changements saisonniers de l'importance des facteurs limitants, passant de la prédation en été à la nourriture en hiver.

[Traduit par la Rédaction]

Introduction

Site fidelity has been defined as (*i*) the tendency of an animal to return to a previously occupied area or (*ii*) to remain within the same area for an extended period of time (White and Garrott 1990), and it has been documented in a variety of species including birds and mammals (Greenwood and Harvey 1982; Switzer 1993). Site fidelity is typically associated with nesting sites (Madsen and Shine 1999), sleeping sites (Clark and Gillingham 1990), breeding areas (Schieck and Hannon 1989), foraging areas (Irons 1998), and territories (Kitchen et al. 2000). In ungulates, site fidelity has been predominately described in relation to the use of seasonal ranges (e.g., Schoen and Kirchhoff 1985; Aycrigg and Porter 1997). Small seasonal ranges reflect high fidelity within a season, while the tendency of an animal to return to the same seasonal range year after

year shows high fidelity among years. Explanations for the prevalence of both types of site fidelity include familiarity with the distribution of food, conspecifics, and predators that enhances individual survival and reproductive success (Greenwood 1980; Schieck and Hannon 1989; Beletsky and Orians 1991).

Seasonal movement and space-use patterns including range fidelity of large herbivores in mountainous and temperate regions have commonly been attributed to changes in food quality and availability, as well as to the risk of predation (Fryxell et al. 1988; Mysterud et al. 2001). Individual variation in space-use patterns is extremely variable among populations of woodland caribou (*Rangifer tarandus caribou* (Gmelin, 1788)) where annual travel distances vary from >3000 km for migratory animals (Bergman et al. 2000) to <200 km for sedentary animals (Stuart-Smith et al. 1997). Based on these distinct differences, Bergerud (1988, 1996) proposed to categorize North American caribou (*Rangifer tarandus* (L., 1758)) as either sedentary or migratory. The sedentary ecotype differs from the migratory ecotype in range size, rates of travel, and calving strategies (Bergerud 1988, 1996). Migratory caribou move beyond the distribution of most predators to calve in large aggregations, while sedentary caribou isolate themselves from each other to decrease the likelihood of predation.

Both ecotypes of caribou show among-year fidelity to areas for calving and mating (Gunn and Miller 1986; Fancy and Whitten 1991; Schaefer et al. 2000). Greater within-season fidelity of sedentary caribou has led to the hypothesis that reduced movements minimize encounter rates with predators (Bergerud and Page 1987; Bergerud 1996; Rettie and Messier 2001) that are supported largely by other prey species (Bergerud and Elliot 1986; Seip 1992; Wittmer et al. 2005a). Sedentary caribou appear to exhibit less among-year fidelity to winter ranges than calving or mating ranges (Schaefer et al. 2000). However, variation in seasonal range fidelity is inconsistent across studies (e.g., Rettie and Messier 2001), indicating that factors underlying differences in fidelity behaviour outside the calving season remain poorly understood.

We studied site fidelity in a sedentary ecotype of woodland caribou referred to as "arboreal lichen feeding" or "mountain" caribou (COSEWIC 2002). These mountain caribou inhabit the wet coniferous forests of southeastern British Columbia, Canada, and adjacent portions of Idaho and Washington, USA (Wittmer et al. 2005b), and are designated threatened or endangered in both countries (U.S. Fish and Wildlife Service 1994; COSEWIC 2002). During winter, these caribou are associated with late-successional forests where their primary food, arboreal lichen, is relatively abundant (Rominger and Oldemeyer 1989; Rominger et al. 1996; Terry et al. 2000). The economic and social implications of maintaining winter range for the threatened mountain caribou can be significant. Areas to be managed as caribou habitat are often delineated using radiolocations of a sample of the population or incidental sightings (Stevenson et al. 2001), so quantifying site fidelity, particularly fidelity among winters, is critical for a sound conservation strategy.

Mountain caribou typically exhibit four distinct elevational movements that are used to define seasons (Apps et al. 2001) and food availability and risk of predation vary among seasons. In early winter caribou descend from high-elevation subalpine habitats to lower elevations where they primarily forage on arboreal lichen as litterfall and on recently wind-thrown trees (Terry et al. 2000; Apps et al. 2001). During early winter food is scarce (Simpson and Woods 1987; Rominger and Oldemeyer 1990) and predation rates are generally low (Wittmer et al. 2005b). As the snowpack deepens and consolidates, caribou move from low elevations to high-elevation late-winter habitat (Apps et al. 2001). These elevational movements occur when snow at high-elevation ranges is sufficiently deep (typically 2–4 m) and firm enough to support caribou as they access the abundant arboreal lichen growing in the canopy of standing trees. In addition to increased food availability, being at high elevations on deep snow separates caribou from areas with higher densities of other ungulates and of predators such as gray wolves (*Canis lupus* L., 1758) that remain at lower elevations (Seip 1992). In spring caribou generally move to lower elevation forests and clearings to feed on emerging green vegetation. Females move back to higher elevations for calving. Both males and females spend summer at high elevations where food is abundant. Predation rates are highest during seasons where caribou fail to spatially separate themselves from their main predators (Seip 1992; Wittmer et al. 2005b).

We analyzed caribou movement patterns to investigate factors that influence fidelity to seasonal ranges and, in particular, to test the hypothesis that caribou site fidelity is a predator-avoidance strategy. We predicted high degrees of within-season and among-year fidelity during summer when mountain caribou are particularly vulnerable to predation (Table 1). In contrast, we predicted lower within-season fidelity during early winter and late winter when predation rates are reduced owing to spatial separation (Seip 1992), as well as to reduced predation risk from bears as a result of their hibernation. We also predicted lower among-year fidelity during early winter when food availability is low and highly variable from 1 year to the next (Table 1). Finally, we evaluated the influence of environmental factors including snow depth and lichen availability on site fidelity during early winter and late winter when predation rates are similar and whether individual variation in site fidelity affected the probability of surviving.

Methods

Study area

The study was conducted in a 9000 km^2 area in the Columbia Mountains, located in the southern extent of continuously occupied caribou habitat in southeastern British Columbia, Canada (51°N, 118°W; Fig. 1), currently supporting a population of approximately 400 individuals (Wittmer et al. 2005b). The topography is characterized by rugged mountains with steep, narrow valleys. Elevations range from 610 to >3000 m, with treeline at approximately 1980 m. The mean annual precipitation was 946 mm at an elevation of 450 m and 2102 mm at an elevation of 1875 m, with the majority falling as snow during winter (Environment Canada 2002). Typical mean daily temperatures at elevations of 450 m and 1875 m were –5.3 and –9.2 °C during January and 18.2 and 10.7 °C during July, respectively.

Biogeoclimatic zones in the study area include ICH (inte-

Table 1. Predicted seasonal fidelity behaviour (within season and among years) based on spatial separation from predators, predation risk (adjusted for seasonal length), and variation in food availability of mountain caribou (*Rangifer tarandus caribou*) in the Columbia Mountains of British Columbia, Canada; seasons are delineated based on observed elevational migrations following Apps et al. (2001).

Season	Elevation	Spatial separation	Cause of mortality		Total number of days†	Predation (number/day)	Food availability	Within-season/among-year fidelity
			Non-predation (females/males)*	Predation (females/males)*				
Summer	High	No	3 (3/0)	10 (8/2)	1325	0.008 (high)	High	High/high
Early winter	Low	No	3 (3/0)	3 (3/0)	821	0.004 (low)	Low	Low/low
Late winter	High	Yes	4 (4/0)	3 (3/0)	976	0.003 (low)	High	Low/high

*Observed number of mortalities associated with either non-predation or predation (from Wittmer et al. 2005*b*).
†Total number of days that caribou were monitored for based on seasonal dates shown in Table 2.

rior cedar (*Thuja plicata* Donn ex D. Don) – Pacific hemlock (*Tsuga heterophylla* (Raf.) Sarg.)) at lower elevations, ESSF (Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) – subalpine Fir (*Abies lasiocarpa* (Hook.) Nutt.)) at mid-elevations, and Alpine Tundra at higher elevations (Meidinger and Pojar 1991). Dominant shrubs at lower elevation include boxleaf (*Paxistima myrsinites* (Pursh) Raf.), thinleaf huckleberry (*Vaccinium membranaceum* Dougl. ex Torr), and Pacific yew (*Taxus brevifolia* Nutt.).

Caribou capture and telemetry

Between February 1992 and March 2002, 67 adult caribou (>2 years) were captured in subalpine habitat during late winter using a net-gun deployed from a helicopter. Two radio collars failed immediately, leaving 65 caribou (54 females, 11 males) that were included in the analysis (Table 2). Because >90% of the population is visible and available for capture at this time of the year (Wittmer et al. 2005*b*), we were able to distribute our sample of radio-collared animals in a geographic distribution that approximated that of the population. All captured caribou were fitted with mortality–motion sensitive very high frequency (VHF) radio collars. Individual female caribou were monitored for 1237 ± 120 days and male caribou were monitored for 1303 ± 230 days.

Telemetry relocations were recorded from a fixed-wing aircraft and marked on aerial photographs. Locations were then transcribed to 1:20000 forest cover maps and Universal Transverse Mercator (UTM) coordinates were recorded to the nearest 100 m. Radiolocations were divided into summer, early winter, late winter, and spring seasons according to the timing of elevational movements each year (Apps et al. 2001) (Table 2). The definition of the calving season was based on the date that radio-collared female caribou in the study area were first and last observed with new calves (earliest: 21 May; latest: 10 June). Tracking flights occurred, on average, every 11 (±5) days and the frequency of flights did not differ among the five seasons (ANOVA, $F_{[4,220]} = 0.94$, $P = 0.443$).
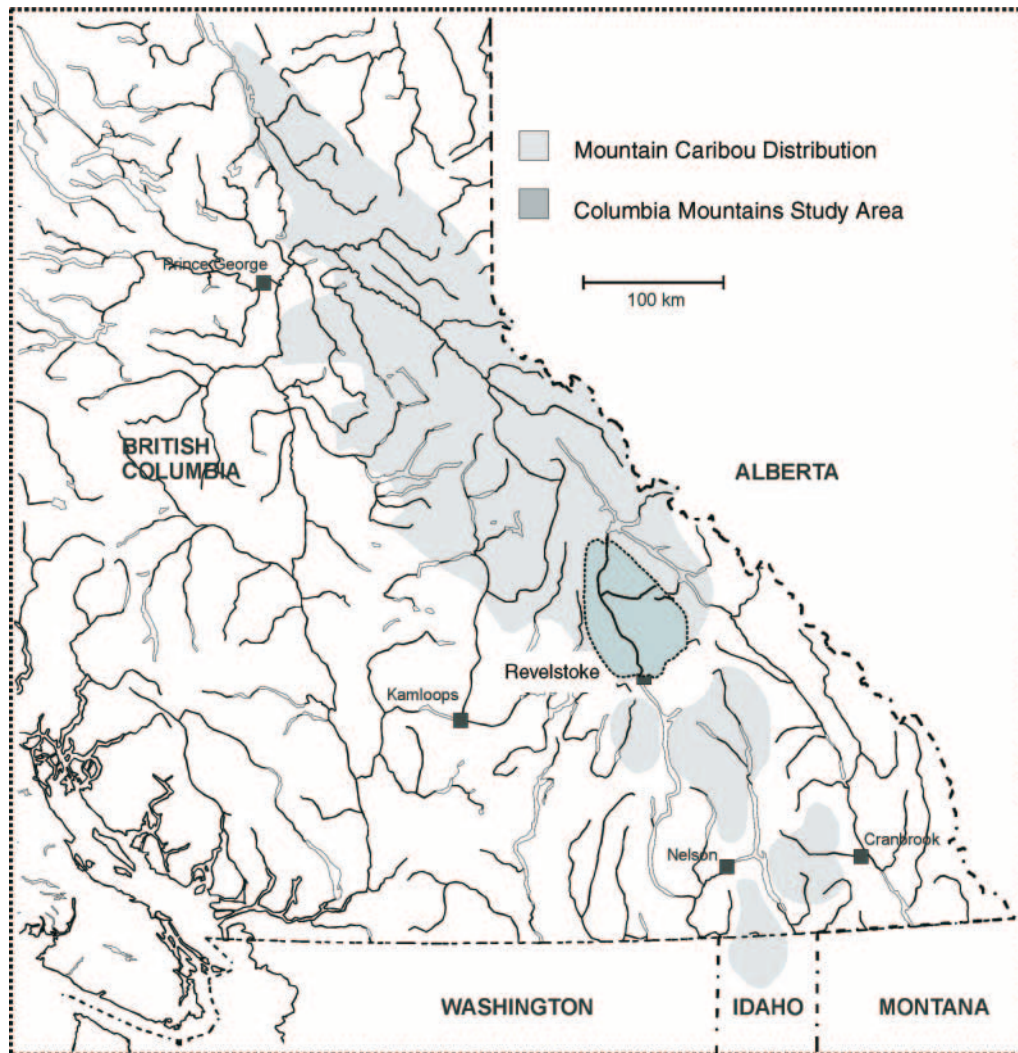
Seasonal predation risk

Wittmer et al. (2005*b*) presented an analysis of the causes and seasonal distribution of mortalities of mountain caribou over their entire distribution in British Columbia. We subsampled the data used in Wittmer et al. (2005*b*) for the four subpopulations (i.e., Columbia-South, Frisby-Boulder, Columbia-North, Kinbasket-South) that make up our study population. A total of 46 (41 females, 5 males) mortalities of radio-collared caribou were recorded in our study area, 30 (27 females, 3 males) of which were categorized into either predation or non-predation (Table 1). Following Wittmer et al. (2005*b*), we then estimated the probability of a caribou dying as a result of predation adjusted for season length and used these estimates to describe the seasonal predation risk of caribou in the Columbia Mountains (Table 1). We pooled female and male mortality data because Wittmer et al. (2005*b*) did not find differences in causes or timing of mortalities between sexes across the distribution of mountain caribou.

Analysis of caribou range fidelity

A variety of methods have been used to assess site fidel-

Fig. 1. Current distribution of mountain caribou (*Rangifer tarandus caribou*) and location of the Columbia Mountains study area in southeastern British Columbia, Canada.

ity from radiolocations (White and Garrott 1990). The use of linear distances between all possible pairs of locations to describe spatial fidelity for individual animals has been shown to be more precise and less biased than commonly used home-range approaches (Garrott et al. 1987; Conner and Leopold 2001). We used the distances between all possible pairs of locations within each season to quantify within-season fidelity. To quantify among-year fidelity, we used a method similar to multi-response permutation procedures (MRPP) (Mielke et al. 1976; Zimmerman et al. 1985). For each season, the distances between all possible pairs of locations within a season were compared with the distances between all possible pairs of locations between 2 different years. If the within-season interlocation distances were equal to the among-year interlocation distances, then the animal did not change its area of use among years and was considered to show site fidelity among years. Individual caribou were used as the sampling unit to avoid pseudoreplication (Aebischer et al. 1993). However, because spring and calving seasons were very short and thus had very small numbers of locations per individual (Table 2), we restricted our

statistical analysis of fidelity behaviour to summer, early-winter, and late-winter seasons.

Distances among locations were analysed using a nested, mixed model ANOVA that treated individual caribou as a random effect nested in sex. Sex, season, and fidelity type (within-season, among-years) were treated as fixed effects. The distances among locations are reported as means ± 1 SE adjusted for random effects. Multiple comparisons between levels of significant effects were performed using Scheffé's procedure (Scheffé 1959) with least-squares means adjusted for other effects. Logistic regression between status (i.e., animals that survived summer and animals killed by predators during summer) and mean interlocation distances was used to measure the effects of within-season and among-year fidelity during summer (when predation risk was highest).

The repeatability, tau (τ), of movement behaviour (i.e., differences between among-year and within-season distances) was estimated as the ratio of among-individual variance to the total phenotypic variance (or the sum of within-individual and among-individual variances) following Lessels and

Table 2. Mean seasonal end dates, number of animal samples (n_A), and number of seasonal radiolocations (n_L) by year of mountain caribou in the Columbia Mountains, British Columbia 1992–2002.

	Calving			Summer			Early winter			Late winter			Spring		
Year	End	n_A	n_L	End	n_A	n_L	End	n_A	n_L	End	n_A	n_L	End	n_A	n_L
1991–1992										23 Apr.	22	99	20 May	21	42
1992–1993	10 June	22	53	30 Oct.	22	217	30 Jan.	22	191	25 Apr.	35	182	20 May	32	64
1993–1994	10 June	—	—	25 Oct.	31	272	26 Dec.*	31	216	21 Apr.	33	248	20 May	31	75
1994–1995	10 June	14	40	21 Oct.	31	213	02 Jan.	30	182	25 Apr.	34	205	20 May	31	62
1995–1996	10 June	31	91	13 Oct.	32	211	09 Jan.	29	125	25 Apr.	32	174	20 May	—	—
1996–1997	10 June	27	54	20 Oct.	28	207	15 Jan.	25	174	20 Apr.	34	154	20 May	34	68
1997–1998	10 June	1	2	29 Oct.	34	184	13 Jan.	26	181	15 Apr.	25	189	20 May	29	85
1998–1999	10 June	21	42	09 Oct.	27	166	16 Jan.	25	128	30 Apr.	22	206	20 May	—	—
1999–2000	10 June	4	8	23 Oct.	5	18	09 Jan.	4	13	22 Apr.	4	33	20 May	—	—
2000–2001	10 June	—	—	21 Oct.	6	21	03 Jan.	4	10	26 Apr.	7	28	20 May	—	—
2001–2002	10 June	—	—	14 Oct.	7	39	14 Jan.	7	22	02 Mar.	4	14			
Multi-year	10 June	55	290	21 Oct.	65	1548	11 Jan.	61	1242	23 Apr.	62	1532	20 May	50	396

*1993.

Table 3. Mean seasonal interlocation distances within and among years; P values adjusted using Scheffé's (1959) criteria.

Season	Time period	Mean distance (km)	Effect	Difference in mean distances (km)	df	Critical t value	Adjusted P value
Summer	Within	6.96±0.66	Among – within	2.32±0.91	96	2.54	0.274
	Among	9.28±0.71					
Early winter	Within	5.66±0.67	Among – within	5.51±0.93	96	5.93	*<0.001*
	Among	11.17±0.72					
Late winter	Within	3.94±0.66	Among – within	8.44±0.89	96	9.52	*<0.001*
	Among	12.38±0.67					

Note: Adjusted P values set in italic type are significant.

Boag (1987). A repeatability of 0 would indicate that all variance was within individuals over successive measurements, and a repeatability of 1 would indicate that repeated measurements of the same individual produced identical estimates, and the variance comes from differences between individuals.

Arboreal lichen availability and snow conditions

To determine the availability of arboreal lichen (*Bryoria* spp. and *Alectoria sarmentosa* (Ach.) Ach.) to caribou during early winter and late winter, its abundance was recorded at a sample of 68 randomly located sites. At these sites, three 2 m × 50 m (100 m²) transects were completed at a random direction radiating from a randomly located starting point following methods described by Terry et al. (2000). A 2 m transect width was chosen to reflect the search path of a foraging caribou that may take a small step to reach lichen-bearing branches. Along the transects lichen abundance was estimated visually using a standard 10 g lichen clump divided into two strata: (1) number of lichen clumps within approximate reach of caribou (0–1.80 m) from the snow surface and (2) number of lichen clumps above reach of caribou at present snowpack depths (1.80–3.60 m).

Mountain caribou foraging behaviour is influenced by snow accumulation (Rominger and Oldemeyer 1990). We measured snow depth at two permanent stations concurrent with each telemetry flight during winter. The low-elevation station representing early-winter conditions was at 915 m el-

evation in the ICH biogeoclimatic zone. The high-elevation station at 1830 m elevation was in the ESSF biogeoclimatic zone to measure snow accumulation typical for late-winter ranges. We analyzed the relationship between mean within-season interlocation distances, during both early winter and late winter, and snow depth using a general linear mixed model (GLMM) that treated individual caribou as a random effect. For hypothesis testing an $\alpha' = 0.05$ was used. Statistical analyses were performed using SAS® (SAS Institute Inc. 1995) and SYSTAT® (Systat Software Inc. 2002).

Results

The ANOVA testing the effect of individual caribou, sex, season, and fidelity type on interlocation distances indicated a significant third-order interaction among individual caribou, season, and fidelity type (nested, mixed model ANOVA: $Z = 6.47$, $P < 0.001$, $n = 65$), but no effect of sex (nested, mixed model ANOVA: $Z = 1.17$, $P = 0.121$, $n = 65$; females = 7.35 ± 0.35 km, males = 9.09 ± 0.75 km). Distances differed among individual caribou owing to inconsistencies in movement behaviour within individuals ($\tau = 0.036$).

The ANOVA also revealed a significant interaction between season and fidelity type (nested, mixed model ANOVA, $F_{[2,96]} = 19.66$, $P < 0.001$). The among-year interlocation distances of individual caribou were significantly larger than the within-season interlocation distances during early winter and late winter, suggesting low among-year fidelity

Table 4. Differences between mean seasonal interlocation distances within and among years; *P* values adjusted using Scheffé's (1959) criteria.

Effect*	Difference in mean distances (km)	df	Critical *t* value	Adjusted *P* value
SU (within) – EW (within)	1.30±0.68	96	1.90	0.607
SU (within) – LW (within)	3.02±0.67	96	4.50	*0.002*
EW (within) – LW (within)	1.72±0.68	96	2.51	0.2867
SU (among) – EW (among)	–1.89±0.74	96	–2.57	0.263
SU (among) – LW (among)	–3.10±0.72	96	–4.29	*0.004*
EW (among) – LW (among)	–1.21±0.73	96	–1.66	0.738

Note: Adjusted *P* values set in italic type are significant.
*SU, summer; EW, early winter; LW, late winter.

Table 5. Availability of arboreal lichen per tree during winter and random site in 10 g units at low-stem regions (0–1.80 m above snow) and high-stem regions (1.80–3.60 above snow) at low-elevation early-winter (ICH) habitat and high-elevation late-winter (ESSF) habitat.

	Season	
	Early winter	Late winter
Number of random 100 m² sites	29	39
Number of trees / site	22.25±11.41	23.18±11.32
Lichen load / tree		
Low stem	0.34±0.38	0.85±0.64
High stem	0.94±0.97	2.80±1.69
Lichen load / site		
Low stem	6.40±6.32	18.41±16.44
High stem	18.49±15.63	62.01±48.29

Note: Values are means ± SE.

to these seasonal ranges (Table 3). During late winter, the among-year interlocation distances of individual caribou were significantly larger than the among-year interlocation distances during summer (Table 4). All other among-year comparisons were not significant. All within-season interlocation distance comparisons were not significant except that summer distances were significantly larger than late-winter distances (Table 4). While not included in the statistical analysis, we also found a tendency of female caribou to return to familiar calving locations among-years (difference in mean distances among-year vs. within-season during calving was 5.47 ± 0.96 km).

The lichen load available to caribou per site was approximately three times higher on late-winter ranges than on early-winter ranges (Table 5). Within-season and among-year interlocation distances, however, were not significantly different between these seasons.

Over the 11-year study period, mean early-winter snow accumulation in December ranged from 26 to 99 cm at 915 m elevation and from 119 to 224 cm at 1830 m elevation. Late-winter snow accumulation in March ranged from 84 to 184 cm at 915 m elevation and from 190 to 425 cm at 1830 m elevation. Average within-season interlocation distances of individual caribou increased with increasing snow depth during early winter (GLMM: $F_{[1,140]} = 5.52$, $P = 0.020$, $y = 4.39 + 0.030x$) but not during late winter (GLMM: $F_{[1,165]} = 0.15$, $P = 0.696$, $y = 3.62 + 0.001x$).

Average within-season and among-year interlocation dis-

tances of caribou killed by predators during summer were not different from those that survived the summer season (logistic regression: within-season: $\chi^2_{[1,8]} = 0.0371$, $P = 0.847$, $y = 1.540 - 0.020x$; among-year: $\chi^2_{[1,8]} = 0.065$, $P = 0.799$, $y = 1.597 - 0.025x$).

Discussion

Ungulates have a variety of antipredator strategies that include space-use patterns to reduce encounters with predators. Seasonal migration beyond the range of resident predators is one predator-avoidance strategy used by some ungulates, including many caribou populations (e.g., Fryxell et al. 1988; Bergerud 1996). Populations that fail to separate themselves from resident predators by migration should exhibit alternative predator-avoidance strategies (Rettie and Messier 2000). Where predation is a major limiting factor of sedentary caribou, fidelity of caribou to seasonal ranges where they did survive in the past may be an effective predator-avoidance strategy (Schaefer et al. 2000; Rettie and Messier 2001). Continued seasonal use of areas where they were previously successful may be specifically critical during calving and summer when sedentary caribou are particularly vulnerable to predation (Bergerud and Page 1987; Rettie and Messier 1998).

We observed caribou exhibiting higher among-year fidelity to seasonal ranges during summer than during early winter and late winter. Fidelity behaviour was significantly different between summer (when caribou were most vulnerable to predators) and late winter when they are spatially separated from their main predators and thus experienced lower predation rates. These results are consistent with the hypothesis that fidelity to seasonal ranges represents a predator-avoidance strategy. However, within-season fidelity was greater during late winter when caribou experienced low predation rates than during summer when the majority of predation occurred, suggesting that other factors also influence site fidelity.

Lack of within-season fidelity during early winter indicates the possibility of a seasonal shift in limiting factors from predation to food during years with high snow accumulation. During most of the winter, mountain caribou feed largely on arboreal lichen (Rominger et al. 1996; Terry et al. 2000). The availability of arboreal lichen is greatly influenced by snow conditions and results in differences in caribou foraging behaviour between early winter and late winter. In early winter, the availability of arboreal lichen on standing trees was low. During this period, caribou forage

on relatively sparse amounts of lichen available on standing trees and are known to use lichen available on wind-thrown trees more intensively because the accessible lichen biomass is much higher than on standing trees (Rominger and Olde-meyer 1989; Terry et al. 2000). During early-winter periods with low snow accumulation, caribou dig through the snow to browse on the leaves of the evergreen shrub boxleaf, as well as feeding on lichen from standing and downed trees (Rominger and Oldemeyer 1990). Our results indicate that within-season interlocation distances during early winter increased with increasing snow depth, suggesting that caribou may have had to search more broadly for downed trees with an abundance of lichen because other foods are less available. Such variability of early winter range fidelity of caribou during our study is likely favoured in areas with substantial temporal variation in ecological conditions (Moran 1992).

In contrast to early-winter ranges, available arboreal lichen is abundant on standing trees on high-elevation late-winter ranges. Arboreal lichen (i.e., *Bryoria* spp.) cannot endure periods of prolonged wetting and therefore cannot persist on trees below the maximum snow depth of the previous years (Goward 1998). The availability of arboreal lichen is thus dependent on snow conditions that allow caribou access into the canopy of standing trees and is reflected by the variation in dates that elevational movements occurred. This abundance of food on late-winter ranges allows caribou to reduce their movements as indicated by the small within-season interlocation distances recorded during this season. Although caribou are well adapted for locomotion in snow (Fancy and Whitten 1987), reduced movements would decrease energy expenditure. The density of mountain caribou is currently very low (Wittmer et al. 2005*b*) and their concentrated feeding behaviour may not deplete the amount of available lichen to levels far below those of surrounding patches. However, in the past and in other ecosystems where caribou are more abundant, they likely deplete lichen (e.g., Messier et al. 1988). We suggest that the lack of among-year fidelity to both early- and late-winter ranges represents a foraging strategy with enough flexibility to enable individuals to avoid returning repetitively to the same areas where slow-growing lichens may become depleted.

Although we observed variation in site fidelity among individuals, the τ of 0.036 indicates that the variation resulted largely from inconsistent movement behaviour by individuals among years. This inconsistency of movement behaviour by individuals indicated that the maintenance of alternative phenotypes expressing site fidelity would not occur within this population of mountain caribou. Similar behavioural plasticity in migration patterns have been described in a variety of cervids including mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) (Brown 1992; Nicholson et al. 1997), Columbian black-tailed deer (*Odocoileus hemionus hemionus* (Rafinesque, 1817)) (McNay and Voller 1995), and white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) (Nelson and Mech 1991; Nelson 1995). In these species, some individuals migrate each year, others were never known to migrate, while others change migratory patterns depending on conditions. The plasticity in site fidelity that we found with mountain caribou revealed a similar pattern to other cervids in that individuals appear to show fidelity to seasonal ranges between some years, but not in others.

Unlike many other cervids (Nelson and Mech 1991; McNay and Voller 1995; Nicholson et al. 1997) however, variation in movement patterns was not correlated with survival.

Changes in the site fidelity expressed by an individual may depend on age, reproductive status, or the social structure of animals (Garrott et al. 1987; Newton 1993; Switzer 1993; Nelson and Mech 1999; Rettie and Messier 2001). We were unable to test for the effect of these factors because accurate estimates were unavailable. However, we suggest that the inconsistency of individual caribou use of seasonal ranges in our study may have been strongly influenced by the dynamic social structure of these animals. Within the wide distribution of suitable habitat, fidelity to specific ranges may be influenced by inconsistent association with conspecifics (Festa-Bianchet 1986; Bergerud 1996). It has been suggested that traditional selection of winter ranges by female white-tailed deer is based on family members following each other (Nelson and Mech 1999). The social organization of mountain caribou particularly during late summer, the breeding season, and winter appears to be flexible with groups varying in size and membership (B. McLellan, unpublished data). When mountain caribou make elevational migrations from mating areas in the autumn to early-winter ranges and then to high-elevation late-winter habitat, individuals may follow older or more experienced animals and thereby do not return annually to seasonal ranges previously used. For these highly gregarious animals, choosing membership in a group rather than returning to a known wintering area is likely an effective antipredator strategy.

The lack of site fidelity during both early winter and late winter has important implications for the conservation of threatened mountain caribou. During winter, these animals rely on old forests that are highly valuable to the forest industry; thus, their conservation has significant economic and social costs. A major component of the current conservation strategy involves first delineating areas to be managed for caribou winter-range requirements. Once the area is delineated, then landscape and stand management prescriptions that are thought to be compatible with caribou habitat requirements are deployed (Stevenson et al. 2001). Delineating where forests will be managed as caribou winter range is based on telemetry locations from a sample of the population, as well as recent incidental sightings. Because caribou show a lack of fidelity to winter ranges, areas of suitable habitat that have not recently been used by caribou may become significant in the future. Managers delineating where habitat will be managed for caribou should not necessarily exclude areas of suitable habitat only because of a lack of recent use.

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