Selection of calving sites by Porcupine herd caribou

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Characteristics of 305 calving sites used by 131 different radio-collared caribou (*Rangifer tarandus*) cows from the Porcupine herd in northeastern Alaska and the northern Yukon Territory were investigated between 1983 and 1990 to determine the factors influencing calving site selection. Cows selected areas north of the foothills primarily to reduce exposure of calves to predators. Sites dominated by *Eriophorum* tussocks were selected secondarily for access to newly emerging vegetation. Highest calf mortality occurred in years when snowmelt was relatively late and calving occurred closer to the foothills and in Canada. Industrial development of the coastal plain of the Arctic National Wildlife Refuge could increase calf mortality if calving were displaced south and east of potential development areas.

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Les caractéristiques de 305 sites de mise-bas utilisés par 131 femelles du Caribou (*Ranfiger tarandus*) munies d'un collier émetteur, au sein du troupeau de Porcupine, dans le nord-est de l'Alaska et le nord du Yukon, ont été relevées de 1983 à 1990 afin de déterminer quels facteurs influencent le choix du site de mise-bas. Les femelles choisissaient des zones situées au nord des contreforts surtout pour diminuer l'exposition des petits aux prédateurs. Les endroits dominés par les touffes d'*Eriophorum* étaient choisis ensuite parce qu'ils permettaient l'accès à de la végétation fraîche. La mortalité des petits s'est avérée particulièrement élevée au cours des années où la fonte des neiges s'est produite relativement tard et où la mise-bas s'est faite plus près des contreforts et à l'intérieur du Canada. Le développement industriel de la plaine côtière de la réserve Arctic National Wildlife Refuge pourrait bien augmenter la mortalité des petits caribous si la mise-bas est déplacée vers le sud et vers l'est des zones potentielles de développement.

[Traduit par la rédaction]

Introduction

The U.S. Congress directed the U.S. Department of the Interior in 1980 to conduct biological and geological studies on the coastal plain of the Arctic National Wildlife Refuge (ANWR) in northeastern Alaska to provide information necessary for future management of the area. The "1002 area" of the coastal plain contains important fish and wildlife habitats, including the most frequently used calving and post-calving habitats for the Porcupine caribou herd (PCH; *Rangifer tarandus granti*). Unfortunately, the coastal plain is also generally considered the most promising onshore petroleum exploration area in the United States (Clough *et al.* 1987). After completing a 5-year baseline study program, the Department of the Interior concluded that major impacts to the PCH could occur if a major oil discovery is located and developed in the 1002 area (Clough *et al.* 1987).

The U.S. Fish and Wildlife Service and the Alaska Department of Fish and Game have conducted cooperative studies since 1982 on the PCH (n = 178 000, 1989) and the adjacent Central Arctic herd (CAH, n = 13 000, 1983) to assess the potential effects of petroleum exploration and development on caribou. A major concern based on studies of the CAH (e.g., Whitten and Cameron 1983; Dau and Cameron 1986) is that development of the 1002 area can displace parturient cows from traditional calving areas, thereby increasing mortality on calves or reducing foraging opportunities for cows and calves. The purpose of this study was to determine why PCH caribou select certain areas for calving and thereby provide information for assessing and mitigating potential effects of oil development on the PCH during the calving period.

Methods

The PCH annually migrates between winter ranges in northeastern Alaska and northwestern Canada and its calving grounds along the Beaufort Sea coast. Detailed descriptions of the range and seasonal movement patterns of the PCH can be found in Garner and Reynolds (1986) and Fancy *et al.* (1989).

Caribou capture and radio-tracking flights

Beginning in 1981, standard VHF radio-collars were deployed on adult and yearling female caribou using methods described by Fancy *et al.* (1989). Beginning in April 1988, however, all adult caribou were immobilized, using a mixture of 3 mg carfentanil citrate (Wildlife Laboratories, Fort Collins, CO) and 7.5 mg acepromazine maleate with Naloxone (450 mg, Wildlife Laboratories) as the antagonist. Individuals were recaptured as needed every 3–5 years to replace transmitters before batteries were exhausted.

Mortality-sensing transmitters were deployed on 118 calves on 2–3 June 1988, using methods described by Garner *et al.* (1985). Previous experience with capturing calves (K. R. Whitten, G. W. Garner, F. J. Mauer, and R. B. Harris, unpublished data) indicated that calves that were abandoned at the time of capture subsequently died within 48 h. Because we could not distinguish between natural and capture-induced abandonment, and inclement weather precluded observations of collared calves for 2 d following capture, we excluded the 14 calves that died within 48 h of capture from further analysis.

Satellite transmitters compatible with the Argos Data Collection and Location System (Fancy *et al.* 1988, 1989) were deployed on 33 PCH cows between April 1985 and August 1990. Data were received monthly from Service Argos (Landover, MD) and processed as described by Fancy *et al.* (1988, 1989). The satellite transmitter package (Telonics, Inc., Mesa, AZ) weighed 1.6 kg (including a VHF radio transmitter to locate the caribou from an aircraft) and had a 1-year battery life. Individual caribou were monitored for ≤5 years by replacing their transmitters annually. Transmitters were programmed to operate 6 $\text{h} \cdot \text{d}^{-1}$ or 6 $\text{h} \cdot 2\ \text{d}^{-1}$, and provided three or four locations per

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day of operation. Mean location errors were 760 m for generation 2 transmitters (68% of locations used in this study) and 480 m for the newer generation-3 transmitters (32% of locations, Fancy *et al.* 1989).

Radio-collared cows ($n = 131$, including those also monitored by satellite) were observed from a fixed-wing aircraft at 1- to 3-d intervals between ca. 28 May and 30 June each year to determine date and location of calving and the fate of their calves. Calving dates and neonatal survival for calves of collared cows were determined from a combination of criteria, including presence of a calf at heel, presence or absence of hard antlers, udder distention, or observations of cows standing over dead calves (Whitten 1991). Cows not showing any overt signs of pregnancy, but not obviously barren (e.g., already possessing velvet antlers), were relocated at least weekly until 30 June to ensure that no births were missed. Each cow that had apparently lost her calf was observed at least one additional time during the calving period to confirm that no calf was present.

We conducted radio-tracking flights covering the entire range of the PCH, using a fixed-wing aircraft to relocate collared caribou, ca. 2–5 times each year between October and early May. Locations during the period between early January and early April, when cows were most sedentary (Fancy *et al.* 1989; S. G. Fancy and K. R. Whitten, unpublished data), were classified into one of three categories (Alaska, Richardson Mountains, or Ogilvie Mountains) to determine relationships between wintering areas and calving sites. For the purpose of this analysis, all wintering locations in the Yukon that were south and west of the Porcupine and Eagle rivers were included in the Ogilvie Mountains category, whereas locations east of the Eagle River and along the axis of the Richardson Mountains were included in the Richardson Mountains category.

Calving distribution

Locations where radio-collared cows were first observed with a calf during intensive monitoring flights each year were used as calving sites. Calving sites were digitized and entered into the ARC/INFO geographic information system (GIS) for analysis of calving distribution and calving site selection. Calving sites for 54 cows that calved in widely scattered locations in the mountains or west of the Katakturuk River were excluded from analysis. We tested the hypothesis that the distribution of calving sites on the coastal plain was random by arbitrarily partitioning the coastal plain into six blocks of similar area (Fig. 1, blocks A–F) to determine the number of calving sites per square kilometre expected within each block, if sites were evenly distributed. Blocks were delineated on the east and west by major rivers or the Alaska–Yukon border and on the north by the coastline. The southern boundaries of the blocks were drawn where the coastal plain and foothills give rise to the mountains of the Brooks and British ranges. The area within each block was determined using the ARC/INFO geographic information system.

Calving site selection

Factors influencing calving site selection were determined by comparing attributes of calving sites for 1983–1990 with those of randomly selected sites within the area bounded by the outermost calving sites (including those in the mountains, but excluding two cows that calved with the CAH; see Fig. 1). We excluded sites where 16 cows were first observed with their calves because each calf was estimated to be >5 d old (based on their size and behavior) and might have been born several kilometres from the location. (These 16 cows were used in the calving distribution analysis above because they were located within the same block before and after calving.) Logistic regression analyses (McDonald *et al.* 1991) were conducted to determine which attributes best discriminated between 305 sites selected for calving and 305 randomly selected sites on the calving grounds.

We determined the elevation, percent slope, and landcover type for each calving site and random site using digital maps with a resolution (i.e., pixel size) of 50 × 50 m in Alaska (U.S.G.S. Eros Data Center, Anchorage, AK; Garner and Reynolds 1987, p. 60) or 100 × 100 m in Canada (Nixon *et al.* 1991). Landcover maps in both Alaska and Canada were based on LANDSAT multispectral scanner data; however, the use of different classification algorithms for each map precluded direct comparisons. Snow cover at each site on 1 June each year (i.e., <25, 25–75, and >75% snow cover) was determined from TIROS-N AVHRR imagery (Eastland *et al.* 1989). For each site, we also recorded latitude and longitude (in UTM coordinates), shortest distance to the coast, shortest distance to a major river, shortest distance to the foothills (i.e., the southern boundary of the blocks in Fig. 1), proportion of area within a 1-km radius that was dominated by tussock tundra, and proportion of area within a 1-km radius that contained landcover types dominated by *Dryas* vegetation types. Distance to the foothills was negative for sites south of the foothills line. *Dryas* vegetation types included dry prostrate dwarf scrub and moist prostrate dwarf scrub types in Alaska and the *Dryas* sedge type in Canada.

Calving site fidelity

We determined whether individual cows showed fidelity to calving sites in different years by comparing distances between all calving sites for each radio-collared cow between 1983 and 1990 with a distribution of distances for random sites obtained through computer simulation. The number of calving sites for each cow varied from 1 to 7 (mean ± SD = 2.24 ± 1.45, $n = 131$); separate analyses were required depending on the number of calving sites included. We calculated the shortest distance between any two calving sites and the shortest distance connecting all calving sites for each cow. Then we generated 8000 sets (i.e., two to seven locations) of random sites from an area delineated by the outermost calving sites (Fig. 1) and calculated the above distance parameters for each simulation. Differences between cumulative frequency distributions of observed and simulated distances were compared using the Kolmogorov–Smirnov test for goodness of fit (Sokal and Rohlf 1969, p. 573).

Calf mortality

Relationships between habitat and mortality risk were investigated by comparing attributes of sites where radio-collared cows were observed with live calves with attributes of sites where cows lost calves. The site where a cow lost a calf was considered to be the site where she was first observed without a calf. We excluded all locations in Canada from this analysis because (*i*) if displacement occurred, it would most likely be to areas immediately south and east of the 1002 boundary; (*ii*) different landcover classification schemes were used in Alaska and Canada, precluding direct comparisons of landcover data; (*iii*) no landcover data were available in Canada for the area north and west of the Malcolm River; and (*iv*) digital elevation and slope data were not available for the northern Yukon, and obtaining these data directly from maps for all locations in Canada could be a very time-consuming process. We randomly selected only one location each year during late May through June 1983–1990 where each cow was first observed with a calf, because serial observations of individual cows with calves may not be independent.

Results

Calving distribution

The distribution of calving sites among the six designated blocks (Fig. 1) on the coastal plain in 1983–1990 was non-random (Table 1, $X^2 = 77.0$, df = 5, $P < 0.0001$). The area between the Hulahula River and the international border (Fig. 1, blocks B, C, and D) contained 1.5 times as many calving sites per square kilometre as expected, whereas the coastal plain east of the international border contained only 0.7 times as many sites as expected. Selection for areas west of the Aichilik River in Fig. 1, blocks B and C, where much of the area is at higher latitude, appears strong even though complete snow cover remains near the coast in most years. A greater proportion of the coastal plain east of the Aichilik River is snow-free or has mottled snow during the early calving period (Eastland *et al.*, 1989; S. G. Fancy and K. R. Whitten, unpublished data).

The east–west distribution of calving sites was related to the herd's winter distribution. Cows that wintered in the Richardson

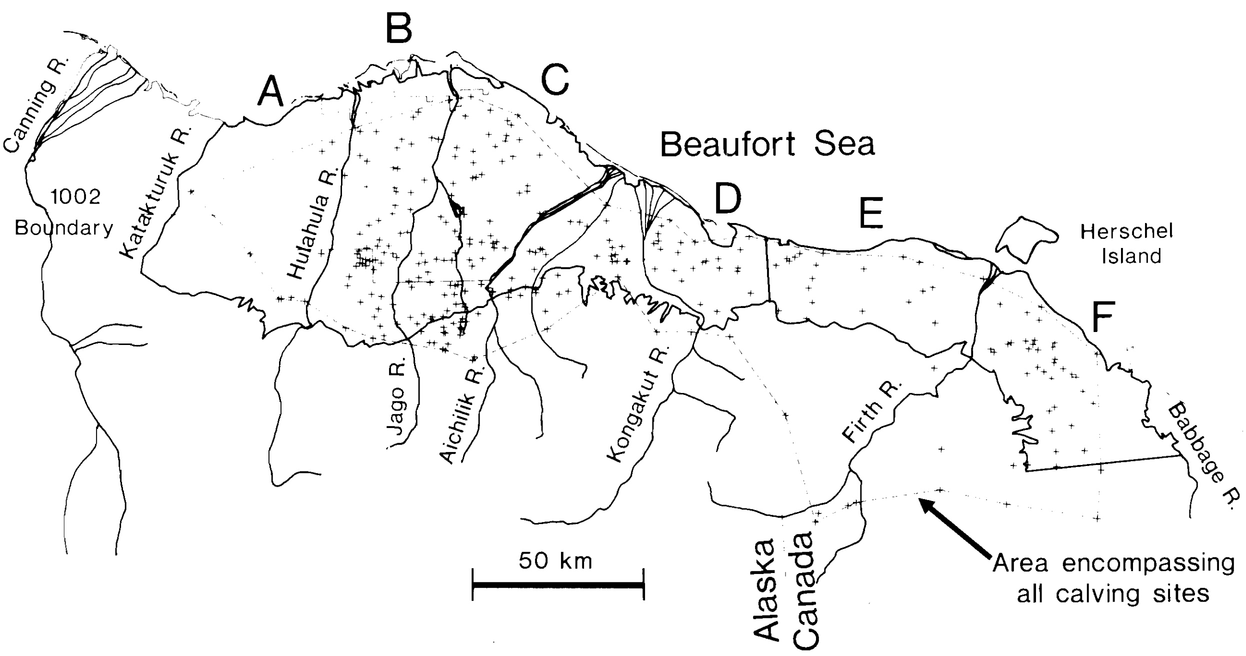

FIG. 1. Calving grounds of the Porcupine herd, showing areas used in analyses of calving distribution, calving site selection, and fidelity. Blocks A–F were used to test for random distribution of calving sites on the coastal plain. The area encompassing all sites where radio-collared cows were first observed with a calf in 1983–1990 (sites are marked by crosses; area is delineated by a dash–dot line) was used in analyses of calving site selection and fidelity.

TABLE 1. Distribution of 267 calving sites in 1983–1990 on the coastal plain of northeastern Alaska and northern Yukon

Block	% of area	Sites observed	Sites expected	Observed: expected	Selection probability[a]
A	21.37	11	57.1	0.19	0.032
B	15.61	66	41.7	1.58	0.259
C	19.26	70	51.4	1.36	0.223
D	16.03	65	42.8	1.52	0.249
E	12.49	18	33.3	0.54	0.088
F	15.24	37	40.7	0.91	0.149

NOTE: Blocks A–F refer to areas shown in Fig. 1.

[a] Relative probability that block will be selected as a calving site.

Mountains calved farther west than those that wintered in Alaska or the Ogilvie Mountains (Fig. 2). In most years, the windswept ridges of the Richardson Mountains allow caribou to begin spring migration and arrive on the calving grounds earlier than cows wintering in other areas with deeper snow (Thompson 1978). We found a significant correlation between date of arrival on the calving grounds and longitude of calving sites (early arriving cows calved farther west) for cows tracked by satellite (Spearman's rank correlation; $n = 39$, $r = 0.646$, $P < 0.001$). However, we found no relationship between arrival date on the calving grounds and date of calving (Spearman's rank correlation; $n = 39$, $r = 0.25$, $P > 0.20$).

Calving site selection

The movements of pregnant cows tracked by satellite between 1985 and 1989 averaged $>10\ \mathrm{km \cdot d^{-1}}$ in a northwest direction during the 12-d period before calving (Table 2). During the 6-d period beginning at calving, cows moved $<5\ \mathrm{km \cdot d^{-1}}$ and movement direction was random. Daily relocations of radio-collared cows indicated that most cows selected a calving site on or 1–3 d before their calving date and remained in that general area for 1–2 weeks. The 24-h activity index, an independent measure of caribou movement (Fancy *et al.* 1989), followed a pattern similar to rates of movement (Table 2).

Selection for landcover types characterized by *Eriophorum* tussock tundra was apparent in both Alaska and Canada (Table 3). In Alaska, 55% of calving sites were located in moist graminoid tundra or mesic erect dwarf scrub types characterized by *E. vaginatum* (Garner and Reynolds 1987, p. 60), whereas only 40% of the randomly selected sites were located in these types. In Canada, 54% of calving sites were located in tussock tundra types, compared with 30% for randomly selected sites. When landcover types in both Alaska and Canada were reclassified as tussock versus nontussock types and combined, we found a highly significant selection for tussock types at calving (Fisher's exact test, $P < 0.0001$).

Logistic regression was used to determine the set of attributes that best discriminated between sites selected for calving and randomly selected sites. Attributes were included in the model if their regression coefficient was significantly different from zero

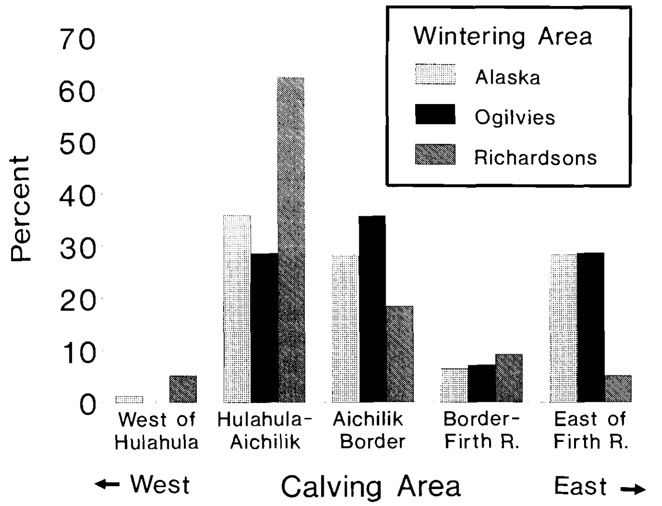

FIG. 2. Relationship between locations of calving sites for 131 individual cows and their previous wintering area.

TABLE 2. Movement and activity (mean ± SE) of parturient cows during 3-d intervals relative to their date of calving

Days relative to calving date	n	Distance travelled (km/d)	24-h activity index	Mean direction (°)	
				Azimuth	P
−12 to −10	42	12.8±1.7	13 713 ± 1270	339	***
−9 to −7	42	13.0±1.5	13 508 ± 1338	326	***
−6 to −4	42	11.9±1.1	13 469 ± 1298	303	***
−3 to −1	42	10.3±1.0	11 917 ± 1098	289	***
0 to +2	40	4.7±0.5	8 316 ± 882	290	ns
+3 to +5	41	4.2±0.6	7 524 ± 839	111	ns
+6 to +8	41	6.9±2.3	10 037 ± 1179	244	ns
+9 to +11	39	5.4±0.5	11 382 ± 1223	212	ns
+12 to +14	38	7.0±0.7	12 700 ± 1347	233	ns
+15 to +17	35	9.0±1.2	14 443 ± 1533	261	ns
+18 to +20	34	9.3±0.9	15 634 ± 1552	270	ns
+21 to +23	33	10.9±1.0	16 994 ± 1924	308	**
+24 to +26	30	13.9±1.2	19 624 ± 1999	317	ns

NOTE: Data were collected between 1985 and 1989 using the Argos Data Collection and Location System (Fancy *et al.* 1989). ns, direction not significant; Rayleigh test (Batschelet 1981, p. 54); **, $P < 0.005$; ***, $P < 0.001$.

at the 95% confidence level (χ^2-test with df = 1; BMDP 1988). The analysis yielded the model ($\chi^2 = 53.84$, df = 3, $P < 0.0001$)

$$w(x_1,x_2,x_3) = \exp(1.571x_1 + 0.015x_2 - 2.830x_3)$$

where x_1 is the proportion of area within 1 km of a site dominated by *Eriophorum* tussocks, x_2 is the distance between a site and the foothills, and x_3 is percent slope. This selection function can be solved for any site to determine the relative probability of that site being selected for calving (McDonald *et al.* 1991). For example, a site 20 km north of the foothills characterized by 100% tussock tundra within 1 km and a slope of 2% is 29 times more likely to be selected for calving than a site 20 km south of the foothills line that has no tussocks and a slope of 45%. Compared with randomly selected sites, calving sites were significantly farther west, farther north, at lower elevations on gentler slopes, closer to major rivers, farther from the foothills, and had more snow and tussock tundra (Table 4).

TABLE 3. Percent occurrence of landcover types at calving sites and randomly selected sites in Alaska and Canada

Location	Randomly selected sites (n = 277)	Calving sites (n = 284)
Alaska		
Barren floodplain	1.7	0.4
Barren scree	1.7	0.4
Dry prostrate dwarf scrub	6.9	3.0
Moist prostrate dwarf scrub	22.4	20.4
Mesic erect dwarf scrub[a]	18.4	24.3
Moist graminoid tundra[a]	21.3	30.9
Moist–wet tundra complex	13.8	10.9
Wet graminoid	10.3	8.3
Very wet graminoid	0.0	0.9
Scarcely vegetated	3.5	0.5
Canada		
Dryas–sedge	5.8	3.7
Dense shrub slope	2.9	1.9
Open shrub heath	12.6	20.4
Low shrub tundra	1.0	0.0
Lichen–barren	30.1	9.3
Tussock tundra with 0–15% shrubs[a]	10.7	22.2
Tussock tundra with 16–25% shrubs[a]	12.6	24.1
Tussock tundra with 26–35% shrubs[a]	6.8	7.4
Unvegetated	16.5	7.4
Alluvial	1.0	3.6

NOTE: No landcover data were available for the area in Canada west of the Malcolm River.

[a] Landcover types dominated by tussock tundra.

Fidelity to calving sites

Although PCH cows showed a high fidelity to the calving grounds between the Katakturuk and Babbage rivers, they did not return to the same sites on the calving grounds each year to calve (Table 5). None of the cumulative frequency distributions of distances between calving sites were different (Kolmogorov–Smirnov test; $P > 0.20$) from the distributions for randomly selected sites. Thus, although cows select areas with certain characteristics (e.g., away from the foothills, tussock tundra) for calving, annual variation in wintering areas and migration routes used by individual cows and variation in snow cover during migration and on the calving grounds make it unlikely that a cow will calve near the same exact location each year.

Calf mortality

Fourteen (13.5%) of 104 calves collared in 1988 that survived >48 h after capture died by 30 June (Table 6). As in previous years, June mortality for calves of radio-collared cows in 1988 was higher than that for collared calves. This result is expected as calf mortality is greatest within 48 h of birth, and many calves are stillborn or die before they can be collared. After adjusting for perinatal moralities (i.e., excluding deaths that occurred <48 h after birth), similar rates of death were obtained for collared calves and calves of collared cows (Table 6).

In our 1988 study of collared calves, no significant difference ($\chi^2 = 0.85$; $P > 0.10$) was found between mortality of calves originally collared within the 1002 area (9 of 55) and those collared south and southeast of the 1002 area (5 of 49). Snowmelt on the coastal plain in 1988 was the latest on record (Eastland *et al.* 1989; S. G. Fancy and K. R. Whitten, unpublished data), and a relatively high proportion of calves present

TABLE 4. Characteristics (mean ± SE) of 305 calving sites and 305 randomly selected sites within the calving grounds, 1983–1990

Variable	Random sites	Calving sites	P^a
Longitude (UTM)	706 393 ± 4065	682 689 ± 3805	0.0001
Latitude (UTM)	7 717 719 ± 1505	7 725 461 ± 1252	0.0001
Elevation (m)	365 ± 18	260 ± 14	0.0001
Slope (%)	9.0 ± 0.7	4.9 ± 0.4	0.0001
Snow cover (class)	2.3 ± 0.1	2.1 ± 0.1	0.0017
Distance to coast (km)	30.2 ± 1.0	30.5 ± 1.1	0.817
Distance to river (km)	4.1 ± 0.3	2.9 ± 0.2	0.002
Distance to foothills (km)	7.4 ± 1.2	14.7 ± 1.0	0.0001
Tussocks <1 km (%)	35.0 ± 1.9	48.6 ± 2.0	0.0001
Dryas <1 km (%)	20.5 ± 1.2	20.7 ± 1.1	0.899

NOTE: No vegetation data were available for 21 calving sites and 28 randomly selected sites.

[a] *t*-test for difference between means.

TABLE 5. Comparisons of distances (mean ± SE) between calving sites of radio-collared cows located in 2–7 different years with distances between randomly selected sites

No. of years	n	Shortest distance between two sites (km)			Shortest distance connecting all sites (km)		
		Observed	Random	$D_{\max}{}^a$	Observed	Random	$D_{\max}{}^a$
2	43	67.1±49.1	93.6±59.7	0.097			
3	19	27.9±12.0	38.9±21.7	0.266	125.0±58.7	145.3±55.1	0.111
4	7	26.2±10.0	26.2±14.3	0.202	192.8±27.4	179.2±48.5	0.184
5	6	17.6±8.6	19.8±10.7	0.145	179.6±47.9	206.7±43.8	0.201
6	5	7.2±2.7	15.7±8.4	0.297	176.3±28.5	229.7±42.6	0.373
7	2	5.9±1.4	13.2±7.1	0.424	229.1±105.3	250.6±42.2	0.498

NOTE: Cumulative frequency distributions of distances between calving sites and 8000 sets of randomly selected sites were compared using the Kolmogorov–Smirnov test (Sokal and Rohlf 1969, p. 573).

[a] All values are nonsignificant ($P > 0.10$); Kolmogorov–Smirnov test statistic.

within the snow-covered 1002 area was captured compared with those captured outside the 1002 area.

Locations where cows that lost calves were first observed without a calf were significantly farther south and closer to the foothills than locations where cows were observed with live calves (Table 7).

Discussion

Concentrations of cows have used the coastal plain between the Hulahula and Aichilik rivers for calving in 17 of the past 19 years, but the location of areas having the highest concentration of caribou during calving varies annually. We believe that most of this annual variation can be explained by variation in snow cover, both on the calving grounds and on winter range. In years of relatively early snowmelt, the highest concentration of calving sites has consistently been located in Alaska west of the Aichilik River and close to the coast, whereas in all years when snowmelt was relatively late, calving sites were concentrated east of the Aichilik River or in the foothills.

Primary wintering areas for the PCH occur in areas of relatively shallow snow, and snow has been shown to influence the initiation and progress of spring migration (Thompson and Roseneau 1978; Garner and Reynolds 1986; D. E. Russell, A. M. Martell, and W. A. Nixon, unpublished data). Cows wintering on wind-blown ridges of the Richardson Mountains are least likely to encounter deep snow that may delay arrival on the calving grounds; these cows tend to calve farther west than cows wintering in Alaska or the Ogilvie Mountains. Cows delayed by deep snow during spring migration may calve before they reach an area with the combination of factors (e.g., greater distance from foothills, tussock tundra, lower elevations, gentler slopes) associated with most calving sites.

TABLE 6. Percent mortality of collared calves or calves of collared cows during late May and June 1983–1990

Year	Calves of collared cows		Collared calves (adjusted^a)
	Overall	Adjusted^a	
1983	35 (20)	7 (14)	9 (59)
1984	16 (25)	10 (21)	7 (60)
1985	35 (43)	10 (30)	15 (60)
1986	—	—	—
1987	34 (41)	18 (33)	—
1988	31 (71)	12 (51)	13 (104)
1989	26 (58)	9 (47)	—
1990	9 (54)	0 (52)	—

NOTE: Data for 1983–1985 were obtained from K. R. Whitten, G. W. Garner, F. J. Mauer, and R. B. Harris (unpublished data). Relocations in 1986 were too infrequent to calculate death rates. Values in parentheses are sample sizes.

[a] Adjusted mortality includes only those calves known to have been >48 h old when last observed alive. Perinatal and possible perinatal mortalities are excluded.

Once they reach the coastal plain, parturient cows continue to

TABLE 7. Characteristics (mean ± SE) of sites within Alaska where calves of radio-collared cows were observed alive and sites where cows that lost calves (including perinatal mortalities) were first observed without their calf during late May and June 1983–1990

Variable	Cows with calves (n = 263)	Lost calves (n = 42)	P^a
Longitude (UTM)	648 849 ± 2442	655 658 ± 4800	0.211
Latitude (UTM)	7 732 351 ± 1160	7 725 792 ± 2513	0.034
Elevation (m)	272 ± 15	316 ± 35	0.292
Slope (%)	6.6 ± 0.8	4.8 ± 1.2	0.194
Distance to coast (km)	31.9 ± 1.2	38.0 ± 3.0	0.065
Distance to river (km)	2.5 ± 0.1	2.0 ± 0.3	0.129
Distance to foothills (km)	18.4 ± 1.1	10.4 ± 2.1	0.001
Tussocks <1 km (%)	45.0 ± 2.2	45.9 ± 5.3	0.881
Dryas <1 km (%)	26.1 ± 1.1	19.7 ± 2.5	0.041
Wet–very wet graminoid <1 km (%)	23.8 ± 1.8	26.2 ± 4.2	0.618
Barrens <1 km (%)	5.0 ± 0.6	8.2 ± 1.7	0.068

[a] t-test for difference between means.

travel 10–12 km · d^{-1} until they bear their calf. In most years, they appear to follow a band of advancing partial snowmelt towards the north and west, and we believe that the apparent selection for areas dominated by tussock tundra during calving is an artifact of their association with this band of mottled snow. The microtopography of *Eriophorum* tussocks promotes melting, evaporative loss of snow cover, and early growth of vegetation (Lent 1980), and in most years when cows arrive on the coastal plain, the northernmost patches of bare ground are associated with tussock tundra landcover types (Eastland *et al.* 1989). Areas north of the melt line are probably not used because foraging is difficult through the heavy, wet snow, and green vegetation and dry sites for calving are lacking.

Our results are consistent with the hypothesis that within the constraints of snow cover and the timing of their arrival on the calving grounds, cows select calving sites primarily to reduce exposure of calves to predators. There is a secondary benefit in being able to take advantage of the first green vegetation (primarily *Eriophorum vaginatum*) and bare patches available on the coastal plain. Bears (*Ursus arctos*), wolves (*Canis lupus*), and golden eagles (*Aquila chrysaetos*) appear to be more abundant in the foothills and mountains than on the coastal plain during the calving season (S. G. Fancy, personal observation), and radio-tracking studies of predators have confirmed that most predators remain south of the coastal plain during calving (Young *et al.* 1990). Our results and those of an earlier calf mortality study (K. R. Whitten, G. W. Garner, F. J. Mauer, and R. B. Harris, unpublished data) indicate that mortality risk (i.e, the probability of a calf dying) during June is higher for calves that spend time closer to foothills or mountains than for those farther north on the coastal plain.

The rate of calf deaths is greatest within 48 h of birth (K. R. Whitten, G. W. Garner, F. J. Mauer, and R. B. Harris, unpublished data; this study).This perinatal mortality appears to be influenced more by maternal or fetal condition and behavior than location of the calving sites. Roffe (1990) found that 78% (43/55) of PCH calves (<48 h old) for which he determined cause of death were stillborn or died of emaciation or malnutrition. However, his results may underestimate predation as a mortality factor during the perinatal period because only carcasses that were largely intact were necropsied, and all carcasses were collected from a relatively predator-free calving concentration area on the coastal plain. The association of perinatal and other calf mortalities with the foothills that we found may be partly explained if cows in poor condition or with poor maternal instincts tended to calve on the periphery of the main calving concentration. However, very young calves are particularly vulnerable to predators (Miller *et al.* 1988), and perinatal deaths in the foothills and mountains could also have been due to predation. Following the prenatal period, predation is involved in the majority of calf mortalities in the PCH. K. R. Whitten, G. W. Garner, F. J. Mauer, and R. B. Harris (unpublished data) reported that predation was involved in 13 of 18 collared calf mortalities, and mortality sites where predators were involved were at higher elevations than sites where calves died for other reasons (e.g., disease, drowning, malnutrition).

Our contention that cows select calving sites primarily to reduce exposure of calves to predators and secondarily for their nutritional value is based on several factors. During calving, barren cows and bulls occur closer to the foothills and mountains where plant phenology is more advanced and foraging opportunities are presumably superior (Whitten and Cameron 1980). Furthermore, in years of relatively early snowmelt, as in 1990, many cows calve north of areas dominated by tussock tundra, thereby decreasing foraging opportunities but increasing the distance from predators. Finally, simulation studies indicate that cows have an energy deficit during early calving because the biomass of *Eriophorum* and other forage species is low (Fancy 1986).

However, tussock tundra may provide the best foraging opportunity among vegetation types available on the coastal plain. Flower buds of *E. vaginatum* are highly digestible and may be an important source of nitrogen and minerals for parturient cows (Kuropat and Bryant 1980; Fancy *et al.* 1989; D. E. Russell, A. M. Martell, and W. A. Nixon, unpublished data). The biomass and digestibility of *Eriophorum* within the 1002 area are higher than in peripheral areas to the south and east (Felix *et al.* 1989; White *et al.* 1989; Christensen *et al.* 1990).

The selective advantage of calving in the northwestern portion of the calving grounds is reflected in annual rates of calf death. Snowmelt on the Alaskan portion of the calving grounds in 1988 and 1987 was the latest and second latest, respectively, recorded in 20 years. In 1987, >67% of calves were born in Canada, and calves born in Alaska were born relatively close to the foothills. In 1988, most calving occurred in the foothills and mountains south of the 1002 area boundary. In contrast, calving in 1989 and 1990 was concentrated north of the foothills and west of the Aichilik River. Snowmelt in 1990 was the earliest ever recorded; by 28 May, the entire coastal plain was >95% snow-free. Overall and adjusted rates of death for calves during 1987 and 1988 were greater than in 1989 and 1990, when calving was concentrated farther from the foothills (Table 6).

Our results suggest that displacement of calving caribou from the 1002 area towards areas of higher predator abundance could result in increased calf mortality. However, if the PCH continues to increase without a proportional increase in predator numbers, the proportion of calves killed by predators could decrease even if calving were displaced closer to areas of higher predator abundance. Additional studies are needed on the relationship between caribou distribution during calving and the potential numerical and functional response of predator populations. Results will be used in simulation models of PCH population dynamics to estimate the potential effects of an oil and gas leasing program in ANWR on the PCH.

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