

HABITAT USE BY FEMALE CARIBOU: TRADEOFFS ASSOCIATED WITH PARTURITION

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Abstract: We compared habitat use, forage characteristics, and group size among preparturient, parturient, and nonparturient female caribou (*Rangifer tarandus*) during and after the birthing season to test hypotheses involving acquisition of forage and risk of predation. We monitored 39 radiocollared females from the Mentasta caribou herd, Alaska, in 1994 and 40 animals in 1995. Group size of females giving birth at higher elevations was smaller ($P < 0.01$) than females without young that occurred at lower elevations at peak parturition; that difference did not persist into post parturition ($P > 0.5$). During peak parturition, females with young used sites with fewer predators ($P < 0.05$), a lower abundance of forage ($P < 0.05$), but with variable forage quality compared with those sites used by females without young. We hypothesized that parturient females used birth sites that lowered risk of predation, and traded-off forage abundance for increased safety. Nonetheless, few differences existed between parturient and nonparturient females in composition of diet or in indices of diet quality; we could not demonstrate a nutritional cost to maternal females from our analyses. We suggest that increasing population density might intensify intraspecific competition among females for birth sites, and thereby increase nutritional costs of using high-elevation areas with less forage but fewer predators.

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Acquiring resources necessary to survive and reproduce is a major component of fitness and

constrains the types of habitats used by mammals (Fryxell and Sinclair 1988, White et al. 1997, Bowyer et al. 1998a). Among large herbivores, habitat selection often is related to availability and quality of forage (Klein 1970, Skogland 1980, Bowyer 1986, Albon and Langvatn 1992, Cameron et al. 1993), but also can depend upon other factors, such as mineral re-

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quirements (Belovsky and Jordan 1981), insect harassment (Mörschel and Klein 1997), exposure to adverse weather (Miller et al. 1985, Ion and Kershaw 1989), and predation (Bergerud et al. 1984, Festa-Bianchet 1988, Bleich et al. 1997).

Constraints on foraging are magnified for females at parturition because neonates are vulnerable to predation, and lactation increases nutrient demands (White and Luick 1984; Bowyer 1991; Rachlow and Bowyer 1994, 1998). Indeed, maternal condition can have strong effects on growth and survivorship of young cervids (Skogland 1984; Keech et al. 1999, 2000). Requirements for nitrogen and phosphorus by female caribou increase around the time of parturition (Klein 1970, McEwan and Whitehead 1970) to meet the costs of gestation and lactation (Robbins 1983), and to replenish body reserves expended during winter (McEwan 1968). Those nutritional demands on caribou coincide with early phenological stages of vegetation growth (Klein 1990, Albon and Langvatn 1992), which are typically high in nitrogen, phosphorus, and digestible energy, and low in structural carbohydrates and toxic secondary metabolites that reduce digestibility (Bryant et al. 1983, Launchbaugh et al. 1993).

Minimizing risk of predation may result in ungulates selecting habitats that compromise their ability to optimize foraging (Berger 1978, 1991; Molvar and Bowyer 1994; Bowyer et al. 1998a, 1999; Kie 1999). Mountain ungulates often seek steep, rugged terrain to reduce risks of predation, especially when accompanied by neonates (Festa-Bianchet 1988, Bleich et al. 1997, Rachlow and Bowyer 1998, Bleich 1999). During migration, mule deer (*Odocoileus hemionus*) make tradeoffs between habitats containing high-quality forage and those with less risk of predation (Nicholson et al. 1997). Bergerud et al. (1984) noted that female caribou with young were separated spatially from those without young during parturition, and hypothesized that predation was the controlling factor; however, the role of nutrient acquisition was not investigated. No studies have examined in detail the potential nutritional tradeoffs associated with habitat use by caribou inhabiting mountainous terrain during parturition.

Depending upon the distribution of predators and forage in the environment, caribou might minimize the ratio of predation risk to forage availability, or make a tradeoff between

those 2 variables (Bowyer et al. 1998a). We determined the relative importance of nutrient acquisition and predator avoidance in the use of sites for parturition by female caribou. If habitat use differed between parturient and nonparturient females at or around the time of birth, we considered 3 hypotheses to explain that outcome (1) parturient females used habitat that maximized forage intake and quality to accommodate the increased cost of late gestation and lactation, (2) parturient females used sites with a lower risk of predation to themselves and their neonates, and (3) females made tradeoffs between forage acquisition and risk of predation.

To distinguish among those 3 hypotheses, we compared forage characteristics at sites used by parturient and nonparturient females immediately before, during, and after the birthing season. If nutrient acquisition was the driving force influencing the use of sites for parturition, we further predicted that (1) forage abundance and quality would be greater at sites used by females with young just after parturition than that at sites used by pregnant females before parturition, (2) forage abundance and quality would be greater at sites used by females with young than that at sites used by females without young, (3) forage abundance and quality would be greater at high-elevation sites used for birthing than at low-elevation sites used following parturition, and (4) caribou would follow a phenological gradient of vegetation to maximize their intake of high-quality forage. Alternatively, if predator avoidance was the primary factor determining habitat use, we predicted that (1) forage abundance and quality would be lower at sites used by females with young than at sites used by females without young, (2) parturient females would spatially separate themselves from concentrations of predators, (3) females would not track a phenological gradient of vegetation, and (4) this tradeoff between avoiding predators and acquiring nutrients would be most evident immediately following parturition when neonates were most vulnerable to predators' (Adams et al. 1995, Bleich et al. 1997), and energetic demands on females increased because of high costs of lactation (Skogland 1984, White and Luick 1984, Adamczewski et al. 1987).

STUDY AREA

We studied habitat use, group size, and diets of female caribou around the time of parturition

in Wrangell St. Elias National Park and Preserve in southcentral Alaska, United States. The range of the Mentasta herd during parturition encompassed 2,100 km², and varied in elevation from about 600 m along the Copper River to 2,200 m on the slopes of Mt. Drum and Mt. Sanford; maximum elevation reached 4,800 m at the summit of Mt. Sanford. About 10–15% of the area was >2,200 m in elevation, which was above habitats typically used by caribou in the Mentasta herd. Topography of this area ranged from nearly flat in low-lying areas to precipitous terrain in the mountains. Vegetation at <800 m was composed primarily of forests of white and black spruce (*Picea glauca* and *P. mariana*, respectively) interspersed with wetlands and tussock tundra that was dominated by cotton grass (*Eriophorum vaginatum*). Vegetation was characterized by shrub communities of willow (*Salix* spp.) and birch (*Betula glandulosa*) at elevations between 800 and 1,200 m, by extensive areas dominated by sedge tundra between 1,200 and 1,700 m, and alpine tundra typified by lichens (*Cetraria*, *Cladonia*, and *Cladonia*) from 1,700 to 2,200 m. Permanent snow, ice, and rock generally prevailed above 2,200 m.

Female caribou of the Mentasta herd (about 600 females in 1994) arrive on ranges where they give birth (62°20'N, 144°20'W) on the western and northern scarps of Mt. Drum and Mt. Sanford in late April; they remain in that area until migrating in October. Caribou begin giving birth in mid-May, with peak parturition usually occurring 1 week later; parturition nearly is complete by the beginning of June. Ungulates in arctic and sub-arctic environments typically exhibit extreme synchrony in births (Rachlow and Bowyer 1991, Bowyer et al. 1998b).

The first snowfall usually occurs in late September and snow persists until early May. Weather at >1,500 m is harsher than at lower elevations, with higher winds, colder temperatures, and occasional snow flurries developing throughout May. About 35 cm of snow fell on the calving grounds on 25 May 1994, and again on 16 May 1995. As a result of those snowfalls, much of the habitat above 1,500 m that had become snow-free was again covered by snow.

The study area contained numerous predators of young caribou. We observed wolves (*Canis lupus*), coyotes (*C. latrans*), grizzly bears (*Ursus arctos*), black bears (*U. americanus*), wolverines (*Gulo gulo*), golden eagles (*Aquila*

haliaetus), and bald eagles (*Haliaeetus leucocephalus*) on the study area. We located 5 dens of wolves in the study area at <1,000 m in elevation.

Insect abundance, which can have dramatic effects on behavior of caribou (Mörschel and Klein 1997), was low during both years of study. We routinely worked at elevations ranging from 800 to 2,000 m throughout the calving season in the same habitats occupied by caribou. Although we did not quantify insect abundance, we noticed few mosquitoes (Culicidae) during that period.

METHODS

Sampling Procedures

In autumn 1992 and spring 1993, we captured 44 adult (≥ 2 yr old), female caribou with a skid-mounted net gun attached to a Hughes-500D helicopter using methods described by Krausman et al. (1985). Each female we captured was fitted with a radiocollar and, weather permitting, was radiotracked daily from 18 May to 10 June in 1994–95 with a small fixed-wing aircraft. We monitored the status of pregnancy in females daily by observing whether antler velvet had been shed, or if females had a young at heel, and less frequently for indications of a distended udders (Whitten 1995).

We sampled characteristics of habitats and recorded group sizes of caribou during 3 sampling periods (1) preparturition (3–5 days before the first young was born), (2) peak parturition (1–3 days after a female gave birth), and (3) post parturition (10–12 days after a female gave birth). Status of parturition was defined as preparturient (before parturition began), parturient (with young) and nonparturient (not pregnant and without young). Size of groups was determined by counting the total number of animals (including young). We attempted to sample sites used by 20 females before parturition, 40 females during peak parturition (20 with young and 20 without young), and 40 females after parturition (20 with young and 20 without young) during each year. We marked all sampling sites by dropping a radiotracking beacon at locations of caribou from a fixed-wing aircraft or helicopter, or by recording the location with a global positioning system (GPS) from the airplane. Because the GPS was only accurate to within 100 m, we often wrote descriptions and made drawings of the site, which

allowed us to relocate the position of the neonate. We then used a helicopter equipped with a GPS unit to return to the locations of neonates for sampling, usually within 24–48 hr of their initial location.

Just prior to the birthing season in 1995, we randomly selected 20 radiocollared females, without regard to their status of pregnancy, for sampling habitat use during that period. Nonparturient females were probably under-represented in that sample because about 85% of females were pregnant each year (K. J. Jenkins, unpublished data). Unfortunately, parturition began 1 week earlier than expected in 1994, which prevented us from sampling habitats used during preparturition in that year.

We then sampled habitat use by females at peak parturition by randomly selecting 20 radiocollared females that were parturient from the sample of 44 radiocollared individuals. We located those females each day via fixed-wing aircraft, and sampled habitats where each female was first seen with a young at heel, usually within 24–48 hr of her giving birth. We obtained comparable samples of habitats used by nonparturient females at peak parturition by using all radiocollared females that were in the appropriate category. Nonetheless, because of the high rate of pregnancy, we had to rely on 15 noncollared females in both 1994 and 1995 to achieve our quota of nonparturient individuals. We identified additional females as nonparturient by antler and udder characteristics (Whitten 1995), and randomly selected a subset of noncollared females from sightings of caribou made during telemetry flights each day. We assumed that those random samples were representative of nonparturient females, and that the large number of females to draw from minimized any bias from potentially re-sampling the same individuals. We synchronized the timing of sampling for parturient and nonparturient females within each period to control for effects of Julian date on forage quality and abundance.

We sampled habitat use during post parturition in the same manner as at the peak of births. We sampled the same parturient females that we had used for the sample at peak parturition about 10 days after they gave birth, providing they still had a young at heel. Females selected during peak parturition but that lost their young before post parturition were omitted from that sample. We replaced those females with other randomly selected females with radiocollars that

had young of known age. We also re-sampled nonparturient females that we had sampled during peak parturition (those with radiocollars), and again relied on randomly selected noncollared females that were without young to complete our sample of nonparturient individuals. To increase our sample of nonparturient females with radiocollars, we considered any female that had lost a young ≤ 5 days prior to the post-parturition period to be nonparturient. We based that decision on data from previous years, which indicated that females moved from their birth sites to areas occupied by nonparturient females within 36–48 hr after losing a neonate (K. J. Jenkins, unpublished data). We assumed that those females were behaving similar to nonparturient animals.

We sampled the distribution of predators on the study area by recording all predators observed while radiotracking collared caribou and recorded locations of predators using a GPS unit. Although this method will not provide a population estimate for predators on our study area, it offers a valid index to compare relative occurrence of predators at differing elevations (Bleich et al. 1997). We logged a total of 180 hr of flight time in a helicopter, and 600 hr in a fixed-wing aircraft flying about 175 m above the ground while monitoring radiocollared caribou. There were typically 4 people in the helicopter, and 2 in the fixed-wing aircraft; all acted as observers.

Descriptions of Sites

We described habitat at each site using the vegetation classification system of Viereck et al. (1992). Topography was recorded as the dominant features of terrain within 1 ha of the site (i.e., flat, gentle slope, steep slope, drainage bottom, ridge, or hills). We estimated the slope of the site as 1 of 6 categories (0°, 1–10°, 11–20°, 21–30°, 31–45°, and >45°). We recorded elevation using the altimeter mounted in the helicopter after landing at the site. Cover of tree and shrub canopy, and snow cover was estimated visually (Kershaw 1964) within 1 ha of the site, and ranked in broad categories (0–6) of increasing cover. Aspect was assigned 1 of 8 categories (N, NE, E, SE, S, SW, W, or NW).

At each site, we sampled vegetation at each 1-m interval along a 50-m transect (i.e., 50 points/transect). We oriented the 50-m tape in a N-S or E-W direction based on the flip of a coin. The tape was centered at the location of

the radio beacon that had been dropped at the site, or by randomly selecting a midpoint at the GPS location. At each 1-m point along the transect, we sampled the first intercept (hit) and recorded 1 of the following categories: deciduous shrub, evergreen shrub, graminoid, forb, lichen, moss, rock, bare ground, snow, water, or litter. Plants were identified to species in most instances, except for dead or newly emergent graminoids. In shrub communities, the canopy of vegetation overhanging the point also was recorded with line-intercept sampling (Bonham 1989). We estimated forage biomass with the double-sampling method (Ahmed et al. 1983), using 6 quadrants each 20×50 cm, spaced at 10-m intervals along the transect, which we pooled into a single sample of 0.6 m^2 . We began by estimating the biomass of each species in 1 quadrat, and then immediately clipping and weighing that vegetation to the nearest 0.01 g. That weight allowed us to calibrate our estimate of biomass on each transect, and was used as a correction factor for the remaining 5 quadrats. By regressing measured versus estimated biomass on the clipped plots, we developed regression equations for each forage class. We converted estimated weights to dry mass by correcting for the moisture content of vegetation on the clipped quadrat.

We collected about 40 g wet biomass of each forage species at each site, along or immediately adjacent to the transect, for subsequent analysis of nutrients. We sampled only new growth for deciduous shrubs. We collected the entire plant for forbs, whereas for graminoids we sampled aboveground biomass, which included both dead and live material; most samples were a mixture of those 2 categories.

At each site, we noted phenology of plant species thought to be important forages for caribou during spring (Whitten and Cameron 1980, Klein 1990). Timing of green-up corresponded generally with percentage of newly emergent foliage in graminoids. Consequently, we assessed effects of elevation on timing of green-up using graminoids and their percentage of live versus dead material. We divided the study area into 3 elevational categories (1) $<1,200$ m, (2) $1,200\text{--}1,500$ m, and (3) $>1,500$ m, with nearly equal numbers of sites at each elevation ($n = 55, 51,$ and 57 , respectively). We then divided the birthing season into 5 periods of 5 days each, and determined the percentage of live graminoids at each of the elevations

throughout the season of births from the clipped plots on each transect.

We collected fecal samples from groups of caribou during pre, peak, and post parturition to compare indices of diet composition and quality. Each sample was a composite of 10–15 fecal groups, typically collected within min of deposition. In 1994, we collected samples during pre, peak, and post parturition without regard to the status of parturition of a particular female, because of difficulty in obtaining feces from individuals of known status. In 1995, we divided our sampling during parturition into high elevation ($>1,700$ m—typically parturient females and nursery groups) and lower-elevation ($<1,450$ m—mostly females without young). Thus, we sampled feces based on differences in elevation of groups, in lieu of knowing the status of parturition for individual females.

Laboratory Analysis

We dried forage samples at 50°C to a constant mass and ground them in a Wiley Mill using a 0.5-mm mesh screen. We analyzed each sample for nitrogen content and *in vitro* dry matter digestibility. Nitrogen was measured at the Forest Soils Laboratory at the University of Alaska Fairbanks, with a LECO CNS 2000 carbon, nitrogen, and sulfur analyzer. *In vitro* dry matter digestibility was determined at the Institute of Arctic Biology, University of Alaska Fairbanks, with the technique of Tilley and Terry (1963). Rumen liquor for digestibility trials was obtained from a fistulated reindeer at the Large Animal Research Station at the University of Alaska Fairbanks. Prior to collection of rumen fluid, the reindeer was accommodated to a diet of newly emergent grasses and forbs and new growth of deciduous shrubs to more closely match diets of caribou on our study area.

Botanical composition of feces was determined from epidermal fragments of plants identified from microhistological characteristics (Dearden et al. 1975) at the Wildlife Habitat Laboratory at Washington State University. Density values for fragments in feces were calculated from 100 microscope views for identification to forage class, and from 150 microscope views for each composite of groups identified to species. We did not use correction factors for digestibility in our dietary analysis and thus may underestimate occurrence of more digestible species. We also analyzed fecal pellets

for fecal nitrogen, and neutral detergent fiber as indices of diet quality (Holechek et al. 1982).

Statistical Analyses

We tested for differences in group size of caribou using analysis of variance (ANOVA), with group size as the dependent variable, and status of parturition, year, and their interaction as main effects. We compared use of 3 broad habitat types on the study area (e.g., shrubs, sedge tundra, and lichen tundra) by females with and without young during peak and post parturition using chi-square analysis (Conover 1980). For this broad-based analysis, we pooled all observations in shrub habitats into a single type (shrubs) because of similarity of those habitats, and to meet assumptions of chi-square analysis. We also omitted 12% of the observations from that analysis because some sites could not be categorized into those 3 habitat types; that procedure helped minimize the bias from a potential lack of independence among cells in the chi-square analysis (Cherry 1998).

We also conducted a more detailed analysis of habitat use with stepwise logistic regression (Agresti 1990) on a suite of habitat measurements related to topography, climate, and vegetation to determine which variables best differentiated between sites used by parturient and nonparturient caribou ($\alpha = 0.15$ to enter and remain). We used Akaike information criteria in selecting the best model (Cressie 1993). We controlled for multicollinearity by eliminating one of any pair of variables with $r^2 \geq 0.50$. Elevation was highly correlated with many other variables; consequently, we omitted that variable from logistic models. Percentage of sites classified correctly was based on a jackknifed reclassification (Agresti 1990).

We tested for differences in elevations of sites used by females with and without young in a separate analysis using ANOVA (Wonnacott and Wonnacott 1990). All statistical comparisons were conducted with SAS statistical software (SAS Institute 1988).

We further investigated the importance of forage biomass by evaluating differences among sites used by preparturient females, and females with and without young using multivariate analysis of covariance (MANCOVA; Johnson and Wichern 1982). Dry mass of each forage class (g/m^2) was used as the dependent variable, with status of parturition, year, and their interaction as main effects, and Julian date as a co-variate.

Progressing Julian dates, which served as an index to climatic conditions, were accompanied by increasing ambient temperatures and day lengths during spring, and thereby influenced growth of vegetation.

Measures of forage quality (nitrogen, in vitro dry matter digestibility) could not be included in logistic-regression models because that analysis required no missing data, and we were unable to collect comparable forage samples at all sites because of either an absence of forage or deep snow that prevented such collections. We used MANCOVA for the analysis of nitrogen and in vitro dry matter digestibility (dependent variables), with status of parturition and forage class as main effects, and Julian date as the covariate. We tested for temporal changes in indices of diet quality (fecal nitrogen, neutral detergent fiber) throughout the period of parturition for groups of females with and without young using the *t*-test (Wonnacott and Wonnacott 1990). Botanical composition of feces was analyzed by testing percent occurrence of each forage class separately with ANOVA; forage class was the dependent variable, and period of parturition or elevation was the main effect. We used the sequential Bonferroni procedure to correct for making multiple comparisons (Rice 1989). We examined differences in elevations of sites used by female caribou with and without young during peak parturition, and elevations of predators using a Wilcoxon test of medians; we met distributional assumptions of that test (Conover 1980).

RESULTS

Group Size

Twenty preparturient females were in larger groups ($\bar{x} = 10.3$, $\text{SE} = 2.37$) than 36 females with young at peak parturition ($\bar{x} = 4.0$, $\text{SE} = 0.75$; $F_{2, 53} = 5.46$, $P = 0.007$), but did not differ from 30 females without young at peak parturition ($\bar{x} = 9.9$, $\text{SE} = 2.46$, $F_{2, 46} = 0.71$, $P = 0.50$). During peak parturition, those same 36 females with young were in smaller groups than 30 females without young ($F_{3, 61} = 3.10$, $P = 0.03$). During post parturition, however, 40 females with young ($\bar{x} = 35.0$, $\text{SE} = 10.65$) and 37 females without young ($\bar{x} = 18.5$, $\text{SE} = 2.94$) were in smaller groups ($F_{3, 71} = 1.75$, $P = 0.17$).

Habitat Use

Use of broad habitat types characterized by vegetation communities (Fig. 1) differed be-

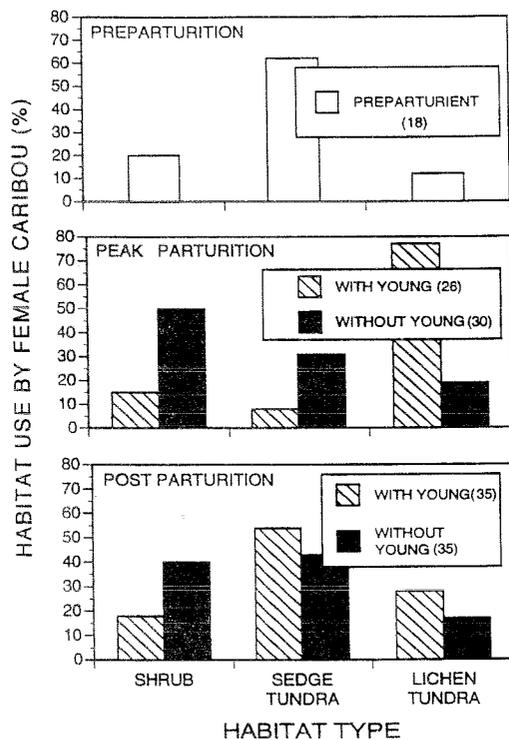


Fig. 1. Habitat use by adult female caribou during 3 periods of parturition, Wrangell St. Elias National Park and Preserve, Alaska, 1994–95. Sample sizes are in parentheses.

tween females at preparturition and females with young at peak parturition ($X^2_2 = 17.93$, $P = 0.001$), but not between females at preparturition and females without young at peak parturition ($X^2_2 = 4.87$, $P = 0.09$). Patterns of use for those broad vegetation types different between females with and without young during peak parturition ($X^2_2 = 18.17$, $P = 0.001$). Females with young predominantly used lichen-tundra habitat, whereas nonparturient females used mostly sedge tundra and shrubs (Fig. 1). During post parturition, patterns of habitat use did not differ between females with young and those without them ($X^2_2 = 4.67$, $P = 0.10$).

We pooled data related to topography, climate, vegetation (Table 1) for 1994 and 1995 because year failed to enter any logistic model ($P > 0.15$). Logistic regression identified 3 variables, low-shrub habitat, sedge-tundra habitat, and bare ground, which best discriminated between sites females used during preparturition ($n = 20$) versus sites used by females with young at peak parturition ($n = 36$; Table 2; $P < 0.05$). At peak parturition, females with

young used habitats that had a higher proportion of bare ground, and a lower occurrence of sedge tundra and low shrubs than sites used by females at preparturition (Table 2). That model correctly classified 80.1% of 56 sites used by those categories of caribou.

Logistic regression also identified 3 variables, dry mass of all graminoids, dry mass of live graminoids, and a slope of $<30^\circ$, which best discriminated between sites females used during preparturition versus sites used at peak parturition by females without young (Table 2; $P < 0.05$). At peak parturition, females without young used habitats with steeper slopes and a greater amount of live biomass of graminoids than did females at preparturition. That model correctly classified 83.5% of 50 sites used by those females.

During peak parturition, low-shrub habitat, sedge-tundra habitat, and dry mass of the new growth of deciduous shrubs, best differentiated between sites used by females with and without young (Table 2). Females with young used sites with less low-shrub and sedge-meadow habitat than those sites used by females without young ($P \leq 0.05$). That model correctly classified 79% of 66 sites.

During post parturition, habitats and species associated with low-elevation sites, including low-shrub habitat, wet mass of lichens, and percent cover of low-bush cranberry (*Vaccinium vitis idaea*) best categorized sites used by females with young ($n = 40$) and those without young ($n = 37$). Only low-shrub habitat, however, was significant (Table 2, $P \leq 0.05$). Females with young used areas with less cover of shrubs than did females without young. This model, however, only classified 66% of 77 sites correctly.

At peak parturition, females with young used higher-elevation sites (Fig. 2) than those used by females without young ($F_{3, 61} = 3.23$, $P = 0.03$). That difference was marginally not significant when females with young moved to lower-elevation sites ($F_{3, 73} = 2.48$, $P = 0.07$; Fig. 2).

Forage biomass (Fig. 3) differed between sites used by female caribou during preparturition and by females with young at peak parturition ($F_{4, 49} = 2.58$, $P = 0.05$). Most of that difference occurred because of a greater biomass of graminoids at sites used by females during preparturition ($F_{3, 52} = 5.97$, $P = 0.0002$). Forage biomass did not differ between sites used by females without young at peak partu-

Table 1. Summary statistics for habitat characteristics of sites used by female caribou, by period of parturition and parturient status, Wrangell St. Elias National Park and Preserve, Alaska, USA, 1994–95.

| Habitat characteristic | Pre parturition (n = 20) | | | Peak parturition | | | Post parturition | | |
|--|-----------------------------|------|-------|---------------------|------|-------|---------------------------|-------|------|
| | Without young (n = 36) | | | With young (n = 40) | | | Without young (n = 37) | | |
| | \bar{x} | SE | n | \bar{x} | SE | n | \bar{x} | SE | n |
| Topographical | | | | | | | | | |
| Elevation (m) | 1,432 | 49 | 1,465 | 1,175 | 68 | 1,373 | 53 | 1,253 | 43 |
| Sin aspect (E-W) | -0.15 | 0.18 | -0.08 | 0.31 | 0.10 | -0.11 | 0.11 | -0.22 | 0.11 |
| Cos aspect (N-S) | -0.14 | 0.12 | -0.06 | -0.05 | 0.12 | -0.05 | 0.09 | 0.16 | 0.11 |
| Slope (°) | 0.95 | 0.05 | 1.11 | 0.90 | 0.12 | 1.05 | 0.10 | 1.05 | 0.08 |
| Climatic | | | | | | | | | |
| Julian date ^a 136.8 | 0.36 | 0.36 | 146.5 | 146.7 | 0.91 | 155.9 | 0.51 | 155.1 | 0.48 |
| Snow cover (0-6) ^b | 0.16 | 0.16 | 1.42 | 0.50 | 0.26 | 0.45 | 0.14 | 0.24 | 0.09 |
| Vegetation dry mass (g/m²) | | | | | | | | | |
| Deciduous shrubs | 4.53 | 1.25 | 3.92 | 8.32 | 1.40 | 8.31 | 1.06 | 10.52 | 1.24 |
| Forb | 0.95 | 0.25 | 2.23 | 3.20 | 0.55 | 5.54 | 0.81 | 5.94 | 0.89 |
| Graminoid | 25.22 | 3.97 | 9.58 | 21.41 | 3.80 | 21.52 | 3.02 | 24.52 | 2.63 |
| Live graminoid | 1.15 | 0.17 | 1.11 | 2.57 | 0.41 | 3.45 | 0.58 | 3.88 | 0.55 |
| Lichen | 4.01 | 2.44 | 1.54 | 4.28 | 1.49 | 2.04 | 0.39 | 1.67 | 0.28 |
| Evergreen | 4.26 | 0.59 | 1.06 | 2.42 | 0.68 | 3.05 | 0.78 | 2.97 | 0.68 |
| Vegetation cover (%) | | | | | | | | | |
| Graminoid | 50.3 | 6.77 | 17.5 | 36.5 | 5.21 | 38.0 | 4.35 | 5.5 | 4.11 |
| Deciduous | 3.0 | 0.98 | 2.5 | 6.5 | 1.30 | 5.0 | 1.27 | 6.5 | 1.65 |
| Forb | 0.2 | 0.14 | 1.0 | 1.0 | 0.53 | 1.0 | 0.30 | 1.0 | 0.24 |
| Lichen | 7.0 | 1.53 | 8.0 | 7.5 | 1.42 | 7.0 | 1.21 | 8.5 | 1.28 |
| Evergreen | 8.0 | 1.66 | 10.5 | 15.0 | 2.99 | 12.5 | 1.58 | 13.0 | 1.81 |
| Moss | 13.5 | 2.16 | 12.5 | 9.0 | 1.14 | 10.0 | 1.31 | 11.0 | 1.40 |
| Rock | 9.5 | 3.60 | 23.5 | 10.0 | 3.03 | 7.5 | 1.70 | 4.5 | 1.90 |
| Bare ground | 3.0 | 0.73 | 7.5 | 4.5 | 1.51 | 7.5 | 1.66 | 4.00 | 0.93 |
| Leaf litter | 2.5 | 0.66 | 3.0 | 4.5 | 1.65 | 5.0 | 1.01 | 4.0 | 0.98 |
| Snow | 1.0 | 0.53 | 13.5 | 3.5 | 3.07 | 5.0 | 2.19 | 1.5 | 1.02 |
| Water | 2.0 | 0.83 | 0.5 | 2.0 | 0.78 | 1.5 | 0.64 | 0.5 | 0.00 |

^a Julian date is considered with climatic variables because it reflected increases in ambient temperature and day length in spring.^b Categorical ranking that increases with cover.

Table 2. Logistic-regression models, coefficients, and SE, for sites used by female caribou at parturition, Wrangell St. Elias National Park and Preserve, Alaska, USA 1994–95.

| Model | Variable | Coefficient ^a | SE | P |
|--|----------------------------|--------------------------|--------|-------|
| Preparturition (1) vs. peak parturition (0) (with young) | Low shrub | -2.2345 | 0.9868 | 0.024 |
| | Sedge tundra | -3.2679 | 1.0448 | 0.002 |
| | Bare ground | 0.2928 | 0.1449 | 0.043 |
| Preparturition (1) vs. peak parturition (0) (without young) | Gentle slope | -1.4574 | 0.7253 | 0.045 |
| | Weight of green graminoids | 1.5530 | 0.5890 | 0.008 |
| | Weight of total graminoids | -0.0662 | 0.0352 | 0.059 |
| Peak parturition (1) (with young) vs. peak parturition (0) (without young) | Low shrub | 2.8858 | 1.1236 | 0.010 |
| | Sedge tundra | 2.5553 | 0.8788 | 0.004 |
| | Deciduous weight (dry) | 0.1605 | 0.0838 | 0.055 |
| Post parturition (0) (with young) vs. post parturition (1) (without young) | Low shrub | 1.6392 | 0.7801 | 0.036 |
| | Lichen weight (wet) | -0.3933 | 0.2477 | 0.112 |
| | Low-bush canberry | 0.4722 | 0.3265 | 0.148 |

^a The coefficient signifies the direction (+ or -) of relative use of the habitat variable by caribou that are coded 0.

rition and those sites used by females during preparturition ($F_{4,44} = 0.15, P = 0.96$). During peak parturition, females with young used sites with less available biomass of forbs, graminoids, and deciduous shrubs, than those used by females without young ($F_{4,61} = 3.39, P = 0.02$). By post parturition, biomass of forages did not differ between sites used by females with and without young ($F_{4,72} = 0.58, P = 0.68$).

We examined differences in forage quality among periods of parturition and reproductive classes separately in 1994 and 1995 (Fig. 4), because there was a year by reproductive class interaction (MANCOVA; $P < 0.05$). In 1994, nitrogen and in vitro dry matter digestibility of forage species differed between sites used by females with and without young during peak parturition ($F_{2,48} = 4.91, P = 0.01$). Nitrogen

content of forages was higher at sites used by females without young, but levels of in vitro dry matter digestibility were lower at those sites. During post parturition, forage quality was similar between sites used by females with and without young ($F_{2,130} = 1.14, P = 0.32$). In 1995, nitrogen and in vitro dry matter digestibility of forages at sites used by females with and without young during peak parturition (Fig. 4) differed significantly ($F_{2,113} = 6.51, P = 0.002$). A posteriori comparisons indicated both nitrogen and in vitro dry matter digestibility were higher at sites used by females without young ($P = 0.001$ and $P = 0.009$, respectively). Those differences no longer existed by post parturition ($F_{2,169} = 0.88, P = 0.42$).

Percentage of live material in samples of graminoids was negatively related to elevation; low-elevation sites had a higher percentage of live material. Graminoids reached 20% live material during 26–30 May at <1,200 m, 31 May–4 June at 1,200–1,500 m, and 5–9 June at >1,500 m.

Diet Characteristics

Mean (\pm SE) fecal nitrogen was $1.6 \pm 0.09\%$ for 6 fecal groups of caribou collected during preparturition, $1.5 \pm 0.18\%$ for 7 groups at peak parturition, and $2.8 \pm 0.34\%$ for 8 groups sampled during post parturition in 1994. Values of neutral detergent fiber for those same periods were $65.2 \pm 0.87\%$, $65.6 \pm 0.73\%$ and $61.9 \pm 1.58\%$, respectively. In 1995, samples were subdivided by elevation. Fecal nitrogen of car-

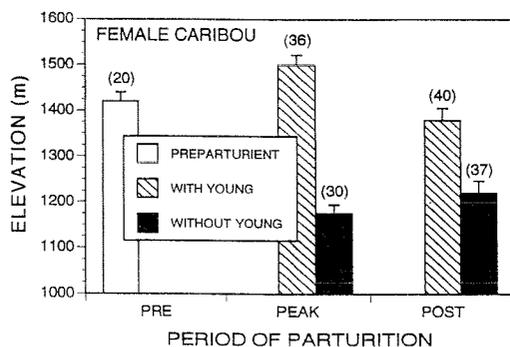


Fig. 2. Mean (\pm SE) elevation used by female caribou during 3 periods of parturition, Wrangell St. Elias National Park and Preserve, Alaska, 1994–95. Sample sizes are in parentheses.

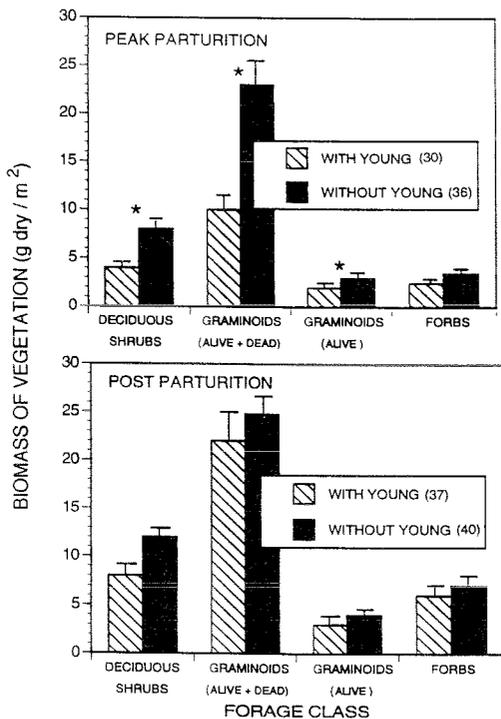


Fig. 3. Mean (+SE) biomass of vegetation at sites used by female caribou with and without young during periods of peak and post parturition, Wrangell St. Elias National Park, Alaska, 1994–95. Sample sizes are in parentheses; * $P < 0.05$ following a Bonferroni correction.

ibou averaged $2.1 \pm 0.43\%$ at high elevation, and $2.4 \pm 0.6\%$ at low elevation. Values of neutral detergent fiber for those same elevations were $65.1 \pm 2.83\%$, and $66.7 \pm 1.48\%$, respectively. Fecal nitrogen and neutral detergent fiber did not differ between preparturition and peak parturition in 1994–95 (yr pooled; $t_{9,1} = 0.38$, $P > 0.71$, and $t_{10,3} = 0.31$, $P > 0.7$, respectively). Fecal nitrogen was significantly higher at post parturition than during preparturition ($t_{8,1} = 3.61$, $P < 0.007$), but neutral detergent fiber was not different ($t_{10,5} = 1.83$, $P > 0.09$). Fecal nitrogen also was higher during post parturition than at peak parturition ($t_{10,5} = 3.53$, $P < 0.005$), but again neutral detergent fiber marginally did not differ ($t_{9,8} = 2.09$, $P > 0.05$). Likewise, composition of fecal pellets in 1995 did not differ in fecal nitrogen or neutral detergent fiber between postparturition sites at high elevation, and post-parturition sites at low elevation ($t_{5,7} = 0.53$, $P < 0.62$, and $t_{4,5} = 0.49$, $P < 0.64$, respectively).

Botanical composition of the fecal pellets differed somewhat in 1994, when fecal pellets con-

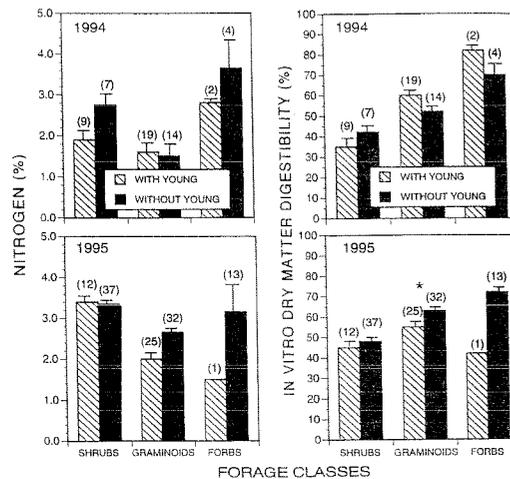


Fig. 4. Mean (+SE) nitrogen content and digestibility of caribou forages at sites with and without young, Wrangell St. Elias National Park and Preserve, Alaska, 1994–95. Sample sizes are in parentheses; * $P < 0.05$ following a Bonferroni correction.

tained more deciduous shrubs ($P = 0.04$) and fewer mosses ($P = 0.006$) during post parturition than during peak parturition or preparturition (Fig 5). Further, fecal pellets collected during peak and post parturition in 1994 contained a lower percentage of grasses than those collected during preparturition. In 1995, botanical composition of fecal pellets collected at high elevation and low elevation sites did not differ for any forage class (Fig. 5).

Distribution of Predators

We pooled years to assess elevations at which grizzly bears and wolves occurred to increase sample size, and because elevations at which we observed those predators did not differ between years, although that outcome was marginal (ANOVA; $F_{7,103} = 1.92$, $P = 0.07$). During peak parturition, caribou females with young were at higher elevations than grizzly bears or wolves (Fig. 6; Wilcoxon test, $z = 2.03$, $P = 0.042$, and $z = 2.61$, $P = 0.009$, respectively). Females without young, however, were not at different elevations than those predators. Likewise, at post parturition, females with young were at similar elevations to grizzly bears and wolves ($z = 0.97$, $P = 0.332$, and $z = 1.48$, $P = 0.14$, respectively), as were females without young ($z = 1.37$, $P = 0.17$, and $z = 0.94$, $P = 0.35$, respectively).

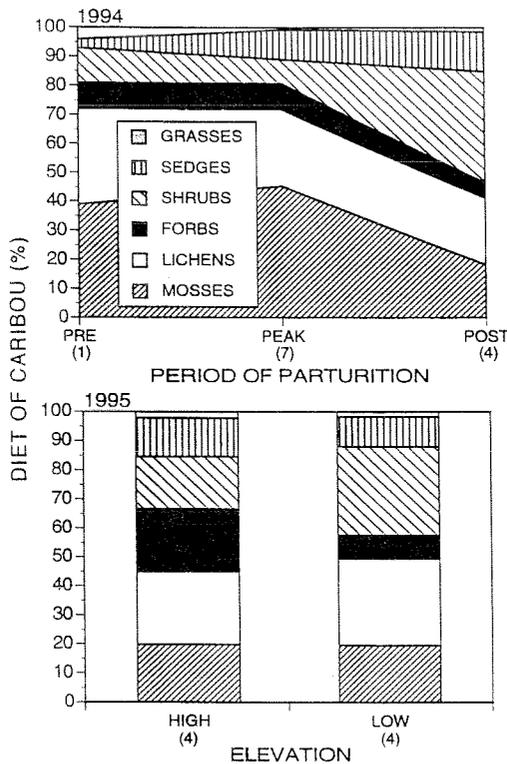


Fig. 5. Diets of caribou as indexed by microhistoriological analyses of feces for periods of parturition (1994) and high and low elevations (1995), Wrangell St. Elias National Park and Preserve, Alaska. Sample sizes are in parentheses; each sample represents 10–15 composited fecal groups.

DISCUSSION

Female caribou with and without young used different habitats at parturition. Patterns of habitat use for nonparturient females did not change markedly through the periods of parturition, whereas females with neonates sought higher-elevation sites during peak-parturition (Figs. 1 and 2). That pattern was consistent with other studies involving caribou herds inhabiting mountains, where parturient females dispersed to higher-elevation sites just prior to giving birth (Bergerud et al. 1984, Bergerud and Page 1987).

Although an analysis of broad vegetation types indicated some differences in use of habitat by female caribou with and without young (Fig. 1), tests involving additional habitat variables surrounding sites used by females provided further insights into their ecology (Table 2). For instance, females with young used sites at higher elevations but with less-steep slopes than did females without neonates, indicating that a

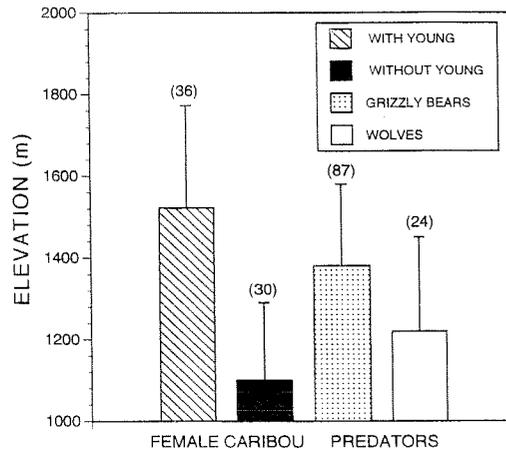


Fig. 6. Median (+ ½ interquartile distance) elevation at which female caribou with and without young and predators occurred during peak parturition, Wrangell St. Elias National Park and Preserve, Alaska, 1994–95. Sample sizes are in parentheses.

level micro-site situated within more rugged and steep terrain may be an important habitat characteristic for calving grounds in the mountains. Indeed, sampling at >1 spatial scale may be necessary to understand habitat use by maternal females (Rachlow and Bowyer 1998). Such detailed measurements of habitat also have been useful in understanding birth-site selection for ungulates (Bowyer et al. 1998a, Rachlow and Bowyer 1998), and revealed patterns not evident from examining only vegetation types (Bowyer et al. 1999).

Our data were inconsistent with the hypothesis that parturient females spatially separated from nonparturient females in response to increased demands for sites with more forage at parturition. Parturient females occurred at sites with less forage than did females without young (Fig. 3). During peak parturition, we observed nearly 50% less biomass of deciduous shrubs, total graminoids, and live graminoids at sites used by females with young than at sites used by females without young, although forb abundance was nearly identical (Fig. 3). That difference in biomass was substantiated by data on plant cover from line transects, which indicated lower abundance of graminoids and deciduous shrubs, and nearly equal cover of forbs at sites used by females with young compared with sites used by females without young (Table 1).

During peak parturition in 1994, nitrogen was higher but in vitro dry matter digestibility lower on sites used by females without young compared with those used by parturient fe-

males. In 1995, however, nitrogen and in vitro dry matter digestibility were lower for graminoids at sites used by females with young, than at sites used by females without young during peak parturition; no differences were detected for deciduous shrubs (Fig. 4). Although somewhat ambiguous because of between-year variation, those data indicated that sites used by females with young at peak parturition did not consistently possess forage of higher quality than for sites used by females without neonates.

Although female caribou with young used plant communities with lower biomass than females without young at peak parturition, we were unable to document consistent effects of this altitudinal separation on nutrients in diets they consumed. Our analysis of caribou feces indicated that females at high elevations had similar diet composition to females at lower elevations (Fig. 4), although forage abundance was generally lower at high-elevation sites (Fig. 3). Despite the lower abundance of forage, caribou may be able to feed in a highly selective manner at those sites, and increase their intake of forage higher in quality than our process for collecting forage revealed. White and Trudell (1980) documented an increase of 10% in the dry-matter digestibility of forage acquired through selective grazing by reindeer compared with the digestibility of forage the authors collected based on availability.

Although caribou frequently ascend in elevation to take advantage of early phenological stages of vegetation (Oosenbrug and Theberge 1980), timing of vertical movements of parturient caribou in the Wrangell Mountains preceded green-up, as evidenced by the later dates of green-up for graminoids at higher elevations. Higher-elevation sites used by females with young (Fig. 2) consisted mostly of lichen-tundra communities with colder temperatures and snow persisting later than at lower elevations. Those harsher climatic conditions limit new growth of plants (Chapin 1983, Kudo 1991), which are high in nitrogen, and thought to be important nutritionally to caribou at parturition (White and Luick 1984, Klein 1990). Lichens can be an important component of the diet during the birthing season (Klein 1970); that observation was supported by microhistological analysis of fecal pellets at parturition (Fig. 5). Lichens, however, were more abundant at lower than at higher elevations (Table 1); caribou

probably did not move to higher sites to gain access to that forage.

Movement of females to high-elevation sites before green-up has been described previously for caribou (Bergerud et al. 1984) and bighorn sheep (*Ovis canadensis*; Festa-Bianchet 1988). Avoidance of predation was hypothesized to be the driving factor underlying movements in those studies. Our data also were consistent with the hypothesis that habitat use by parturient females reflected minimizing the effects of predation on neonates; we could find few nutritional benefits at sites used at parturition by pregnant and lactating females. Additionally, sites where caribou gave birth were higher in elevation than most locations where we observed predators (Fig. 6). Females could not use low-elevation sites with more forage and simultaneously avoid predators because risk of predation and forage availability exhibited a positive relation; hence, females were confronted with a tradeoff between those 2 variables (Bowyer et al. 1998a). A female and her young, however, could lower the chance of a predator encounter by spacing away to higher elevation sites as reported in other studies of mountain caribou (Bergerud et al. 1984, Bergerud and Page 1987). Supportive data on predator avoidance at parturition also are available for caribou inhabiting arctic environments (Fancy and Whitten 1991).

High elevations may offer additional protection from predation we did not measure. Sites consisting of heterogeneous terrain and snow patches can provide a cryptic background for a female and her neonate, which likely enhances their ability to escape detection by predators (Eastland et al. 1989). Indeed, at peak parturition, more snow occurred at sites used by parturient females than at sites with nonparturient females (Table 1). Bergerud and Page (1987) suggested that upward movements in elevation by caribou could decrease the likelihood of encountering a predator by spacing away from travel corridors of predators along valley bottoms. Bergerud and Page (1987) also observed that parturient females at higher elevations were in smaller groups, making them less conspicuous to predators. Parturient females on our study area consistently occurred in smaller groups than nonparturient females at the peak of the birthing season. High-elevation sites also could enhance the ability of maternal caribou to detect and avoid predators as hypothesized

for female moose (*Alces alces*) by Bowyer et al. (1999). This increased ease in vigilance afforded by being above most approach routes of predators could allow a female and young an opportunity to escape by moving away from an approaching carnivore.

If minimizing risk of predation to offspring were the deciding factor in habitat use by parturient females, we would expect substantial differences between sites used by females with neonates and those without young at heel. Those differences existed as indicated by elevational differences in sites used (Fig. 2), and the differential habitat use revealed with logistic regression (Table 2). We also predicted that after the loss of their neonate, parturient females would behave as nonparturient females in their use of habitat, because risk of predation had lessened. Indeed, when females in high-elevation sites lost young to predation, they usually descended to sites occupied by females without young within 24–36 hr (K. J. Jenkins, unpublished data). We also observed use of lower-elevation sites by females when their young were at or near 10 days old, compared with the elevation of sites used just after they gave birth (Fig. 2). That period coincided with increased mobility of young, and a decreased vulnerability to predators (Miller et al. 1985), especially to bears (Adams et al. 1995). Females that had moved to lower elevations were in larger groups, which could be advantageous to a female caribou and her young by lessening the chance that she or her neonate would be selected from the group by a predator (Hamilton 1971). The period 10 days after parturition also coincided with greatest energetic demands on female caribou because of the high costs associated with lactation (White and Luick 1984), which could be responsible for movements to low-elevation sites that supported a greater biomass of forage (Fig. 4). Indeed, White and Trudell (1980) suggested that low biomass of forage combined with a high percentage of dead material could limit the rate of forage intake by caribou. Both those conditions existed for graminoids at high-elevation sites where caribou gave birth in our study area (Figs. 1 and 3).

Behavior whereby parturient females balanced the need for forage with the risk of predation to young has been reported for caribou (Bergerud et al. 1984), mountain sheep (*O. dalli*; Festa-Bianchet 1988, Rachlow and Bowyer

1998), and moose (Molvar and Bowyer 1994, Bowyer et al. 1999). Much of our data on habitat use by parturient and nonparturient caribou support the interpretation that females with neonates were attempting to avoid predators. Nonetheless, inconsistent differences in forage quality, fecal nitrogen, and diet between reproductive classes of females indicate that those with neonates may have reduced risk of predation without incurring a huge nutritional cost in doing so.

MANAGEMENT IMPLICATIONS

Conservation of mountain-dwelling ungulates necessitates an understanding their habitat requirements, especially for critical periods such as the birthing season. We caution, however, that our results are for a low-density population of caribou. Density dependence influences most life-history characteristics of ungulates (McCullough 1999), and we would expect differences in habitat use by caribou occurring at higher densities with respect to carrying capacity, including use of less-desirable birth sites by females. This potential plasticity in patterns of habitat use through time requires flexibility in developing and modifying management plans for conservation of habitat for caribou.

Many populations of ungulates in Alaska have been held at low density by large carnivores; predator control holds the potential to increase those populations (Gasaway et al. 1992). Although management that effectively reduced predation probably would achieve such a goal, we are less certain that female caribou would alter patterns of habitat use in response to a lowered density of predators. Behaviors of ungulates often reflect the likelihood of encountering a predator in a particular habitat irrespective of whether the predator is present (Hirth 1977, Molvar and Bowyer 1994, Bleich 1999). Some responses of ungulates to predation risk may subside relatively quickly (Berger 1999), but others may take decades (Hirth 1977), centuries (LaGory 1986), or even millennia (Berger 1998) to wane. Consequently, females and their neonates may not adjust their use of habitats to reflect an immediate reduction in risk from predators. Managing predators to alter patterns of habitat use by parturient females clearly requires more study prior to implementing such plans, especially in national parks, where predator control currently does not occur.

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