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COMPARATIVE FORAGING ECOLOGY AND SOCIAL DYNAMICS OF CARIBOU (Rangifer tarandus)

A

THESIS

Presented to the Faculty
of the University of Alaska Fairbanks
in Partial Fulfillment of the Requirements
for the Degree of

DOCTOR OF PHILOSOPHY

By
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Fairbanks, Alaska
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By

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ABSTRACT

The Southern Alaska Peninsula Caribou (Rangifer tarandus) Herd (SAPCH) and its two sub-groups were the focus of a study addressing the hypotheses: (1) food limitation during winter caused a decline in the herd; and, (2) higher calf productivity within the Caribou River group than within the Black Hill group was related to greater forage availability on the seasonal ranges of the Caribou River group. Intense, systematic range and calving surveys in 1991 and 1992 supported the hypothesis of food limitation during winter, and indicated that greater calf production in the Caribou River group was related to earlier commencement of the season of plant growth and greater forage availability on the summer range of that group, coupled with earlier parturition among females of the Caribou River herd.

In a comparative study involving the two SAPCH groups and the West Greenland Caribou Herd, daily variation in sizes of foraging groups, densities of caribou within feeding sites, distances between individuals within feeding sites, distances moved by foraging groups, and frequency of group movement was modeled using the following ecological parameters: predation risk, insect harassment (by mosquitos), range patchiness, feeding-site patchiness, feeding-site area, and range-wide density of caribou. Models revealed that intraseasonal social dynamics of foraging caribou were governed in most instances by patterns of forage availability and distribution across landscapes and within feeding sites, in some instances by insect harassment and social pressures, but in no instance by levels of predation risk inherent to the ranges on which they foraged.

In a study of the interrelationships between characteristics of graminoids and intensity of grazing by caribou, vegetation on each of the Black Hill and Caribou River ranges was sampled and tested for responses to clipping. Biomass density (g/m^3) of forage, shoot density ($\#/m^2$), and nutrient and mineral densities (g/m^3) and concentrations (g/100g tissue) correlated positively with use of sites by caribou. Productivity and responses to clipping were independent of previous use, but consistent within ranges. These results indicate that caribou are sensitive to local variation in forage quantity and quality, and preferentially use sites with higher returns of nutrients and minerals.

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INTRODUCTION

The foraging and social ecologies of vertebrate herbivores are closely associated (Monaghan & Metcalfe 1985). For example, changes in forage availability can influence trends of increase or decrease within populations (Sinclair 1977; McCullough 1979; Sinclair *et al.* 1985; Messier *et al.* 1988). The density of herbivores within a population, moreover, can influence the selectivity with which individuals are able to forage (Skogland 1980, 1985*b*; White 1983; Molvar & Bowyer 1994). The selectivity with which herbivores forage has important consequences for the evolutionary fitness of individuals (White 1983; Stephens & Krebs 1986). Choices made by social herbivores regarding where to feed and what to consume are influenced not only by the structure and distribution of their forage (Jarman 1974; Hirth 1977), but also by the presence of competing conspecifics (Pimm *et al.* 1985; Skogland 1989*b*). Furthermore, among social herbivores, the distribution of forage across spatial scales affects the degree of aggregation displayed by herbivores while foraging (McNaughton1984; Molvar & Bowyer 1994), and this, in turn, affects forage productivity (McNaughton 1983; McNaughton *et al.* 1989). Forage productivity, finally, cycles back on the productivity of herbivores (Reimers *et al.* 1983; Owen-Smith 1990). What emerges from the preceding observations, then, is an ecosystem perspective in which herbivores constitute active, dynamic components of ecosystems (Ryszkowski & French 1982; McNaughton *et al.* 1988; Naiman 1988), both shaping and being influenced by the distribution of forage and nutrients across and within landscapes (Ruess & McNaughton 1987; Ruess & Seagle 1994).

As a highly social herbivore existing in extremely seasonal environments, caribou (Rangifer tarandus) occupy a seemingly tenuous position, contending with periods of alternately limited and abundant forage during annual and superannual cycles, while at the same time responding to phenotypic "urges" to congregate or disperse in response to environmental and social stimuli (Lent 1966; Nixon 1991). The levels of interaction between caribou populations and their forage, and the roles of caribou sociality as passive or active components of ecosystems have been addressed separately in many previous studies (White 1983; Thing 1984; Skogland 1985*b*, 1989*a*). This study, however, attempts to integrate the foraging ecology and social dynamics of caribou into one body. In the process, I have drawn heavily on concepts developed from studies of another highly social herbivore inhabiting extremely seasonal environments: the wildebeest (Connochaetes taurinus).

This thesis comprises three chapters, each of which represents a separate manuscript submitted for publication to professional journals. As such, each chapter retains its original author designations (as a footnote to the title page of each chapter), abstract, introduction and conclusion. References, however, have been consolidated into a single section at the end of the thesis. Although each chapter has two or more authors, the research presented is largely original in concept. I collaborated with Pernille Bøving in a portion of this research, but have written this thesis myself. Chapter 2, which was drafted while I was in residence at the University of Copenhagen, includes some data collected by Pernille Bøving during her M.Sc. research, and these data are cited where appropriate. David Klein contributed to the inception of the study and development of the research design. Each chapter addresses a different level or aspect of caribou foraging and social ecology. Chapter 1 addresses the roles of seasonal availability of forage in limiting absolute numbers and productivity of caribou. Chapter 2 assesses the relative contributions of several environmental variables to short-term (intraseasonal) social dynamics of caribou. Finally, Chapter 3 investigates reciprocal relationships between characteristics of feeding sites and variable levels of usage of them by caribou.

CHAPTER 1

RANGE ECOLOGY OF A FOOD-LIMITED CARIBOU HERD IN ALASKA[1]

1.1 Abstract

The Southern Alaska Peninsula Caribou (Rangifer tarandus) Herd declined by over 80% in 10 years, after reaching a peak density in 1983 of > 2 caribou/km^2. Concurrent with the population decline was a steady decline in calf productivity. Two sub-herds have been recognized as using distinct, dissimilar seasonal ranges on the Southern Alaska Peninsula. Since 1989, production of calves by mid-summer has been consistently higher among caribou calving and wintering on the Caribou River range than among those calving on Black Hill and wintering around Cold Bay, Alaska. Intense, systematic range and calving surveys in 1991 and 1992 indicated that lichen abundance was extremely low over the Southern Alaska Peninsula (< 4% cover), but slightly higher around Cold Bay than on Caribou River. Forage is plentiful on the Black Hill and Caribou River calving and summer ranges, but higher density of calving caribou on Black Hill compromises the ability of individuals to forage as selectively as those on Caribou River. Early growth of plants (green-up) commenced 1 month later on Black Hill than on Caribou River in 1992, and calving peaked 1 week later on

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[1] Post E.S. & Klein D.R. Range Ecology of a Food-Limited Caribou Herd in Alaska. Submitted to *Canadian Journal of Zoology.*

Black Hill than on Caribou River in 1992. With compromised foraging conditions in winter, the Southern Alaska Peninsula Caribou Herd appears to be experiencing a food-limited decline, possibly because of overgrazing of lichens during the recent population peak. Higher calf production in mid-summer on Caribou River than on Black Hill ostensibly is related to earlier green-up coupled with greater per-capita forage availability on Caribou River, which allows pregnant females there to ingest high-quality forage for 1 month preceding parturition.

1.2 Introduction

The tendency for populations of vertebrate herbivores to fluctuate has been well documented (Sinclair 1977; McCullough 1979). Early studies of population fluctuation in an ecosystem perspective suggested that the superabundance of forage relative to herbivore biomass precluded the possibility of limitation of herbivores by food shortage (Hairston *et al.* 1960; Slobodkin *et al.* 1967). More recently, a large body of research focusing on population fluctuations of herbivores in East Africa, possibly the world's most productive grassland ecosystem (McNaughton 1984), has identified the limiting influences of forage quantity and quality, as determined by seasonal rainfall, on several ungulates (Sinclair 1975; Botkin *et al.* 1981). For example, wildebeest (Connochaetes taurinus) (Sinclair 1979; Sinclair & Norton-Griffiths 1982; Sinclair *et al.* 1985; Dublin et al. 1990), greater kudu (Tragelaphus strepsiceros) (Owen-

Smith 1990), white-eared kob (Kobus kob leucotis) (Fryxell & Sinclair 1988) and African buffalo (Syncerus caffer) (Sinclair 1977; Dublin *et al.* 1990) are limited by the seasonality of forage availability, to which they have adapted by migrating, a response that also reduces their vulnerability to limitation by sedentary predators (Fryxell *et al.* 1988; Skogland 1991).

In Arctic ecosystems, the most prevalent resident herbivore is the caribou or wild reindeer (Rangifer tarandus), which occurs in large herds of up to several hundred thousand in Siberia and North America, and which also is characterized by dramatic population fluctuations and by migration between seasonal ranges (Murie 1935; Skoog 1968). Despite the relative nutrient limitation of Arctic ecosystems (McKendrick *et al.* 1980) and their lower productivity than that described from East Africa, limitation of caribou populations in North America, where caribou coexist with wolves (Canis lupus), brown bears (Ursus arctos), and other natural predators, has traditionally been ascribed to predation (Bergerud 1974; Miller & Broughton 1974; Bergerud & Elliot 1986). These conclusions have been based on comparisons of the relative abundances of caribou and wolves, their fluctuations relative to one another, or increases in caribou numbers following reductions in wolf numbers; in no instance was a detailed range evaluation conducted during a population decline. Alternatively, investigations of caribou declines in North America that have included range evaluations have identified forage limitation as a possible contributing factor (Pegau 1975;

Couturier *et al.* 1990). Indeed, on islands and in other areas where natural predators of caribou and wild reindeer are absent or scarce, declines of Rangifer typically are attributed to forage limitation during severe winters (Reimers 1977; Skogland 1985*a*; Gates *et al.* 1986; Meldgaard 1986; Tyler 1987; Leader-Williams 1988), overgrazing of lichens on winter ranges during population highs (Skogland 1990), or deterioration of summer range conditions at high densities of caribou (Couturier *et al.* 1990). Recent evidence for limitation of Rangifer populations by forage availability on both winter and summer ranges has led to debate over the relative importance of seasonal range conditions to reproductive success and population dynamics in this species (Reimers 1977; Messier *et al.* 1988; Skogland 1990).

The Southern Alaska Peninsula Caribou Herd (SAPCH) is a mainland Alaskan herd (Figure 1) that declined by > 80% in just 10 years, following a population high of > 10,000 in 1983, during which range-wide density of caribou was > 2.1/km^2 (Pitcher *et al.* 1990). Concomitant with this population decline was a steady drop in calf production in summer from a high of 33 calves:100 cows preceding the decline to a recent low of about 14 calves:100 cows in 1992. Preliminary investigations into the cause of the declines in caribou numbers and productivity in the SAPCH noted that skeletal variables were smaller than those of the neighboring Northern Alaska Peninsula Caribou herd and other mainland Alaskan herds, and that lichens appeared to be scarce on the winter ranges of

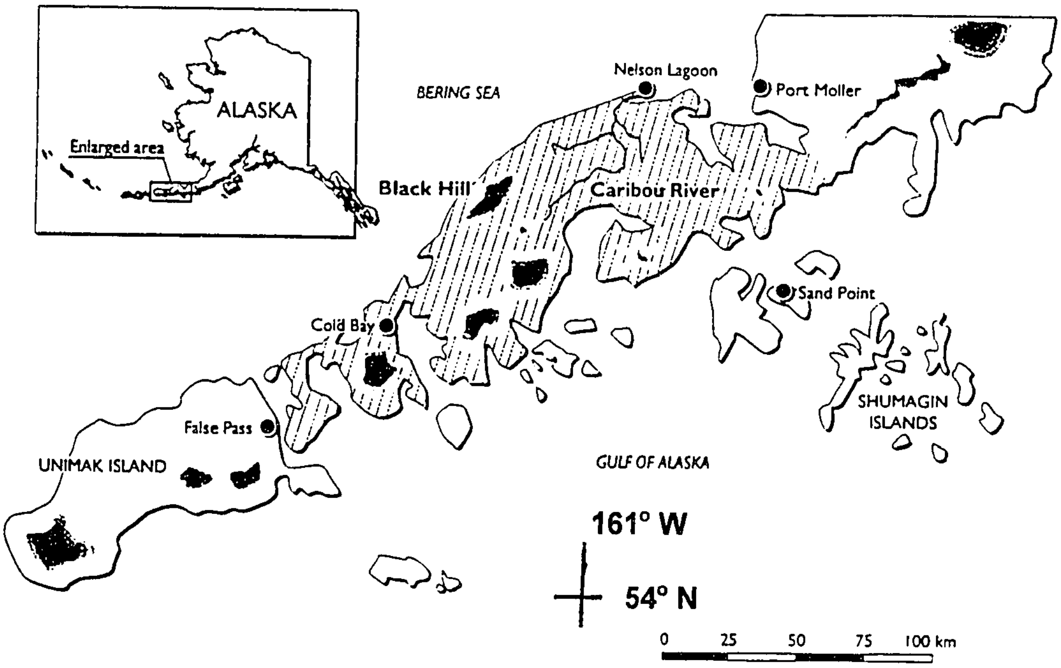

Figure 1. Range of the Southern Alaska Peninsula Caribou Herd (hatched area).

the SAPCH (Pitcher *et al.* 1990). These observations led to speculation that the herd was experiencing a food-limited decline.

Since 1989, two distinct sets of calving, summer, and winter ranges have been recognized on the Southern Alaska Peninsula, giving rise to the possibility that there are actually two subpopulations within this herd (Pitcher *et al.* 1990). The Black Hill group calves and spends summer in the mid-elevation foothills around Black Hill and Trader Mountain, then migrates into the low-lying Empetrum nigrum-dominated dwarf-shrub heath around Cold Bay for winter (Figure 1). In contrast, the Caribou River group is resident year-round in the sedge meadow plains transected by the Caribou River (Figure 1). Since 1989, data on calf production have been collected separately for the two calving ranges, and show consistently higher calf productivity on the Caribou River range than on the Black Hill range (Figure 2).

The existence of two groups with disparate productivities using different types of seasonal ranges within a single, declining caribou herd provided a unique opportunity to assess the potential roles of availability of seasonal forage in limiting numbers and productivity of a caribou population in mainland North America. We addressed the hypothesis that the SAPCH was declining due to food-limitation during winter. Thus, we predicted that availability of lichens on the Southern Alaska Peninsula would be lower than on ranges of other stable or increasing populations of Rangifer; furthermore, as low or lower than on ranges of

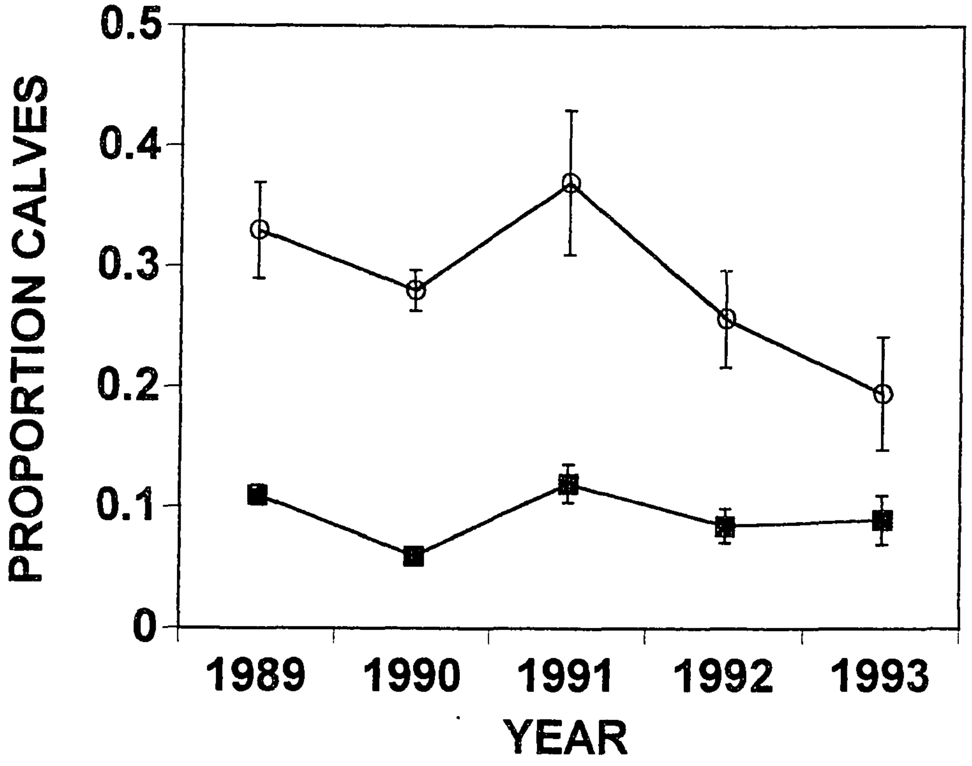

Figure 2. Mid-summer calf productivity (proportion calves and 95% CIs) in the Caribou River (open circle) and Black Hill (closed square) components of the Southern Alaska Peninsula Caribou Herd, Alaska, from 1989 - 1993. Proportion calves = # calves / (# calves + # cows).

Rangifer populations which had been shown to be limited by forage availability during winter. To address the debate over the relative contributions of winter and summer foraging conditions to productivity within Rangifer populations, we relied on comparisons between the Black Hill and Caribou River groups. Hence, if conditions on winter ranges were more important than those on summer ranges, we predicted that lichen availability during winter would be greater for the Caribou River group. Conversely, if conditions on summer ranges were more influential in affecting caribou productivity, we predicted that availability of forage during summer would be greater for the Caribou River group, and that the plant growing season would be longer on the summer range of the Caribou River group. Finally, we hypothesized that greater proportions of calves in mid-summer in the Caribou River group would be associated with earlier commencement of the calving season in that group, whether due to the influences of winter or summer range conditions.

1.3 Study Site and Methods

The Southern Alaska Peninsula (Figure 1) lies between 56°0' - 54°47'N and 161°15' - 163°30'W, composing a total area of approximately 4,900 km^2. The region is of volcanic origin, and is bounded by the Bering Sea on the north and Pacific Ocean on the south, separated at the widest point by about 55 km. The area is treeless, and characterized by a maritime climate with relatively long, cool summers and mild winters, heavy precipitation and strong winds. Elevational relief varies from broad, sea-level flood plains to mountains and active volcanoes 1,500 - 2,500 m in height. Low-lying areas are traversed by rivers, creeks, and lakes and are dominated by wet- and mesic-sedge meadows consisting mainly of Carex nesophila, Potentilla palustris, and Equisetum arvense. Mid-elevation zones comprise a mosaic of tundra-like dwarf-shrub heath (hereafter referred to as heath) dominated by Empetrum nigrum and Betula nana, and mesic-sedge meadows consisting mostly of C. nesophila and Eriophorum angustifolium bordering water courses and lake margins.

Seasonal ranges were quantified according to major plant communities identified by ground-truthing during sampling of forage cover and biomass. Aerial photographs (scale 1:63,360) of seasonal ranges of caribou were overlain with a transparent plastic grid of 1-mm squares; 100 points were located randomly on each range, and the type of habitat encountered by each point was recorded (Marcum & Loftsgaarden 1980). Range areas were estimated as the total number of 1-mm squares composing each range, converted to km^2.

Estimation of percent cover and biomass of forage on seasonal ranges was based on a randomly oriented, stratified, systematic sampling design (Scheaffer *et al.* 1990). Sampling sites were chosen at random from pools of potential sites, designated as those in which caribou had been observed foraging during aerial surveys conducted prior to sampling. Seasonal ranges were stratified according to major habitat types, and three sampling sites were chosen within each stratum. Within each sampling site, three nonoverlapping transects (100 m) were laid randomly; along each transect, sampling frames were laid at intervals of 10 m. Percent cover of forage species was measured using a point frame with 10 pins spaced at 10-cm intervals. As a pin was lowered, the first species encountered was recorded. Biomass of forage species was measured using a 0.25 m^2 frame from which all standing, live vegetation was collected. Forage samples were dried in the field and stored in paper bags. In the laboratory, forage samples were sorted according to forage classes (lichens; graminoids, including families Poaceae, Cyperaceae, and Juncaceae; forbs; deciduous shrubs, including families Salicaceae and Betulaceae; and ericaceous shrubs, including the family Ericaceae), dried in an oven to a constant weight at 60°C for 24 h, and weighed on a Mettler balance to the nearest 1 mg. Winter ranges were sampled in December 1991 (Black Hill) and March 1993 (Caribou River); summer ranges were sampled in July 1991 and 1992 (Caribou River and Black Hill) and September 1992 (Caribou River and Black Hill). Comparisons of forage availability between ranges were based on *Z*-tests of proportions of forage classes and *t*-tests of means of biomass within forage classes on winter and summer ranges.

Habitat use by caribou of both the Black Hill and Caribou River groups was recorded in five seasons: mid-winter (December), late winter (late February, early

March and early April), pre-calving (mid-May), calving (late May through late June), and post-calving (July). Seasonal use of habitats was based on observations of foraging caribou during radio-tracking surveys conducted from fixed-wing aircraft as part of routine censusing of caribou numbers and productivity by staff of Izembek National Wildlife Refuge. Surveys were flown in December 1990; May, June, July, and December 1991; May, June, and July 1992; and February, March, and April 1993. Locations, sizes and compositions of groups were noted on maps (scale 1:63,360), along with information about the types of habitat in which the groups occurred. During surveys in winter, when snowcover precluded identification of habitat types from the air, habitats used by groups were identified later from aerial photographs. Data on habitat selection were analyzed using the chi-square test of homogeneity. To avoid bias to which this test is susceptible (Aebischer *et al.* 1993), we used individual animals, rather than groups or radio locations as sample units. Furthermore, to reduce the risk of Type I error, we set $\alpha = 0.01$ for tests of significance. Tests of selection for or avoidance of specific habitat types were based on construction of Bonferroni simultaneous confidence intervals of percent use minus percent availability (Marcum & Loftsgaarden 1980; Thomas & Taylor 1990), with the following confidence levels: 90% family ($\alpha = 0.10$) and 97.5% individual ($\alpha = 0.025$) for instances with four habitat categories; 85% family ($\alpha = 0.15$) and 97% individual ($\alpha = 0.03$) for cases with five habitat categories. Individual confidence levels were determined using the formula C.L. = $1 - \alpha/k$, where k = the number of categories of habitat; family confidence levels were determined using the formula C.L. = $k(100)(1 - \alpha)\%$ (Marcum & Loftsgaarden 1980). Values of α for Bonferroni simultaneous confidence levels were set according to recommendations in Marcum & Loftsgaarden (1980), with α becoming larger as the number of categories being simultaneously compared increased.

Identification and analysis of seasonal diets of caribou in both groups were based on fresh fecal samples collected from groups observed from the ground. Fecal samples were collected in the following seasons: mid-winter (December 1991), late winter (February, March and April 1993), calving (late May through late June 1991 and 1992), and post-calving (July 1991 and 1992). Pellets were collected from between 15 to 20 individual fecal groups for each season, and combined into one original and seven pseudo-replicate samples for each season. Samples were ground (0.1 mm screen) and analyzed microhistologically for composition of plant tissue to forage class (lichens, graminoids, forbs, deciduous shrubs, ericaceous shrubs, and mosses) under 100 fields of view at the Habitat Lab of Washington State University (Todd & Hansen 1973). Seasonal diets were estimated from fecal samples by converting proportions of lichens, graminoids, deciduous and ericaceous shrubs, and mosses in the feces to proportions in the diet using correction factors based on digestibility during feeding trials with captive caribou and reindeer (Duquette 1984). Proportions of forbs in seasonal diets were calculated by subtracting from one the sum of the corrected proportions of other forage classes, because no correction factors for forbs in caribou or reindeer diets exist as of yet; potential bias from this method could overestimate the proportion of forbs in the diet (Russell *et al.* 1990). Diet selection by the Black Hill and Caribou River groups was estimated for the seasons in which fecal samples were collected, using the chi-square test of homogeneity (Marcum & Loftsgaarden 1980; Thomas & Taylor 1990), with construction of Bonferroni simultaneous confidence intervals of percent use minus percent availability to assess selection for or avoidance of individual forage classes (Marcum & Loftsgaarden 1980) with 80% family ($\alpha = 0.20$) and 96.7% individual ($\alpha = 0.033$) confidence levels. Confidence levels and values of α were determined as described previously.

Progression of the growth season for plants was monitored in 20, 0.5 m^2 plots located randomly on each of the two calving ranges. Preliminary observations were made on 28 May 1992 on Black Hill and 29 May 1992 on Caribou River. Subsequently, plots were re-visited every 3rd day during alternating 2-week intervals on each of the two ranges. Observations on Black Hill ended 5 July 1992, whereas those on Caribou River ended 7 July 1992. As a means of indexing the progression of the growing season, the numbers and names of all plant species present in plots were recorded on each visit. Upon the last day of observation in each area, a final number of plant species was present in each plot. Mean numbers of species present for each range were subsequently calculated for each day of observation, and converted to proportions of the final number of species present on each day for each range. Mean proportions of the final number of species present on each range were plotted against Julian day, and the resulting curves linearized by conversion of the proportions to probits. Probit analysis (Finney 1952) was used to calculate dates of 50% emergence of forage species on each of the two calving ranges. The length of the plant growth season on each range was estimated as the number of days from 10 to 90% emergence of forage species, using nonlinear modeling procedures (SYSTAT, Inc. 1992).

The timing and synchrony of calving seasons on the Black Hill and Caribou River calving ranges were estimated using observed proportions of calves (number of calves per total number of cows plus calves) recorded during aerial and ground-based surveys (Caughley & Caughley 1974; Bowyer 1991; Rachiow & Bowyer 1991) through May and June 1992. Weighted proportions of calves (Caughley & Caughley 1974) were plotted against Julian day, converted to proportion births (Caughley & Caughley 1974; Rachlow & Bowyer 1991), and re-plotted against Julian day. Plots of proportion of births over time were analyzed using probit analysis (Finney 1952) to estimate mean dates of birth. The length of the calving season (number of days between the first observed birth and 80% births) (Rutberg 1984) was estimated using nonlinear modeling procedures

(SYSTAT, Inc. 1992) for each of the two ranges. The *F*-test of polynomial regressions fitted to plots of percent births over time was used to test for differences in timing and synchrony of the calving seasons on the two ranges (Rachiow & Bowyer 1991).

1.4 Results

1.4.1 Composition of Seasonal Ranges

The winter range at Cold Bay, used by caribou calving on Black Hill, was dominated by heath, with much lower cover of wet-sedge meadow, barren soil, standing water, willow thicket, and riparian-sedge meadow (Table 1). With the nonvegetated classes excluded and the remaining categories re-scaled to 100%, the Cold Bay winter range consisted of 72 ± 4.5% (95% CI) heath, 22 ± 4.1% wet-sedge meadow, 3 ± 1.7% willow thicket, and 3 ± 1.7% riparian sedge meadow. The total vegetated area of the Cold Bay winter range composed 1,073.5 ± 333.5 km^2.

The calving range at Black Hill consisted mostly of heath, followed by barren soil, willow thicket, riparian-sedge meadow, wet-sedge meadow, and standing water (Table 1). Excluding nonvegetated classes and rescaling to 100%, the Black Hill range comprised 77 ± 4.2% (95% CI) heath, 10 ± 3.0% willow thicket, 7 ± 2.6% riparian sedge meadow, and 6 ± 2.4% wet-sedge meadow, and a total vegetated area of 789 ± 199 km^2.

Table 1. Compositions of seasonal ranges used by caribou on the Southern Alaska Peninsula, Alaska 1991 - 1993. Values are percents of total cover with 95% confidence intervals, based on a nonmapping technique (Marcum & Loftsgaarden 1980), with sample sizes given in parentheses.

RANGE	Heath	Wet Sedge	Mesic Sedge	Riparian Sedge	Willow Thicket	Barren Soil	Water
Cold Bay (100)	53 ± 5.0	16 ± 3.7	0	0	3 ± 1.7	16 ± 3.8	10 ± 3.0
Black Hill (100)	64 ± 4.8	0	5 ± 2.2	6 ± 2.4	8 ± 2.7	13 ± 3.4	4 ± 2.0
Caribou River (100)	17 ± 3.8	33 ± 4.7	35 ± 4.7	3 ± 1.7	1 ± 0.1	1 ± 0.1	10 ± 3.0

The Caribou River range, used year-round by the Caribou River group, comprised comparatively little heath, but was dominated instead by mesic-sedge meadow and wet-sedge meadow, with a comparable percentage of standing water (Table 1). Relatively little of the total range was covered by riparian-sedge meadow, willow thicket, or barren soil. With nonvegetated classes excluded and re-scaling of vegetated classes to 100%, the Caribou River range consisted of 39 ± 4.9% (95% CI) mesic meadow, 37 ± 4.8% wet-sedge meadow, 19 ± 3.9% heath, 4 ± 2.0% riparian-sedge meadow, and 1 ± 0.1% willow thicket. The Caribou River range consisted of 1,335 ± 377 km^2 of total vegetated area.

1.4.2 Seasonal Habitat Selection

Comparisons of caribou distribution across habitat types to availabilities of those habitats provided the basis for assessment of habitat selection by season. Chi-square analysis of caribou distributions around Cold Bay during mid-winter suggested that caribou used some habitats disproportionately to their availability ($\chi^2 = 52.7$, $P < 0.001$); however, analysis of Bonferroni simultaneous confidence intervals indicated that habitat use was proportionate to availability for all classes ($P > 0.05$ in all instances) (Table 2). On Caribou River, habitat use was disproportionate to availability during mid-winter ($\chi^2 = 104$, $P < 0.001$), as caribou preferentially foraged in mesic meadows and avoided wet-sedge meadows (Table 2). Use of other habitat types on Caribou River during mid-winter did not differ from availability ($P > 0.05$ in all instances).

Table 2. Seasonal habitat selection by caribou in the Black Hill and Caribou River groups, Alaska, 1991 - 1993. Selection = % use - % available, and was considered significant if $P < 0.01$ based on the Chi-square test of homogeneity (Thomas & Taylor 1990). Positive values indicate selection for, whereas negative values indicate selection against habitat types; "---" indicates that a particular habitat type was not a component of that range.

Season	Heath	Mesic Sedge	Wet Sedge	Riparian Sedge	Willow Thicket
MID-WINTER					
Black Hill	+ 0.08	- 0.02	---	- 0.03	- 0.03
Caribou River	+ 0.08	+ 0.20***	- 0.23***	- 0.04	- 0.01
LATE WINTER					
Black Hill	+ 0.10	- 0.04	---	- 0.03	- 0.03
Caribou River	+ 0.37***	- 0.10	- 0.22***	- 0.04	- 0.01
PRE-CALVING					
Black Hill	+ 0.06	- 0.06**	---	+ 0.10	-0.10**
Caribou River	- 0.19***	- 0.35***	- 0.27***	+ 0.83***	- 0.01

continued

Table 2. Continued.

Season	Heath	Mesic Sedge	Wet Sedge	Riparian Sedge	Willow Thicket
CALVING					
Black Hill	- 0.58***	+ 0.28***	---	+ 0.40***	- 0.10
Caribou River	- 0.19***	+ 0.19***	- 0.01	+ 0.02	- 0.01
POST-CALVING					
Black Hill	+ 0.22***	- 0.05	---	- 0.07***	- 0.10
Caribou River	- 0.19*	+ 0.22*	+ 0.02	- 0.04	- 0.01

* $P < 0.01$
** $P < 0.005$
*** $P < 0.001$

Analysis of data on use and availability from late winter around Cold Bay indicated that these values differed ($\chi^2 = 25.4$, $P < 0.001$), but construction of Bonferroni simultaneous confidence intervals revealed no significant differences for individual categories ($P > 0.05$ in all instances) (Table 2). During late winter on Caribou River, however, use differed from availability ($\chi^2 = 90.8$, $P < 0.001$), as caribou avoided wet-sedge meadows and selected heath (Table 2).

During the 2 - 3 weeks preceding calving, caribou on Black Hill discriminated significantly between habitat types ($\chi^2 = 15.3$, $P < 0.005$), avoiding willow thickets and mesic-sedge meadows (Table 2). Use of heath and riparian-sedge meadows did not differ from availability during this period on Black Hill ($P > 0.05$ in both instances). On Caribou River, the pre-calving season was characterized by strongly disproportionate use of habitat types ($\chi^2 = 229.5$, $P < 0.001$). Caribou on Caribou River preferentially used riparian-sedge meadows, while avoiding wet-sedge meadows, mesic-sedge meadows, and heath (Table 2). Use of willow thickets did not differ from availability on Caribou River preceding calving ($P > 0.05$).

Caribou calving on Black Hill displayed disproportionate use of habitat types during the calving season ($\chi^2 = 370.8$, $P < 0.001$). Calving females avoided heath, while selecting for riparian-sedge meadows and mesic-sedge meadows (Table 2). Willow thickets were used in proportion to availability ($P > 0.05$). Calving cows also used certain habitat types disproportionately on Caribou River

($\chi^2 = 191.8$, $P < 0.001$). There, use of mesic-sedge meadows exceeded their availability, while heath was avoided (Table 2). Caribou calving on Caribou River used wet-sedge meadows, riparian-sedge meadows, and willow thickets in proportion to availability ($P > 0.05$ in all instances).

Following the calving season, caribou on Black Hill maintained strongly disproportionate use of habitat types ($\chi^2 = 1101$, $P < 0.001$), shifting their preference to heath, and avoiding riparian-sedge meadows (Table 2). Use of willow thickets and mesic-sedge meadows did not differ from availability on Black Hill following calving ($P > 0.05$ in both cases). The post-calving season on Caribou River also was characterized by disproportionate use of habitat types ($\chi^2 = 13.9$, $P < 0.01$), as caribou there continued using mesic-sedge meadows in excess of their availability, while avoiding heath (Table 2). Finally, wet-sedge meadows, riparian-sedge meadows, and willow thickets were used in proportion to availability on Caribou River during the post calving season ($P > 0.05$ in all cases).

1.4.3 Forage Availability on Seasonal Ranges

Analysis of data on percent cover revealed that graminoids were the most abundant forage available on both winter ranges (Cold Bay: 25.4 ± 3.2%, 95% CI; Caribou River: 27.0 ± 2.5%), whereas lichens were exceedingly scarce in both areas (Cold Bay: 2.9 ± 1.3%; Caribou River: 0.73 ± 0.48%) (Figure 3*a*). Pairwise comparisons revealed no differences in the abundance of these forage classes

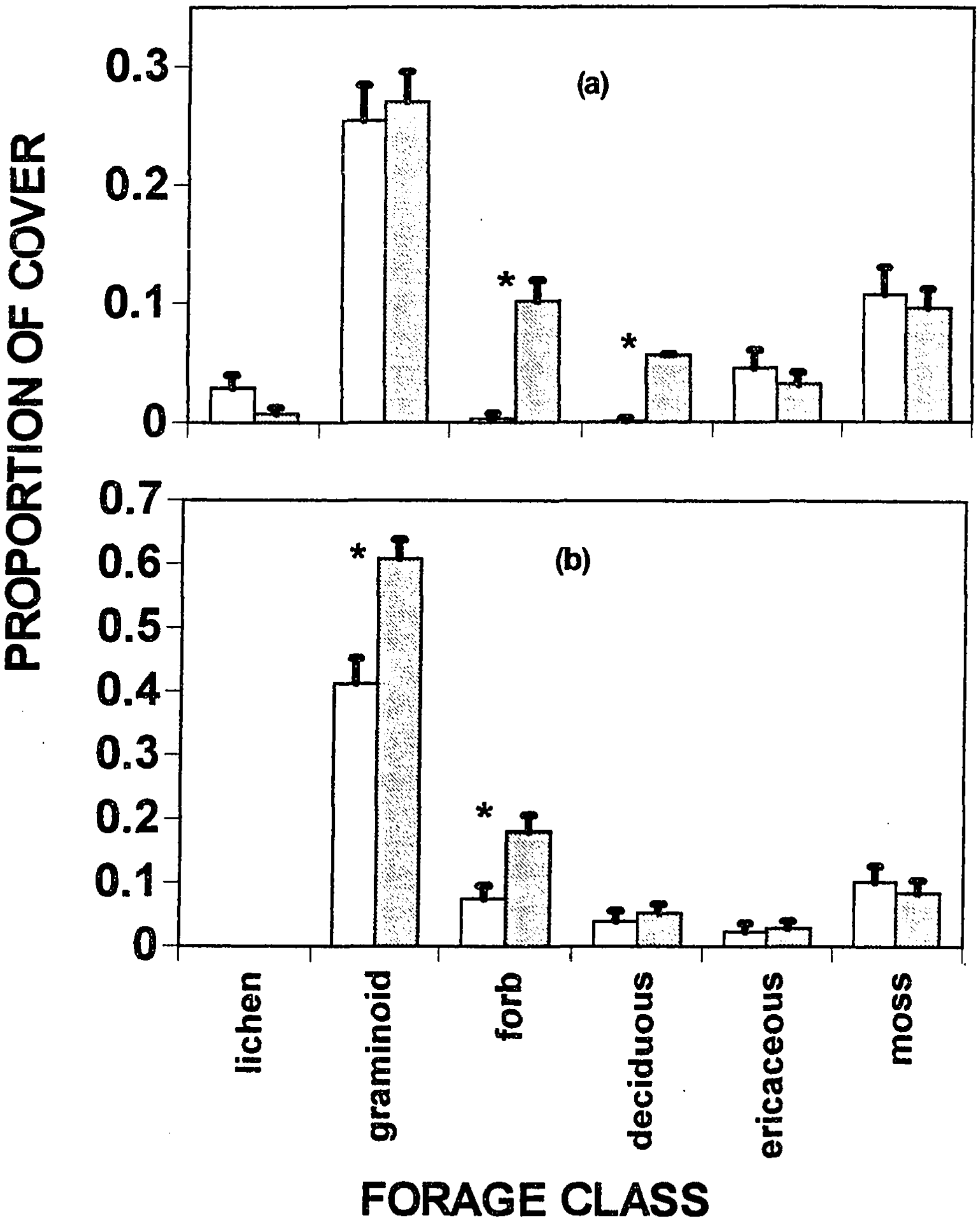

Figure 3. Proportions of total ground cover (mean + 1 SE) represented by classes of caribou forage on winter (a) and summer (b) ranges of the Black Hill (shaded bars) and Caribou River (open bars) groups, Alaska, 1991 - 1993. * = $P < 0.05$, based on the Z-test within classes. Note different scales for winter and summer.

between the two ranges (graminoids: $Z = 0.39$, $P > 0.05$; lichens: $Z = 1.91$, $P > 0.05$). On the winter range at Cold Bay, little forage was available as ericaceous shrubs (4.5 ± 1.5%), forbs (0.30 ± 0.41%), and deciduous shrubs (0.08 ± 0.21%). The winter range at Caribou River contained a comparable percentage of ericaceous shrub forage (3.1 ± 0.9%; $Z = 0.79$, $P > 0.05$), but significantly greater proportions of forbs (10.2 ± 1.7%; $Z = 4.27$, $P < 0.05$) and deciduous shrubs (5.6 ± 1.3%; $Z = 3.18$, $P < 0.05$). Moss was equally abundant on both winter ranges (Cold Bay: 10.7 ± 2.3%; Caribou River: 9.6 ± 1.6%; $Z = 0.39$, $P > 0.5$).

Biomass of lichens was low on both winter ranges, although greater on the Cold Bay range (Cold Bay: 9.47 ± 0.70 g/m^2; Caribou River: 2.63 ± 0.24 g/m^2; $t = 9.28$, $P < 0.05$) (Figure 4*a*). In contrast, biomass of graminoids was relatively high on both ranges, and nearly twice as great on Caribou River than on the Cold Bay winter range (Caribou River: 42.1 ± 0.84 g/m^2; Cold Bay: 23.3 ± 0.86 g/m^2; $t = 32.3$, $P < 0.05$). Biomass of deciduous shrubs was low on both ranges, but greater on the Caribou River range (Caribou River: 2.58 ± 0.08 g/m^2; Cold Bay: <0.01 g/m^2; $t = 30.4$, $P < 0.05$). Only traces (<0.01 g/m^2) of forb biomass were detectable on both winter ranges.

Analysis of data on percent cover from summer ranges revealed that graminoids were the most abundant forage on both calving ranges, and that graminoids were more common on Caribou River than on Black Hill (Caribou River: 60.8 ± 3.2%; Black Hill: 41.2 ± 4.2%; $Z = 3.70$, $P < 0.05$) (Figure 3*b*).

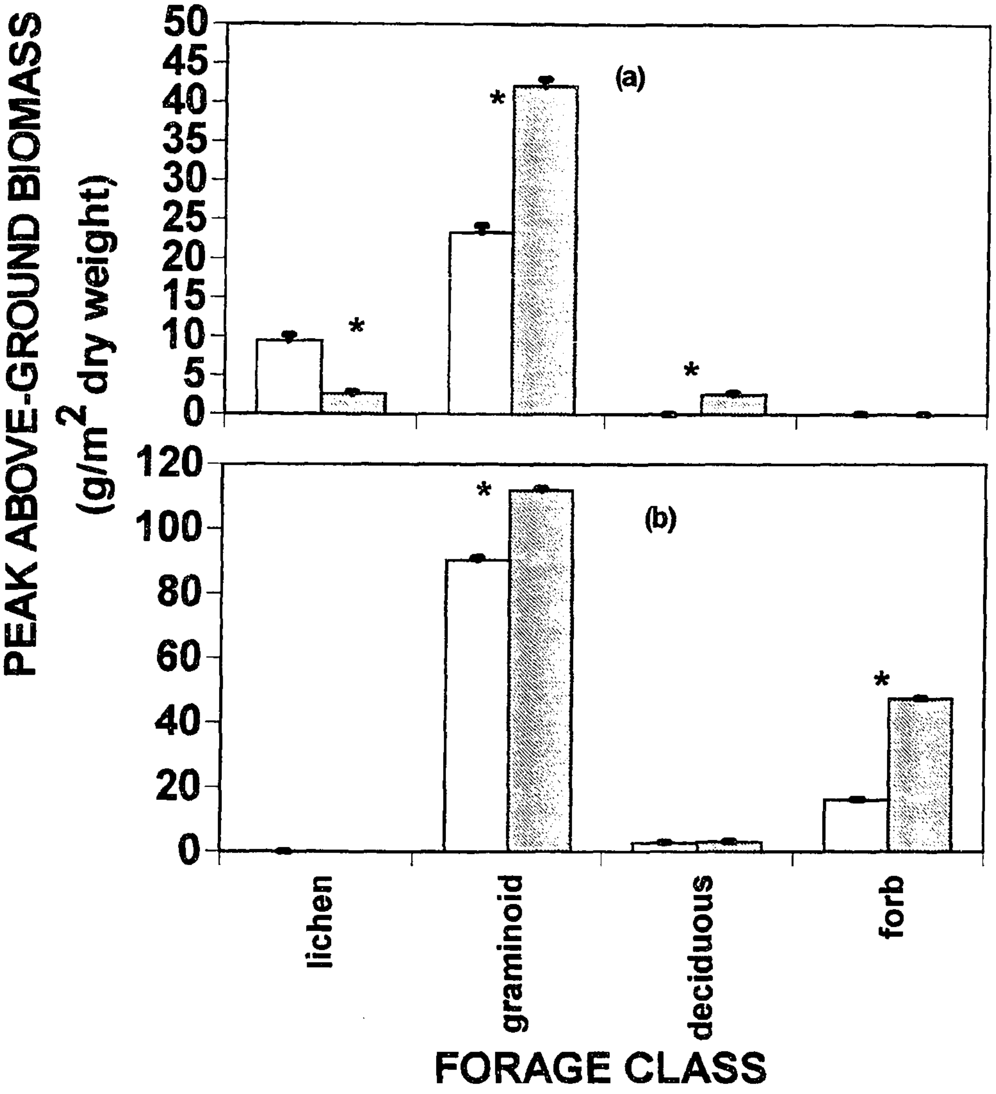

Figure 4. Peak above-ground biomass (mean + 1 SE) of caribou forage available on winter (a) and summer (b) ranges of the Black Hill (shaded bars) and Caribou River (open bars) groups, Alaska, 1991 - 1993. * = $P < 0.05$, based on *t*-tests within classes.

Forbs were the next most frequent of forage on both summer ranges, and they were more than twice as abundant on Caribou River (18.0 ± 2.5%) as on Black Hill (7.5 ± 2.2%) ($Z = 2.83$, $P < 0.05$). Deciduous shrubs accounted for 5.2 ± 1.4% of the total cover on Caribou River and 3.9 ± 1.6% of the total cover on Black Hill, although this difference was not significant ($Z = 0.58$, $P > 0.50$). Ericaceous shrubs were uncommon on both Caribou River (2.9 ± 1.1%) and Black Hill (2.3 ± 1.3%), and their availability did not differ between the two summer ranges ($Z = 0.35$, $P > 0.70$). Moss accounted for 8.4 ± 1.8% of the total cover on Caribou River and, equivalently, 10.1 ± 2.5% of the total cover on Black Hill ($Z = 0.55$, $P > 0.50$). Lichens was not detected during sampling of either summer range.

Forage biomass on summer ranges followed the same pattern of abundance as forage cover (Figure 4*b*). Graminoid biomass was greater on Caribou River (111.9 ± 1.9 g/m^2) than on Black Hill (90.3 ± 3.1 g/m^2) ($t = 5.98$, $P < 0.05$). Similarly, forb biomass was nearly three times greater on Caribou River (47.5 ± 0.61 g/m^2) than on Black Hill (16.1 ± 0.65 g/m^2) ($t = 9.75$, $P < 0.05$). Biomass of deciduous shrubs was low on both ranges, and did not differ between ranges (Caribou River: 3.1 ± 0.12; Black Hill: 2.7 ± 0.64; $t = 0.63$, $P > 0.50$).

1.4.4 Seasonal Diets

Microhistological analysis of fecal samples provided the basis for estimation of seasonal diets. Feces gathered during mid-winter around Cold Bay consisted mostly of moss, followed by ericaceous shrubs and lichens (Table 3). Similarly, mid-winter feces from Caribou River consisted mainly of ericaceous shrubs, moss and lichens (Table 3). Late-winter feces from Cold Bay were composed principally of moss, lichens, and ericaceous shrubs, whereas late winter feces from Caribou River consisted mostly of moss, graminoids, and forbs (Table 3). During the calving season, fecal samples gathered on Black Hill contained mostly graminoids, moss, and forbs, whereas feces collected at that time on Caribou River were composed mainly of forbs (Table 3). Finally, fecal samples from Black Hill during the post-calving season comprised mostly graminoids and forbs, whereas those from the post-calving season on Caribou River contained mostly forbs (Table 3).

Conversion of fecal proportions using correction factors based on feeding trials with captive reindeer and caribou (Duquette 1984) yielded estimates of proportions of each forage class present in seasonal diets. Mid-winter diets did not differ between the two ranges ($\chi^2 = 2.65$, $P > 0.05$) (Figure 5*a*). Lichens and moss were the most abundant classes in diets from both Cold Bay (lichens: 31.3 ± 12.0%; moss: 38.5 ± 13.0%) and Caribou River (lichens: 35.3 ± 12.0%; moss: 29.2 ± 12.0%). Forbs composed 16.6 ± 9.6% of the mid-winter diet on the Cold Bay range and 18.2 ± 10.0% of the diet on the Caribou River range. Ericaceous shrubs accounted for 9.1 ± 7.4% and 11.8 ± 8.3% of the diet on the Cold Bay and Caribou River ranges respectively. Finally, deciduous shrubs composed only

Table 3. Compositions of caribou fecal samples collected seasonally on ranges used by the Black Hill and Caribou River groups, Alaska, 1991 - 1993, as determined by microhistological analysis at the Washington State University Habitat Lab. Values are percentages based on sample sizes given in parentheses.

Season	Lichen	Graminoid	Forb	Deciduous Shrub	Ericaceous Shrub	Moss
MID-WINTER						
(15) Black Hill	18.8	3.6	7.9	1.9	25.5	42.3
(15) Caribou River	21.2	3.1	5.4	5.1	33.1	32.1
LATE WINTER						
(18) Black Hill	29.3	12.5	4.1	1.3	20.3	32.5
(18) Caribou River	9.0	27.4	13.8	2.9	12.5	34.4

continued

Table 3. Continued.

Season	Lichen	Graminoid	Forb	Deciduous Shrub	Ericaceous Shrub	Moss
CALVING						
(20) Black Hill	15.7	25.6	18.7	2.9	16.3	20.8
(20) Caribou River	3.2	34.1	52.0	2.7	2.8	5.2
POST-CALVING						
(20) Black Hill	7.7	38.3	30.6	2.1	11.1	10.2
(20) Caribou River	2.2	31.9	59.8	0.7	3.1	2.3

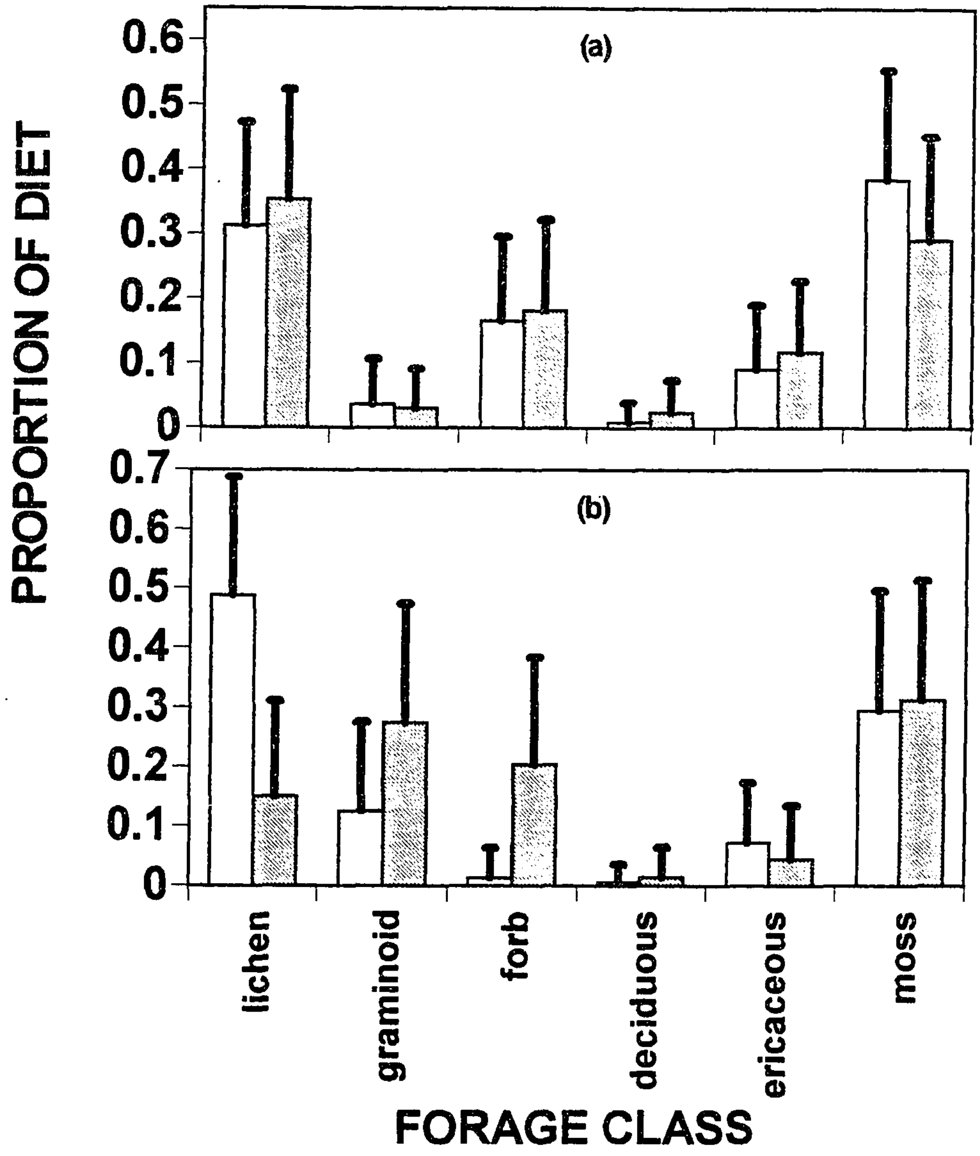

Figure 5. Compositions of diets (mean + 1 SE) of caribou in mid-winter (a) and late winter (b) in the Black Hill (shaded bars) and Caribou River (open bars) groups, Alaska, 1992 and 1993. Diets were estimated from fecal contents using fecal correction factors in Duquette (1984).

small fractions of the mid-winter diets on both ranges (Cold Bay: 0.91 ± 2.5%; Caribou River: 2.4 ± 4.0%).

Late-winter diets differed significantly between the two ranges ($\chi^2 = 41.30$, $P < 0.05$) (Figure 5*b*). Lichens were the most abundant class in diets of caribou at Cold Bay (48.8 ± 12.9%), accounting for nearly three times as much of the total diet as they did on Caribou River (15.0 ± 8.7%) ($Z = 2.07$; $P < 0.05$). Graminoids contributed 12.5 ± 8.5% and 27.4 ± 10.8% to the total diets from Cold Bay and Caribou River respectively, although this difference was not significant ($Z = 1.04$, $0.50 > P > 0.20$). Forbs represented only 1.3 ± 2.9% of the Cold Bay diet and 20.4 ± 9.8% of the Caribou River diet, but this difference was only marginally significant ($Z = 1.70$, $0.1 > P > 0.09$). Deciduous and ericaceous shrubs accounted for small fractions of the diets on both ranges (Cold Bay: deciduous = 0.6 ± 2.0%, ericaceous = 7.3 ± 6.7%; Caribou River: deciduous = 1.4 ± 2.8%, ericaceous = 4.5 ± 5.4%). Finally, a relatively large proportion of the diet was composed of moss on both the Cold Bay (29.5 ± 12.0%) and Caribou River (31.3 ± 11.0%) winter ranges.

Compositions of diets during the calving season on both ranges also differed significantly ($\chi^2 = 40.1$, $P < 0.05$) (Figure 6*a*). Although lichens were a major component of the diet during the calving season on Black Hill (26.2 ± 10.0%), they were a minor component on Caribou River (5.3 ± 5.1%); however, this difference was not significant ($Z = 1.77$, $0.1 > P > 0.09$). Graminoids

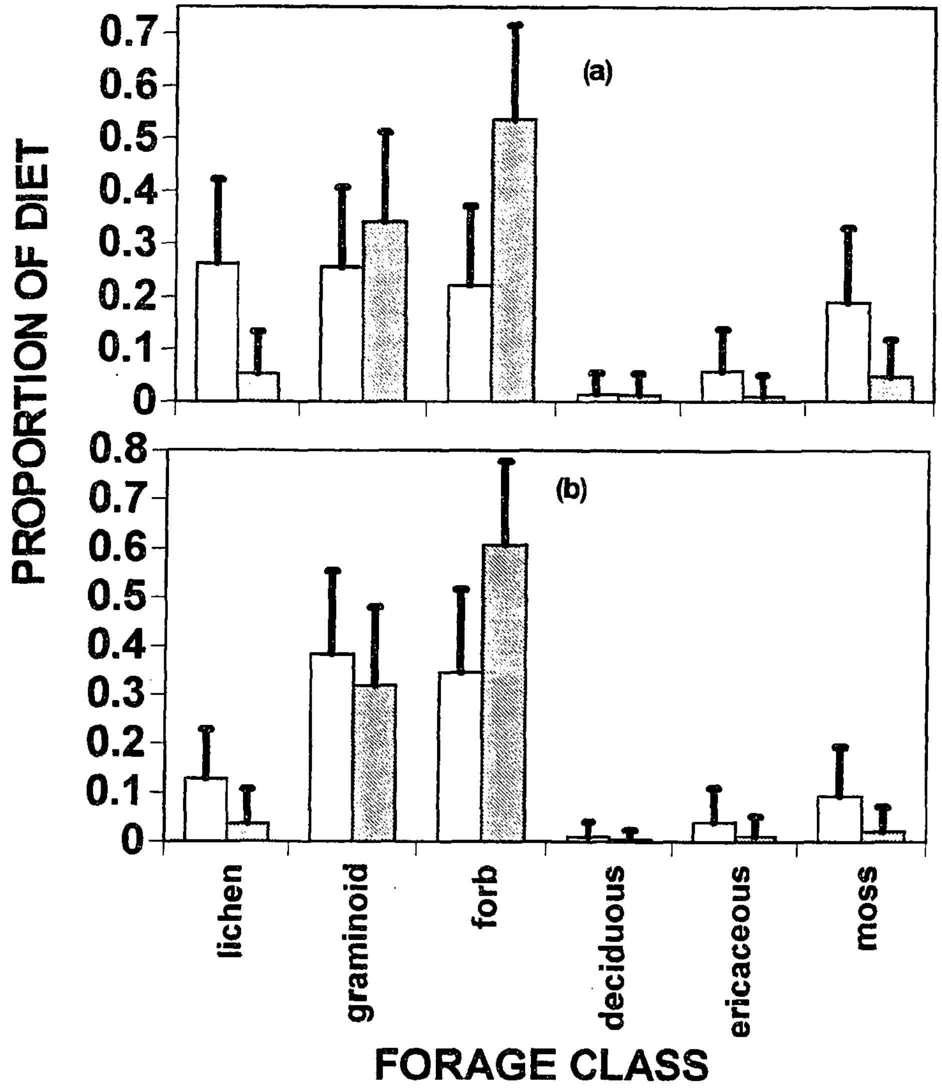

Figure 6. Compositions of diets (mean + 1 SE) of caribou during the calving (a) and post-calving (b) seasons in the Black Hill (shaded) and Caribou River (open bars) groups, Alaska, 1992 and 1993. Diets were estimated from fecal contents using fecal correction factors in Duquette (1984).

composed 25.6 ± 10.0% of the diet during the calving season on Black Hill and 34.1 ± 11.0% of the total diet on Caribou River. Forbs, however, were more than twice as abundant in the Caribou River diets (53.6 ± 11.0%) as they were in the Black Hill diets (22.1 ± 10.0%) ($Z = 2.00$; $P < 0.05$). As in winter diets, deciduous and ericaceous shrubs contributed little to the total diet on either range (Black Hill: deciduous = 1.4 ± 2.7%, ericaceous = 5.8 ± 5.4%; Caribou River: deciduous = 1.3 ± 2.6%, ericaceous = 1.0 ± 2.3%). Moss was more abundant in the Black Hill diets (18.9 ± 9.0%) than in the Caribou River diets (4.7 ± 4.9%), but not significantly so.

Finally, chi-square analysis indicated that post-calving diets differed significantly between ranges ($\chi^2 = 19.3$, $P < 0.05$), but individual comparisons within forage classes revealed no significant differences ($P > 0.05$ in all instances) (Figure 6*b*). On Black Hill, diets of caribou in the post-calving season contained 12.8 ± 7.5% lichens, whereas during the same season on Caribou River, caribou diets contained only 3.7 ± 4.2% lichens. Graminoids contributed 38.3 ± 11.0% and 31.9 ± 10.0% to the total diets on Black Hill and Caribou River respectively. As in diets for the calving season, forbs were the major dietary component on Caribou River (60.8 ± 11.0%), composing almost twice as much of the total diet as they did on Black Hill (34.6 ± 11.0%), although this difference was not significant ($Z = 1.66$; $P > 0.05$). The abundance of deciduous and ericaceous shrubs in post-calving diets reflected their abundance in diets during other seasons, representing small fractions on both summer ranges (Black Hill: deciduous = 1.0 ± 2.2%, ericaceous = 4.0 ± 4.4%; Caribou River: deciduous = 0.4 ± 1.4%, ericaceous = 1.1 ± 2.3%). As in diets during the calving season, moss was relatively scarce, accounting for 9.3 ± 6.5% of the diet on Black Hill and 2.1 ± 3.2% of the total diet on Caribou River.

1.4.5 Seasonal Diet Selection

Comparisons of dietary proportions to proportions of forage available seasonally provided the basis for estimation of diet selection. During mid-winter, use of forage classes was disproportionate to availability on both the Cold Bay ($\chi^2 = 82.5$, $P < 0.001$) and Caribou River ($\chi^2 = 81.2$, $P < 0.001$) ranges (Table 4). Caribou wintering around Cold Bay used lichens and moss in significantly greater proportions than were available, while using graminoids and forbs in proportions significantly less than their availability (Table 4). Use of deciduous and ericaceous shrubs by caribou around Cold Bay did not differ from availability ($P > 0.05$ in both instances). On the Caribou River winter range, use of lichens and moss was significantly greater than their availabilities, whereas use of graminoids was significantly less than availability (Table 4). Use of forbs and deciduous and ericaceous shrubs did not differ from availability on Caribou River ($P > 0.05$ in all instances).

Late-winter use of forage classes differed significantly from their availability on both ranges (Black Hill: $\chi^2 = 62.9$; Caribou River: $\chi^2 = 28.0$; $P < 0.001$ in both

Table 4. Seasonal diet selection by caribou in the Black Hill and Caribou River groups, Alaska, 1991 - 1993. Selection = % use - % available, and was considered significant if *P* < 0.01 based on the Chi-square test of homogeneity (Thomas & Taylor 1990). Positive values indicate selection for, whereas negative values indicate selection against forage classes.

Season	Lichen	Graminoid	Forb	Deciduous Shrub	Ericaceous Shrub	Moss
MID-WINTER						
Black Hill	+ 0.25**	- 0.54**	- 0.52**	+ 0.01	- 0.01	+ 0.14**
Caribou River	+ 0.34**	- 0.45**	+ 0.001	- 0.08	- 0.06	+ 0.12**
LATE WINTER						
Black Hill	+ 0.42**	- 0.46**	+ 0.01	+ 0.005	- 0.03	+ 0.05
Caribou River	+ 0.14**	- 0.21**	+ 0.02	- 0.09	- 0.01	+ 0.14**

continued

Table 4. Continued.

Season	Lichen	Graminoid	Forb	Deciduous Shrub	Ericaceous Shrub	Moss
CALVING						
Black Hill	+ 0.26**	- 0.38**	+ 0.11	- 0.05	+ 0.02	+ 0.03
Caribou River	+ 0.05**	- 0.30**	+ 0.35**	- 0.04	- 0.02	- 0.04
POST-CALVING						
Black Hill	+ 0.13**	- 0.25**	+ 0.23**	- 0.05	+ 0.01	- 0.06
Caribou River	+ 0.04	- 0.32**	+ 0.42**	- 0.05**	- 0.02	- 0.07

** $P < 0.001$

instances) (Table 4). On the winter range at Cold Bay, use of lichens was significantly greater than their availability, and use of graminoids was disproportionately less than their availability. Caribou wintering around Cold Bay used forbs, deciduous and ericaceous shrubs and mosses in proportion to their availabilities ($P > 0.05$ in all instances). On the winter range at Caribou River, lichens and moss were used in significantly greater proportions than they were available, while, as in mid-winter, graminoids were used significantly less than their availability (Table 4). Use of forbs and deciduous and ericaceous shrubs did not differ from availability during late winter on Caribou River ($P > 0.05$ in all instances).

Diets during the calving season reflected disproportionate use of some forage classes on both ranges (Black Hill: $\chi^2 = 49.3$, $P < 0.001$; Caribou River: $\chi^2 = 35.8$, $P < 0.001$) (Table 4). Caribou calving on Black Hill used only lichens in excess of their availability, but used graminoids significantly less than their availability. Use of forbs, deciduous and ericaceous shrubs and moss did not differ from availability on Black Hill during calving ($P > 0.05$ in all instances). On the calving range at Caribou River, use of lichens and forbs was disproportionately greater than their availabilities (Table 4). Graminoids were used significantly less than their availability, while deciduous and ericaceous shrubs and moss were used in proportion to their availabilities on Caribou River.

Finally, during the post-calving season, diets differed significantly from percent cover of forage classes on both summer ranges (Black Hill: $\chi^2 = 35.9$, $P < 0.001$; Caribou River: $\chi^2 = 45.9$, $P < 0.001$) (Table 4). On Black Hill, caribou used lichens and forbs in excess of their availabilities and graminoids less than their availability. Use of deciduous and ericaceous shrubs and moss by caribou on Black Hill did not differ from their availabilities ($P > 0.05$ in all instances). On Caribou River, only forbs were used in excess of their availability during post-calving (Table 4). Graminoids and deciduous shrubs were used disproportionately less than their availability, while ericaceous shrubs and moss were used in proportion to availability.

1.4.6 Plant Phenology and Growing Season

As of 28 May 1992, when phenology plots were established on the two summer ranges, more than 50% of the final number of forage species to emerge ($n = 16$) at Caribou River already were present (Figure 7). In contrast, < 1% of the final number of forage species to finally emerge on Black Hill ($n = 19$) were present on 28 May 1992. Probit analysis of proportion of species emergent vs. Julian date revealed that the dates on which 50% of the final number of forage species were present on each range were 24 May ± 1.14 days (mean ± 1 SE) for Caribou River ($R^2 = 0.98$, $P < 0.001$) and 20 June ± 1.05 days for Black Hill ($R^2 = 0.97$, $P < 0.0001$). Nonlinear regression analysis of the progression of the plant growth season on Caribou River resulted in estimates of dates of 10% and 90% emergence of forage species as 29 April and 20 June, respectively ($\hat{Y} = 1/(1+e$

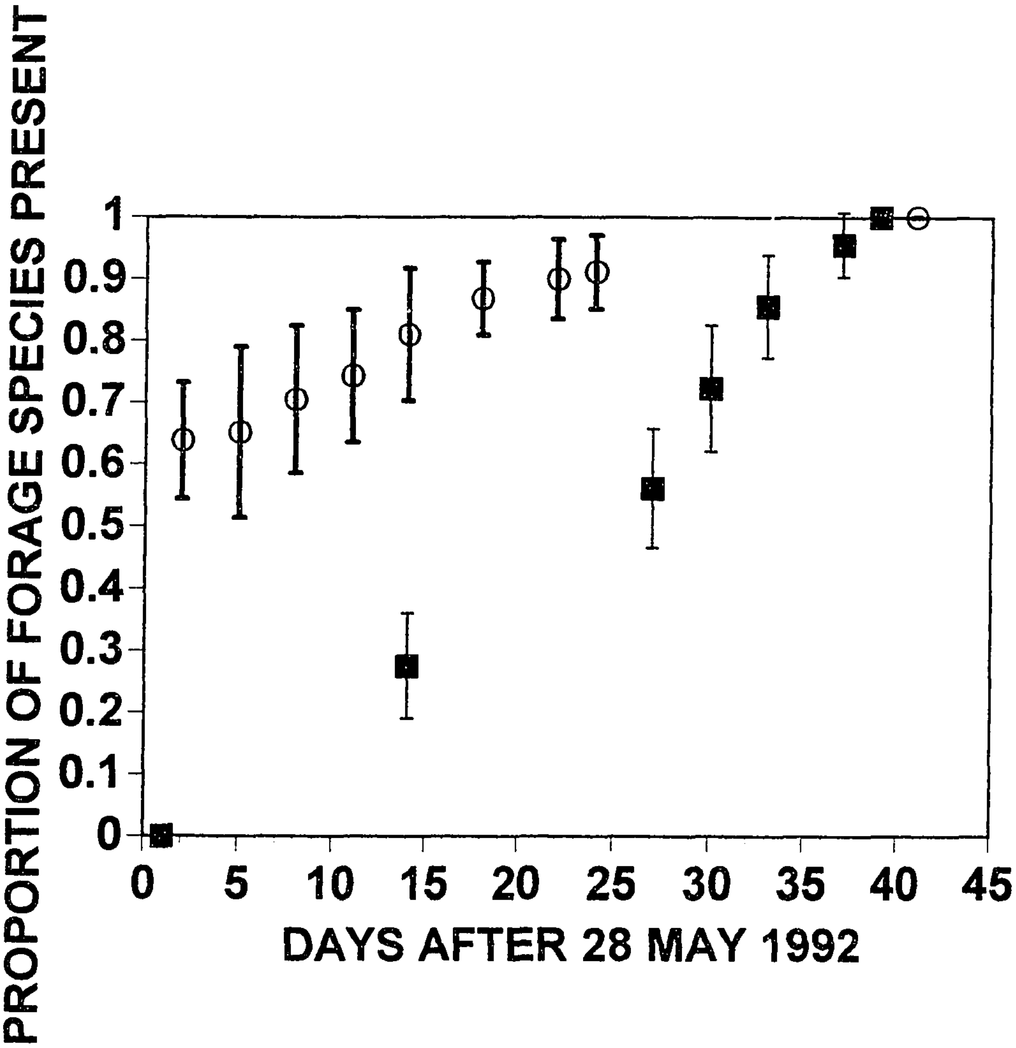

Figure 7. Phenological progression of forage plant species emergence on the Black Hill (closed square) and Caribou River (open circle) calving ranges, Alaska, 1992. Data are average daily proportions (with 95% CIs) of the final number of species present in 20 plots on each range on the last day of observation. Black Hill: start of the growing season = 5 June. Caribou River: start of the growing season = 29 April.

$^{(12.2 - 0.084X)}$); $R^2 = 0.98$, $P < 0.0001$). Similarly, dates of 10% and 90% emergence of forage species on Black Hill were estimated as 5 June and 4 July, respectively ($\hat{Y} = 1/(1+e^{(26.4 - 0.16X)}$; $R^2 = 0.97$, $P < 0.0001$). The length of the plant growing season (number of days from 10% emergence to 90% emergence) was only 29 days on Black Hill, significantly shorter than the growth season of 52 days on Caribou River ($F = 385.2$, $df = 1,14$, $P < 0.0001$).

1.4.7 Timing and Synchrony of Calving

The first calf born on Caribou River in 1992 was observed on 31 May, whereas on Black Hill, the first calf of 1992 was observed on 5 June (Figure 8). Conversion of proportion calves (# calves/(# cows + calves)) to proportion births on each day of observation formed the basis for probit analysis of the progression of the calving seasons on both ranges. The mean date of calving (date of 50% births) on Caribou River in 1992 was 5 June ± 1.53 days (mean ± 1 SE) ($R^2 = 0.91$, $P < 0.001$). On Black Hill, the mean date of calving in 1992 was 12 June ± 1.4 days ($R^2 = 0.80$, $P < 0.016$). Not only was calving later on Black Hill than on Caribou River, but the length of the calving season (number of days from 10% births to 80% births) was 7 days longer on Black Hill, as revealed by nonlinear regression analysis of proportion births vs. date on both ranges (Black Hill: length = 17 days, $R^2 = 0.89$, $P < 0.001$; Caribou River: length = 10 days, $R^2 = 0.95$, $P < 0.0001$; $F = 17.02$, $df = 1,12$; $P < 0.0025$).

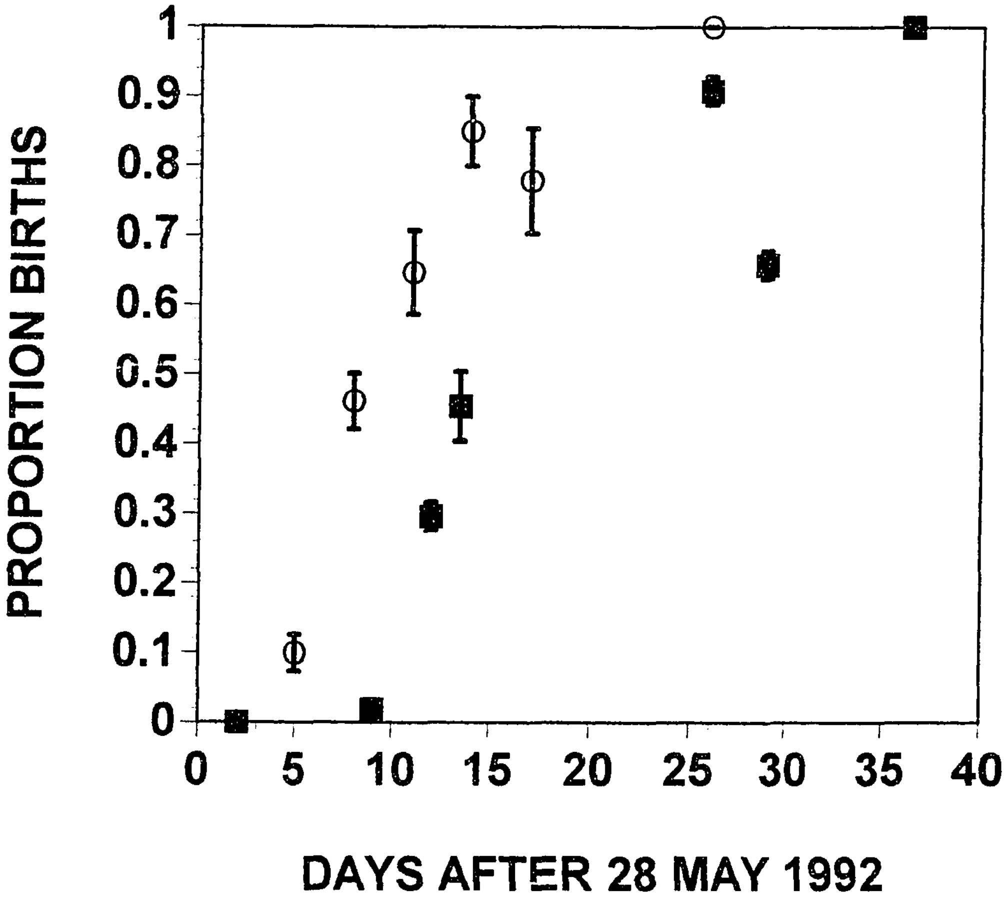

Figure 8. Progression of caribou calving seasons on the Black Hill (solid squares) and Caribou River (open circles) calving ranges on the Southern Alaska Peninsula, Alaska, 1992. Black Hill: mean (± 1 SE) date of calving = 12 June ± 1.38 days. Caribou River: mean (± 1 SE) date of calving = 5 June ± 1.53 days.

1.5 Discussion

1.5.1 Winter Foraging Ecology

Values of lichen cover and biomass on the Southern Alaska Peninsula (Figures 3*a* and 4*a*) represent the lowest reported for ranges of caribou and wild reindeer in mainland North America or Norway. Lichen abundance on the Southern Alaska Peninsula is substantially lower than reported for ranges of other stable or increasing herds, including: the Western Arctic (40% cover) (Saperstein 1993), Central Arctic (11 - 24% cover) (Biddlecomb 1992) and Delta (20 - 85 g/m^2) (Fleischmann 1990) herds in Alaska; the Porcupine (33 - 78 g/m^2) (Russell *et al.* 1993) and George River (51% cover, 122 g/m^2) (Crête *et al.* 1990*a*) herds in Canada; and the Snøhetta (25 - 97 g/m^2) and Rondane (300 g/m^2) herds in Norway (Skogland 1983). Indeed, with $<$ 4% lichen cover, winter ranges on the Southern Alaska Peninsula are more lichen depauperate than ranges in West Greenland (Thing 1984), where caribou are declining despite a lack of natural predation or human harvest (Grønlands Fiskeri- og Miljøundersøgelser 1986), and St. Matthew Island, where lichen abundance was estimated at about 13% of total ground cover in the year preceding the die-off of reindeer there (Klein 1968, 1987). These data support earlier suggestions that the SAPCH is currently experiencing a decline due to food-limitation during winter.

Although lichens are rare on the Southern Alaska Peninsula, caribou wintering around Cold Bay still showed a preference for heath over sedge meadows in mid- and late winter (Table 2) and were able to obtain diets averaging 35 - 45% lichens (Figure 5). In contrast, caribou wintering around Caribou River preferred mesic-sedge meadows in mid-winter, switched to heath in late winter (Table 2), and obtained 15 - 30% lichens in their diets (Figure 5). Although these percents show that lichens are at most only one-half as abundant in winter diets of SAPCH caribou compared to other caribou in mainland North American (Boertje 1984, 1990; Duquette 1984; Russell *et al.* 1993), they nonetheless illustrate the intensely selective nature of caribou feeding as well as the importance of lichens as a highly digestible source of energy for wintering caribou (Klein 1982; Danell *et al.* 1994).

Although moss composed 30 - 40% of the mid- and late-winter diets on the Southern Alaska Peninsula (Figure 5), whether caribou were actually selecting for moss as was indicated by tests for selectivity is difficult to determine(Table 4). Perhaps scarcity of lichens necessitated foraging into the moss layer to obtain lichen fragments. Despite its low digestibility (White & Trudell 1980*b*; Boertje 1990), moss can become an important dietary component in winter for caribou and wild reindeer populations that have exhausted their lichen ranges and have no opportunity to move onto new ranges (Reimers 1977,1982; Klein 1982; Thomas & Edmonds 1983; Gates et al. 1986; Leader-Williams 1988).

The low abundance of lichens on the Southern Alaska Peninsula might be the result of overgrazing of winter ranges during the peak population of caribou.

Lichen mats are quite fragile and susceptible to fragmentation and trampling by the cratering behavior of caribou at high densities (Pegau 1970*a*; Klein 1982). Moreover, strong winds like those on the Southern Alaska Peninsula have a tendency to exacerbate fragmentation of lichen beds by scattering their fragments (Klein 1987), further prolonging the lengthy process of regrowth of lichens following grazing (Pegau 1970*b*; Klein 1987; Henry & Gunn 1991). Early reports from the Southern Alaska Peninsula, however, also noted that lichens appeared to be less abundant there than on other caribou ranges in Alaska (Murie 1935), but quantitative estimates were not available. Skoog (1968) thought this may have been due to the adverse effects of periodic eruptions of the numerous active volcanoes on the Alaska Peninsula and Unimak Island.

1.5.2 Summer Foraging Ecology

Summer diets of caribou and wild reindeer typically consist mainly of deciduous shrubs (Salix and Betula) across a wide variety of ranges and habitats, including interior Alaska (Skoog 1968; Boertje 1984), Arctic Alaska (White *et al.* 1981), Arctic Canada (Banfield 1954), and West Greenland (Thing 1984). Exceptions occur in areas where deciduous shrubs are scarce and caribou diets are dominated by monocots (Leader-Williams 1988; Crête et al. 1990*b*) or forbs (Skogland 1980; White & Trudell 1980*a*). Although deciduous shrubs were scarce on summer ranges on the Southern Alaska Peninsula (Figure 3b), they always were less abundant in summer diets than their availability on summer ranges (Table 4), indicating avoidance of this forage class. Deciduous shrubs are highly digestible and nutritious early in the growing season, but SAPCH caribou apparently used other, more favorable forage that was easier to obtain. Caribou calving at Caribou River showed strong preference for forbs, while avoiding graminoids that were more abundant (Table 4). In contrast, caribou calving on the Black Hill range displayed selectivity only for lichens (Table 4), despite the relative abundance of graminoids (Figure 3). We detected no lichens in our sampling of the calving range at Black Hill, and that they composed about 25% of the diets in the calving season on Black Hill indicates that these caribou were intensely selecting for high-energy forage during a period of great nutritional demand, while vascular forage was phenologically scarce.

The avoidance of willow thickets by caribou on Black Hill during the pre-calving season likely indicates a lack of attractive forage in that habitat type during that period. Caribou foraging on the Caribou River range during the pre-calving season selected for riparian meadows, however, which appeared to be qualitatively rich in emerging sedges at that time. Moreover, during the calving season, a period of high vulnerability to predation for both cows and calves (Lent 1966), caribou on Black Hill used riparian meadows in excess of their availability, perhaps in pursuit of emerging forbs. Caribou calving at Caribou River shifted their preference from riparian meadows preceding calving to mesic-sedge meadows, selecting emergent forbs in the process (Table 4). The change of preference from riparian meadows to heath after calving on Black Hill likely reflects the progression of emergence of forage species from low-lying to upland areas on that range. In contrast, the tendency of caribou on the Caribou River range to remain in mesic-sedge meadows after calving and during post-calving may indicate a lack of phenological differences between the sea-level habitat types on that range.

1.5.3 Plant Phenology and Timing and Synchrony of Calving

The relationship between the timing of parturition and commencement of the plant growing season has been discussed extensively with reference to caribou and wild reindeer (Reimers *et al.* 1983; Skogland 1985*b*, 1989*b*), but with little detailed data on plant phenology. In this study, we showed that timing of parturition in caribou can vary by 1 week between ranges separated by less than 40 km (Figure 8). Because winter diets of the two groups were similar, we reject the possibility that variation in timing of calving was, in this instance, related to different dietary regimes of females during winter (Cameron & Ver Hoef 1994). With data we presented, however, it is not possible to determine the energy expended by caribou of both groups in obtaining those diets. Nonetheless, differences in commencement of the plant growing season on the two calving ranges (Figure 7) likely influenced parturition dates in this instance. Green-up commenced on Caribou River at the end of April in 1992, but did not begin on Black Hill until the end of May. The availability of newly emergent, highly nutritious forage at the end of gestation is an important influence on the timing of parturition among other deer (Cervidae) species (Bowyer 1991), and was likely the key to earlier parturition among female caribou wintering on Caribou River. Alternatively, it is possible that the timing of parturition, and therefore conception, had been favored by natural selection to coincide with earlier green-up on Caribou River.

Considering that winter diets of the two groups were similar, it is plausible that pregnancy rates were approximately equivalent in both groups (Allaye-Chan 1991; Kojola 1993). Therefore, differences in calf productivity on the Black Hill and Caribou River ranges were likely related to differential forage quality or rates of predation on the two calving ranges. Post *et al.* (unpublished) reported, however, that predation risk did not differ significantly between Black Hill and Caribou River. Most mortality of caribou calves occurs within 48 h of parturition (Whitten *et al.* 1992) and is related to body condition of, and thus forage conditions encountered by, pregnant females during the last third of gestation (Allaye-Chan 1991; Rognmo 1983; Skogland 1985*b*, 1989*a*) as has been shown for several ungulates (Thorne *et al.* 1976; Guinness *et al.* 1978; Bunnell 1980). We suggest, then, that lower overall calf productivity on Black Hill reflects greater perinatal mortality influenced by lower availability of forage preceding parturition and throughout the summer foraging season on that range.

Synchrony of parturition also poses consequences for neonatal survival among ungulates living in seasonal environments (Sekulic 1978; Bunnell 1982; Festa-Bianchet 1988; Gaillard et al. 1993), in part because quality of forage available to both lactating females and newborns declines rapidly throughout the growing season (Kuropat & Bryant 1983; Klein 1990; Albon & Langvatn 1992). Generally, less-synchronous births produce greater variability in survival of newborns, as early and late born individuals tend to suffer greater mortality (Bunnell 1980). While vulnerability of offspring born early in the season is usually related to marginal forage conditions and the inability of females to meet energetic demands of lactation (Bunnell 1980), late-born individuals face insufficient nutrition and a shorter summer growing season (Festa-Bianchet 1988). Furthermore, advantages from predator-swamping of highly synchronous parturition diminish as the birth season is prolonged, thereby increasing vulnerability of newborns to predation (Estes 1976; Fryxell 1987). A less-synchronous calving season on Black Hill (Figure 16) therefore, for a variety of reasons, could compromise survival of calves born on that range.

1.6 Conclusions

The paucity of lichens on the Southern Alaska Peninsula, which was lower than lichen availabilities reported for mainland caribou and wild reindeer ranges in North America, Norway, and Greenland, supports earlier speculation that the SAPCH was exhibiting a food-limited decline. The hypothesis that differences in calf productivity between the Black Hill and Caribou River groups were related to winter availabilities of forage on their respective ranges must be rejected because lichens were more prevalent on the winter range of the Black Hill group (Figures 3*a* and 4*a*) and winter diets of both groups were similar (Figure 5). Although other classes of forage were more abundant on the Caribou River winter range (Figures 3*a* and 4*a*), they did not contribute significantly more to winter diets at Caribou River (Figure 5). The calving range at Caribou River, however, had more abundant graminoids and forbs than did the Black Hill range (Figures 3*b* and 4*b*), supporting the hypothesis that differences in summer ranges might contribute to disparate calf production on the two ranges. In addition to providing less total forage, the Black Hill range is used by a higher density of calving caribou than is the Caribou River range (Post & Klein, unpublished). Caribou feed with great selectivity when forage availability is high relative to caribou density; conversely, they become more general foragers when this relationship shifts (Skogland 1985*b*). Therefore, caribou on Black Hill may be unable to forage as selectively as those on Caribou River, a possibility that appears to be supported by a more even distribution of diet proportions across forage classes on Black Hill (Figure 5). Finally, we supported our hypothesis that the plant growth season is shorter on Black Hill than on Caribou River (Figure 7). Later commencement of green-up on the calving range at Black Hill contributed to later calving and poorer calf production on that range compared with Caribou River.

CHAPTER 2

SOCIAL DYNAMICS OF FORAGING CARIBOU (Rangifer tarandus): EFFECTS OF ENVIRONMENT AND CONSPECIFICS[2]

2.1 Abstract

Foraging caribou (Rangifer tarandus) were observed on two summer ranges in Alaska and one in West Greenland. Daily variation in size of foraging groups, density of caribou within feeding sites, distance between individuals within feeding sites, distance moved by foraging groups, and frequency of group movement were recorded and modeled using the following ecological variables that were assessed empirically: predation risk, insect harassment, range patchiness, feeding-site patchiness, feeding-site area, and range-wide density of caribou.

Across data combined from all three ranges, group size correlated most strongly with feeding-site patchiness (negatively) and range-wide density of caribou (positively); density of caribou within feeding sites was positively correlated with range patchiness; individual distance correlated negatively with group size; distance of group movement correlated most strongly, and positively, with insect harassment; and frequency of group movement was positively correlated with insect harassment. Predation risk did not enter any

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[2] Post E.S., Bøving P.S. & Klein D.R. Social Dynamics of Foraging Caribou (Rangifer tarandus): Effects of Environment and Conspecifics. Submitted to *Ecology*.

model.

Within Greenland, group size was most strongly, and negatively, correlated with feeding-site patchiness; feeding-site density correlated negatively with feeding-site area; individual distance correlated positively with feeding site area; distance of group movement was not correlated with any variables; frequency of group movement was positively correlated with insect harassment.

Across data combined from the two Alaska ranges, Caribou River and Black Hill, group size was highly negatively correlated with range patchiness; density of caribou within feeding sites was most highly, and negatively, correlated with feeding-site patchiness; individual distance was most strongly, and negatively, correlated with feeding-site density; distance of group movement was strongly positively correlated with insect harassment; frequency of group movement was positively associated with insect harassment.

Within Caribou River, group size was highly negatively correlated with feeding-site patchiness; density of caribou within feeding sites was most strongly, and negatively, correlated with feeding-site patchiness; individual distance was uncorrelated with all variables; distance of group movement was most highly, and positively, correlated with insect harassment; and frequency of group movement was marginally, negatively associated with feeding-site patchiness.

Within Black Hill, group size was positively correlated with feeding site area; density of caribou within feeding sites was marginally positively correlated with insect harassment; individual distance was strongly negatively correlated with group size; distance of group movement correlated positively with insect harassment; and frequency of group movement was strongly positively associated with insect harassment.

Short-term (intraseasonal) social dynamics of foraging caribou were governed in most instances by patterns of forage availability and distribution across landscapes and within feeding sites, in some instances by insect harassment and social pressures, but in no instance by levels of predation risk inherent to ranges on which they foraged. Although predation certainly has been a force in evolution of caribou sociality, caribou apparently balance demands of foraging in a short and highly variable growth season with the possibility of encountering predators by investing in efficient foraging behavior and relying on more immediate responses to presence of predators.

2.2 Introduction

Sociality may have evolved primarily in response to predation risk (Williams 1966; Treisman 1975; Vermeij 1982; Lima & Valone 1991), but there is considerable evidence indicating that the adaptive value of gregariousness is not limited to reducing predation risk (for a review, see Pulliam & Caraco 1984;

Wenzel & Pickering 1991). Numerous studies of gregariousness among herbivores have demonstrated that sociality enhances foraging efficiency, either through enhanced predator detection by the group (Berger 1983; Monaghan & Metcalfe 1985; Smith 1986), or through reduction of variation in time spent searching for food (du Toit 1990, Pöysä 1991, Focardi & Paveri-Fontana 1992). Moreover, studies of gregariousness among ungulates (hoofed mammals of the orders Artiodactyla and Perissodactyla) indicate that social foraging can enhance forage production above levels observed in systems where social foraging is minimal or absent (Lock 1972; McNaughton 1979*b*, 1985; McNaughton *et al.* 1988; Molvar *et al.* 1993).

Although social foraging is beneficial in some instances, there are certainly environmental conditions that inhibit sociality in situations in which it would seem to be adaptive. For example, browsers are generally asocial feeders, due to the nature of their forage: a bite of stem or leaf removes that food item from the pool of resources potentially available to conspecifics, and browsing habitats offer limited visibility for maintaining social contact within groups (Jarman 1974; Hirth 1977). Furthermore, the patchy distribution of resources experienced by most browsers may prevent formation of large foraging groups even when the threat of predation exists (Damuth 1981; Sinclair 1983). Conversely, there are environmental conditions that promote sociality despite increased costs associated with group living. For example, forest-dwelling cervids such as moose (Alces alces) and white-tailed deer (Odocoileus virginianus) normally feed solitarily or in small groups in closed-canopy vegetation, but become gregarious in open habitat, despite increased agonistic behavior when social (Geist 1974; Hirth 1977; Molvar & Bowyer 1994). The complexity of factors influencing sociality (some of them in opposing ways) has been the basis for many comparative studies of ungulates that have attempted to explain variation in sociality according to factors that either promote or deter formation of groups. These studies have shown that, beyond the influence of predation risk, sociality varies with availability and distribution of forage (Bell 1971; Sinclair 1977; Ryszkowski & French 1982; Lott 1991), weather conditions (Eastland 1991), reproductive season and time of day (Clutton-Brock *et al.* 1982), and insect harassment (Skogland 1989*b*). Such comparative studies have been useful for elucidating influences on sociality of ungulates by comparing differences between populations or within populations during different seasons. They do not, however, necessarily explain variability in sociality within a population within a season. Such variation is apparent during, for example, an aerial census of a herd of caribou (Rangifer tarandus), in which a range of group sizes from two to over 1,000 can be seen in a single day.

The purpose of our study was to investigate the influences of several ecological variables on various aspects of sociality in caribou. Barren-ground caribou are a highly social species, occurring during some seasons in groups of several hundred to thousands of animals. Group sizes of caribou fluctuate seasonally, attaining their highest levels after calving during early summer and decreasing into winter (Skoog 1968; Kelsall 1968). Several explanations have been presented for fluctuations in group sizes of caribou. Increases in group size from winter to summer have been explained as responses by caribou to an increasing supply of forage (Skogland 1989*b*), vulnerability of newborn calves to predation (Bergerud 1971), insect harassment (Roby 1978), and socialization of calves to facilitate cohesion during migration (Skogland 1989*b*; Fancy *et al.* 1990). Conversely, reduction of group size from summer to winter has been explained primarily as a response by caribou to patchiness and decreasing availability of forage due to snow cover (Skogland 1989*b*).

The bases for these explanations have been studies comparing caribou herds on different ranges within a season, or within a single herd during different seasons. Alternatively, we attempted to explain variation in sociality of caribou on the basis of comparisons between herds as well as between groups within herds during one season, summer. We compared the intraseasonal social dynamics of caribou in Alaska (where natural predators exist) and West Greenland (where natural predators are absent) to describe the magnitudes and differential influences of predation risk and environmental variability on caribou sociality. Specifically, we predicted that predation risk, insect harassment, area of the feeding site and range-wide density of conspecifics all act as positive influences on sociality of caribou; alternatively, for ranges and feeding-sites of constant area, patchiness of forage distribution on range-wide and feeding-site levels act to deter sociality in caribou.

2.3 Study Areas and Herds

2.3.1 Alaska

The Southern Alaska Peninsula Caribou Herd was the herd of study in Alaska. The Black Hill and Caribou River groups within this herd, as well as their ranges, were described in detail in Chapter 1.

2.3.2 Greenland

In West Greenland, the Kangerlussuaq-Sisimiut Caribou Herd (KSH) ranges over the southern west coast of Greenland, from about 66° to 69°N. The portion of the herd that we studied occurred mostly in the area stretching from Nordre Isortoq and Isortoqelven (67°6'N) down to Sukkertoppen Iskappe (66°5'N). The area is bounded on the west by Davis Strait and on the east by the Inland Ice, and most of the area is characterized by a continental climate with mean daily minimum and maximum air temperatures from May through July of

1.6°C and 12.5°C, respectively. Winters in the region are typically dry with thin snow cover, except toward the coast (Thing 1984). The landscape comprises low mountain ridges (< 1,800 m) lying in an east-west orientation. South-facing slopes are covered by a thin soil layer and dominated by willows (Salix glauca) and xerophyllic graminoids. North-facing slopes are dominated by dense mats of narrow-leafed Labrador-tea (Ledum palustre), dwarf birch (Betula nana) and mosses, interspersed with grasses (Holt 1983; Thing 1984).

2.4 Methods

Caribou were observed during May through July, 1991 and 1992 in Alaska, and during May through mid-July 1993 in Greenland. Observations of caribou were recorded during aerial and terrestrial surveys during with fixed routes of travel. A total of 147 groups was observed in Alaska (38 on Black Hill and 109 on Caribou River) and a total of 111 groups was observed in West Greenland. Although we did not record observations of any group more than once during any single survey, it is probable that individuals (but not groups) were observed on more than one occasion during the course of our investigation. Our analyses are not likely to be biased by repeated observations of individuals, however, because variable environmental and social conditions in different locations on different days are probably not strongly autocorrelated (Hjeljord *et al.* 1990; Molvar &

Bowyer 1994). When caribou were observed, their locations were recorded on maps or in detailed notes that were later transferred to maps and aerial photos (scales: Alaska, 1:63,360; Greenland, 1:40,000). Only observations of foraging caribou (i.e., animals actually feeding in an area, rather than moving through it) are included in the analysis. Furthermore, observations that could not be accurately transferred to or recorded on maps or aerial photos were excluded from analysis. We assessed the following ecological variables and quantified their influences on caribou sociality:

Predation risk was assumed to be associated with the presence of predators on a caribou range. In Alaska, on ranges used by the SAPCH, nearly every known predator of caribou exists, including brown bears (Ursus arctos), wolves (Canis lupus), wolverines (Gulo gulo), lynx (Lynx canadensis), and golden eagles (Aquila chrysaetos) (personal observation, INWR files), as well as humans; the SAPCH has been hunted heavily in recent years. Hence, caribou in the SAPCH were considered to be under the risk of predation. Predation risk on the Southern Alaska Peninsula was calculated as the mean number of predators observed per day during periodic forays along fixed routes on both caribou ranges. On Black Hill, we made 24 daily forays, and on Caribou River we made 69. Accordingly, the number of predators of caribou observed on each day was summed and divided by the number of days of observation on each range.

Differences in predation risk between the calving ranges on Black Hill and Caribou River were assessed by comparing the median number of predator observations per day for the periods during which the sites were visited.

In West Greenland, the KSH has existed without nonhuman predators for about 4,000 years (Meldgaard 1986). Until recently, however, the herd had been hunted by humans briefly in winter (Thing 1984). Because there is no predation on the calving ranges of the KSH, this herd has evolved for roughly some 2,000 generations without natural predators on its calving range, and we considered this herd to be free of predation risk.

Insect harassment was limited to that by mosquitos (Cuculidae) because we did not observe warble or bot flies (Oestridae) or their avoidance behavior in caribou on any of the ranges. Insect harassment was estimated during observations of caribou behavior in a related study (Bøving 1994). While caribou groups were under behavioral observations, we rated the relative activity and abundance of mosquitos around ourselves on a scale from 0 (none present, whether due to wind speed, temperature, or a combination) to 3 (mosquitos abundant and extremely active).

Range patchiness is a quantification of the heterogeneity of the mosaic of vegetation communities and inorganic substrates (e.g. rivers, lakes, gravel bars, stone outcroppings, etc.) constituting the calving ranges studied. A transparent plastic grid of 1 mm^2 squares was superimposed over aerial photographs (scales 1:63,360 for Alaska and 1:40,000 for Greenland) of each of the three calving ranges. For each range, 20 points were located randomly, and from each point a line of fixed length was extended in a random direction (the line corresponded to 317 m on-the-ground distance). We quantified the number of times the line crossed transitions between plant communities or inorganic substrates such as water or barren soil, as indicated by variation in color or shades of color on the photographs. Thus, the more transitions encountered by the line, the greater the patchiness of the range. The number of transitions per line was summed for each range and divided by 20 (total # of lines) to derive a single value of range patchiness for each study area.

Feeding-site patchiness is a quantification of the heterogeneity of plant communities and inorganic substrates within feeding sites. Feeding sites were identified as local areas in which animals were observed foraging. Boundaries of feeding sites were subsequently delineated from aerial photos by transition zones from one major vegetation community to another or as gullies, gravel bars, expanses of exposed soil, ravines, lake edges, and riverbanks surrounding feeding sites. Quantification of patchiness within feeding sites was based on the same method used to quantify range patchiness, except that lines were confined within the natural boundaries of the feeding sites. Using the same aerial photos and plastic grid used to assess range patchiness, one point was located randomly within each feeding site, and a line corresponding to 317 m on-the-ground distance was extended from it in a random direction. The number of times a line crossed minor inorganic patches such as bare ground or pools of water, as well as variations in density of vegetation within plant communities, as indicated by changes in shades or colors on the photos, was recorded for each line and constituted feeding-site patchiness. In this way, patchiness was quantified for 12 feedings sites in West Greenland, 33 on Caribou River, and 29 on Black Hill. The mean patchiness of feeding sites for each range was an average of the individual values from the sample on each range.

Feeding site area was quantified after the natural boundaries of feeding sites had been delineated from aerial photographs. Feeding sites were overlain with a plastic grid of 1 by 1 mm squares, and the number of squares composing each site was counted. Areas were converted from mm^2 to km^2 based on the scale of the photograph calculated as the number of 1 by 1 mm^2 squares composing the site; areas were converted to km^2.

Several aspects of caribou sociality were assessed for associations with the above ecological variables, as well as for certain associations among themselves. Variables related to sociality included:

Group size was recorded as the number of adult caribou within a feeding site separated from each other by < 100 m. Calves were not included in calculations of group size. Individuals were recorded as groups of size one for statistical purposes.

Density of caribou within a feeding site was calculated as group size divided by feeding site area. Feeding-site density is expressed as caribou/km^2.

Density of caribou within a **range** was calculated as herd size (Post, unpublished data for Alaska; Bøving 1994 for Greenland) divided by range area (Post, unpublished data for Alaska; Thing 1984 for Greenland). Range density is expressed as caribou/km^2.

individual distance of caribou within a feeding site was estimated as the average distance (to the nearest 1 m) between members of a group. Individual distance is expressed in meters.

Distance moved by groups within feeding sites was estimated during behavioral observations (Bøving 1994). Groups were scanned at intervals of 15 minutes using Altmann's (1974) scan-sampling technique. Distance of group movement was that distance moved (estimated in meters) by the center of the group between scans.

Frequency of movement of groups within feeding sites was derived from data obtained during behavioral scans. Movement was coded as either 0 (no movement between 15-minute scan intervals) or 1 (movement between 15-

minute scan intervals), and was modeled using stepwise logistic regression (SYSTAT, Inc. 1992). Data were analyzed using stepwise multiple regression (SYSTAT, Inc. 1992), with log transformations of data where necessary to meet assumptions of normality and homoscedasticity (Neter *et al.* 1990). Models were constructed to test hypotheses, rather than for predictive purposes. Aptness of final models was assessed by graphical examination of residuals and analysis of variance-inflation-factors for each independent variable in the final models (Neter *et al.* 1990); consequently, models contain no strongly inter-correlated independent variables. Results were considered significant at $P \leq 0.05$. In two-sample cases, differences between medians were tested using the Wilcoxon-Mann-Whitney test according to Siegel and Castellan (1988).

Data were analyzed at five different levels: over all data, to assess general patterns and influences of sociality among caribou on different ranges; within Greenland; within Alaska, combining data from Caribou River and Black Hill; within Caribou River; and within Black Hill.

2.5 Results

2.5.1 Characteristics of Herds and Ranges Studied

Despite similarities of herd sizes, range-wide density of animals (caribou / km^2) was higher in Alaska than in Greenland (Table 5). Within Alaska, density was higher on the Black Hill than on the Caribou River calving range. Similarly, average group size (Table 5) was greater in Alaska than in Greenland ($P <$ 0.0001, $n_1 = 147$, $n_2 = 111$), and greater on Black Hill than on Caribou River ($P <$ 0.0001, $n_1 = 38$, $n_2 = 109$).

Mean density of caribou within feeding sites (Table 5) did not differ between Alaska and Greenland ($P = 0.997$, $n_1 = 147$, $n_2 = 111$). Density within feeding sites, however, was significantly greater on Black Hill than on Caribou River ($P \leq 0.0001$, $n_1 = 38$, $n_2 = 109$). Individual distance between animals in groups tended to be lower in Alaska than in Greenland ($P = 0.0283$, $n_1 = 68$, $n_2 =$ 97), as well as lower on Black Hill than on Caribou River, although not significantly ($P = 0.072$, $n_1 = 19$, $n_2 = 49$). Distance of group movement within a feeding site did not differ between Alaska and Greenland ($P = 0.108$, $n_1 = 68$, $n_2 =$ 97), but was significantly greater on Black Hill than on Caribou River ($P = 0.003$, $n_1 = 19$, $n_2 = 49$). Frequency of group movement did not differ significantly between Alaska and Greenland ($P = 0.452$, $n_1 = 10$, $n_2 = 14$).

Range patchiness was lower in Alaska than in Greenland ($P = 0.0039$, $n_1 =$ 40, $n_2 = 20$), and lower on Black Hill than on Caribou River ($P = 0.031$, $n_1 = n_2 =$ 20) (Table 6). Also, feeding sites were larger in Alaska than in Greenland ($P =$ 0.0002, $n_1 = 62$, $n_2 = 12$), but there was no difference between sizes of feeding sites within Alaska, on Black Hill and Caribou River ($P = 0.258$, $n_1 = 29$, $n_2 = 33$).

Table 5. Characteristics of caribou herds studied in Alaska (1992) and West Greenland (1993) (means ± 1 SE). Sample sizes are given in parentheses.

Herd	Population Size	Range Density (#/km^2)	Mean Group Size
SOUTHERN ALASKA PENINSULA	2,800	0.57	80 ± 22 (n = 147)
WEST GREENLAND	2,900‡	0.16	4.7 ± 0.55 (n = 111)
CARIBOU RIVER	800	0.53	12 ± 2.6 (n = 109)
BLACK HILL	2,000	2.11	273 ± 76 (n = 38)

continued

Table 5. Continued.

Herd	Mean Feeding Site Density (#/km^2)	Mean Individual Distance (m)	Mean Distance of Group Movement (m)	Mean Frequency of Group Movement †
SOUTHERN ALASKA PENINSULA	57 ± 9 (n = 147)	17 ± 1.4 (n = 68)	30 ± 9.4 (n = 68)	0.48 ± 0.65 (n = 10)
WEST GREENLAND	49 ± 7.4 (n = 111)	21 ± 1.3 (n = 97)	46 ± 8.3 (n = 97)	0.50 ± 0.63 (n = 14)
CARIBOU RIVER	20 ± 3.9 (n = 109)	19 ± 1.7 (n = 49)	11 ± 2.7 (n = 49)	
BLACK HILL	162 ± 29.8 (n = 38)	13 ± 1.8 (n = 19)	81 ± 30.4 (n = 19)	

†Calculated as the mean proportion of scans during which groups moved while under behavioral observation. ‡From Bøving (1994).

Table 6. Characteristics of caribou ranges studied in Alaska (1992) and West Greenland (1993) (means ± 1 SE).

Range	Range Area (km^2)	Mean Range Patchiness	Mean Feeding Site Area (km^2)	Mean Feeding Site Patchiness	Predation Risk*
SOUTHERN ALASKA PENINSULA	4,900†	1.6 ± 0.22 (n = 40)	0.86 ± 0.14 (n = 62)	1.6 ± 0.20 (n = 62)	0.53 ± 0.11 (n = 93)
WEST GREENLAND	18,000‡	4.6 ± 0.87 (n = 20)	0.14 ± 0.35 (n = 12)	6.5 ± 0.93 (n = 12)	0

continued

Table 6. Continued.

Range	Range Area (km^2)	Mean Range Patchiness	Mean Feeding Site Area (km^2)	Mean Feeding Site Patchiness	Predation Risk*
CARIBOU RIVER	1,500	2.1 ± 0.35 (n = 20)	0.70 ± 0.16 (n = 33)	2.0 ± 0.33 (n = 33)	0.44 ± 0.93 (n = 69)
BLACK HILL	950	1.2 ± 0.23 (n = 20)	1.05 ± 0.25 (n = 29)	1.2 ± 0.19 (n = 31)	0.79 ± 0.35 (n = 24)

‡ From Thing (1984). † From Pitcher et al. (1990). * Calculated as the mean number of predator observations per day.

Feeding sites were more homogeneous in Alaska than in Greenland ($P < 0.0001$, $n_1 = 62$, $n_2 = 12$), and less patchy on Black Hill than on Caribou River ($P = 0.038$, $n_1 = 31$, $n_2 = 30$).

On average, a potential predator of caribou was seen about once every other day on the Southern Alaska Peninsula (Table 6). Predation risk appeared to be slightly higher on Black Hill than on Caribou River, but this difference was not significant ($P = 0.472$, $n_1 = 69$, $n_2 = 24$). On the calving range in West Greenland, predation risk was nonexistent.

2.5.2 Factors Influencing Group Size

At all levels of analysis, group size was influenced by a variety of factors, but in no instance was predation risk a significant determinant of variation in group size (Table 7). For all sites combined, group size was modeled by an exponential function which increased with range-wide density of animals and insect harassment, but decreased with increasing feeding-site patchiness (group size = $13.41\ e^{(1.26 \text{ range density } + 0.34 \text{ insect harassment } - 0.259 \text{ feeding-site patchiness})}$, $R^2_a = 0.63$, $P \leq 0.0001$, $df = 161$). Examination of standardized regression coefficients and coefficients of partial determination revealed that while feeding-site patchiness explained the greatest portion of the total variation in group size ($r^2 = 0.37$), range density had the greatest influence on changes in this dependent variable (Table 7).

Table 7. Standardized regression coefficients and coefficients of partial determination (r^2) for variables predictive of group size of caribou foraging in Alaska (1992) and West Greenland (1993).

Area	Range Density	Range Patchiness	Feeding Site Area	Feeding Site Patchiness	Feeding Site Density	Insect Harassment	Predation Risk
ALL SITES	0.521*** $r^2 = 0.206$	NS	NS	-0.437*** $r^2 = 0.368$	NS	0.245*** $r^2 = 0.049$	NS
GREENLAND	-	-	NS	-0.451*** $r^2 = 0.114$	NS	0.228* $r^2 = 0.039$	-
ALASKA	-	-0.493*** $r^2 = 0.578$	NS	-0.436*** $r^2 = 0.177$	NS	0.249*** $r^2 = 0.046$	NS

continued

Table 7. Continued.

Area	Range Density	Range Patchiness	Feeding Site Area	Feeding Site Patchiness	Feeding Site Density	Insect Harassment	Predation Risk
CARIBOU RIVER	-	-	NS	-0.759*** $r^2 = 0.616$	NS	0.214* $r^2 = 0.045$	-
BLACK HILL	-	-	1.674** $r^2 = 0.266$	-1.273** $r^2 = 0.276$	NS	NS	-

* $P \leq 0.05$

** $P \leq 0.01$

*** $P \leq 0.0001$

NS = $P > 0.05$

Within Greenland, group size was described by an exponential function which increased with insect harassment, but decreased with increasing feeding-site patchiness (group size = 29.37 $e^{(1.51 \text{ insect harassment} - 0.31 \text{ feeding-site patchiness})}$, $R^2_a = 0.13$, $P = 0.001$, $df = 91$). In this instance, heterogeneity of forage distribution within feeding sites had the greater influence on variability in group size ($r^2 = 0.11$, Table 7).

Within Alaska, group size was modeled by an exponential function in which landscape- and feeding site-level patchiness had negative influences while insect harassment had a positive influence (group size = 2368.5 $e^{(1.129 \text{ insect harassment} - 0.341 \text{ feeding-site patchiness} - 2.309 \text{ range patchiness})}$, $R^2_a = 0.79$, $P \leq 0.0001$, $df = 64$). Of the three variables influencing fluctuations in group size within Alaska, range patchiness had the largest standardized coefficient and explained most of the variance in group size accounted for by the model (Table 7).

On the calving range at Caribou River, group size was best explained by an exponential function which decreased with increasing feeding-site patchiness and increased with increasing insect harassment (group size = 20.7 $e^{(1.32 \text{ insect harassment} - 0.343 \text{ feeding-site patchiness})}$, $R^2_a = 0.65$, $P \leq 0.0001$, $df = 46$). Clearly, feeding-site patchiness had the greater influence, accounting for nearly 62% of the total explained variance in group size (Table 7).

Finally, on Black Hill, group size was modeled with an exponential function, increasing with feeding site area and decreasing with increasing feeding-site patchiness (group size = $0.516\ e^{(2.467 \text{ feeding site area} - 5.225 \text{ feeding-site patchiness})}$, $R^2_a = 0.49$, $P = 0.002$, $df = 16$). Feeding-site area had the greater standardized coefficient, but patchiness explained more of the total variance associated with changes in group size (Table 7).

2.5.3 Factors Influencing Density of Animals Within a Feeding Site

Density of caribou within feeding sites varied widely across and within all ranges studied. Feeding-site density was influenced by all variables investigated, except for range density and predation risk (Table 8).

For combined data, feeding-site density was best described by an exponential function in which range patchiness and group size positively influenced density, while feeding-site patchiness and insect harassment negatively influenced feeding-site density (feeding-site density = 1.11 group size $e^{(0.923 \text{ range patchiness} - 0.239 \text{ insect harassment} - 0.068 \text{ feeding-site patchiness})}$, $R^2_a = 0.79$, $P \leq 0.0001$, $df = 160$). The most substantial portion of the total variance in feeding-site density was accounted for by range patchiness, which also had the greatest standardized coefficient (Table 8).

Within Greenland, feeding-site density decreased with increasing feeding site area and patchiness, a relationship which was apparently driven by feeding site area (Table 8) (feeding-site density = 483 e $^{(-9.31 \text{ feeding site area} - 0.167 \text{ feeding-site}}$

Table 8. Standardized regression coefficients and coefficients of partial determination (r^2) for variables predictive of feeding site density of caribou foraging in Alaska (1992) and West Greenland (1993).

Area	Range Density	Range Patchiness	Feeding Site Area	Feeding Site Patchiness	Insect Harassment	Predation Risk	Group Size
ALL SITES	NS	0.984*** $r^2 = 0.532$	NS	-0.130* $r^2 = 0.010$	-0.195*** $r^2 = 0.045$	NS	0.857*** $r^2 = 0.215$
GREENLAND	-	-	-0.407*** $r^2 = 0.311$	-0.274** $r^2 = 0.052$	NS	-	NS
ALASKA	NS	-0.502*** $r^2 = 0.084$	-0.663*** $r^2 = 0.083$	-0.584*** $r^2 = 0.380$	0.337*** $r^2 = 0.101$	-	NS

continued

Table 8. Continued.

Area	Range Density	Range Patchiness	Feeding Site Area	Feeding Site Patchiness	Insect Harassment	Predation Risk	Group Size
CARIBOU RIVER	-	-	-0.547*** $r^2 = 0.318$	-0.741*** $r^2 = 0.424$	0.197** $r^2 = 0.037$	-	NS
BLACK HILL	-	-	NS	NS	0.412 $r^2 = 0.121$ $P = 0.08$	-	NS

* $P \leq 0.05$

** $P \leq 0.01$

*** $P \leq 0.0001$

NS = $P > 0.05$

$^{\text{patchiness)}}$, $R^2_a = 0.35$, $P \leq 0.0001$, $df = 94$). In Alaskan feeding sites, density of caribou tended to increase with insect harassment, but decrease with increasing range patchiness, feeding-site area and feeding-site patchiness (feeding-site density = 14.6 feeding-site area$^{-0.75}$ $e^{(1.12 \text{ insect harassment} - 0.335 \text{ feeding-site patchiness} - 1.724 \text{ range patchiness})}$, $R^2_a = 0.63$, $P \leq 0.0001$, $df = 63$). Of the four variables influencing feeding-site density within Alaska, feeding-site area had the greatest standardized coefficient, while feeding-site patchiness had the greatest coefficient of partial determination (Table 8).

On the Caribou River calving range, density of caribou within feeding sites decreased with increasing feeding-site area and patchiness, but increased with insect harassment (density = 91.8 $e^{(1.35 \text{ insect harassment} - 0.372 \text{ feeding-site patchiness} - 0.92 \text{ feeding site area})}$, $R^2_a = 0.76$, $P \leq 0.0001$, $df = 45$). The greatest influence on feeding-site density came from feeding-site patchiness, which explained about 54% of the total variance accounted for in this model (Table 8). On the Black Hill Calving range, density of caribou within a feeding site was marginally influenced by only one variable, insect harassment, with which it tended to increase exponentially (feeding-site density = 34.19 $e^{(0.807 \text{ insect harassment})}$, $R^2_a = 0.12$, $P = 0.08$, $df = 17$).

2.5.4 Factors Influencing Distance Between Individuals Within Groups

For combined data, mean individual distance between caribou within feeding groups was only weakly influenced by one variable, group size (Table 9). Individual distance decreased exponentially as group size increased for data combined from all sites (individual distance = 22.85 group size$^{-0.127}$; $R^2_a = 0.08$, $P \leq 0.0001$, $df = 163$).

Within Greenland, individual distance was positively linearly related to the size of the feeding site, and negatively linearly related to feeding-site density and insect harassment (individual distance = 19.40 + 160.77 feeding-site area - 2.72 feeding-site density - 3.34 insect harassment; $R^2_a = 0.36$, $P \leq 0.0001$, $df = 91$). Examination of the standardized coefficients and coefficients of partial determination for these variables indicates that this relationship is influenced most by feeding-site area (Table 9).

In Alaska, variation in individual distance was best explained by a linear model including feeding-site area, feeding-site patchiness, and feeding-site density, all of which tended to reduce individual distance (individual distance = 41.14 - 2.43 ln(feeding-site area) - 2.68 feeding-site patchiness - 5.80 ln(feeding-site density); $R^2_a = 0.31$, $P \leq 0.0001$, $df = 64$). Of these variables, feeding-site density exerted the greatest effect on individual distance (Table 9).

On the Caribou River range, individual distance was not significantly influenced by any of the variables investigated (Table 9). On Black Hill, distance between individuals within feeding sites was negatively related to group size in an

Table 9. Standardized regression coefficients and coefficients of partial determination (r^2) for variables predictive of individual distance of foraging caribou in Alaska (1992) and West Greenland (1993).

Area	Range Density	Range Patchiness	Feeding Site Area	Feeding Site Patchiness	Feeding Site Density	Group Size	Insect Harassment	Predation Risk
ALL SITES	NS	NS	NS	NS	NS	-0.289*** $r^2 = 0.083$	NS	NS
GREENLAND	-	-	0.642*** $r^2 = 0.254$	NS	-0.249* $r^2 = 0.042$	NS	-0.391** $r^2 = 0.084$	-
ALASKA	-	NS	-0.267* $r^2 = 0.064$	-0.579*** $r^2 = 0.134$	-0.720*** $r^2 = 0.141$	NS	NS	-

continued

Table 9. Continued.

Area	Range Density	Range Patchiness	Feeding Site Area	Feeding Site Patchiness	Feeding Site Density	Group Size	Insect Harassment	Predation Risk
CARIBOU RIVER	-	-	NS	NS	NS	NS	NS	-
BLACK HILL	-	-	NS	NS	NS	−0.919*** r^2= 0.835	NS	-

* $P \leq 0.05$

** $P \leq 0.01$

*** $P \leq 0.0001$

NS = $P > 0.05$

exponential function which accounted for nearly 84% of the variation in this dependent variable (individual distance = 96.5 group size$^{-0.380}$; $R^2_a = 0.84$, $P \leq 0.0001$, $df = 16$).

2.5.5 Factors Influencing Distance of Group Movement

For data combined from all sites, distance moved by foraging groups was exponentially related to group size and insect harassment, and increased positively with these variables (distance moved = 2.85 group size$^{0.239}$ $e^{(0.363 \text{ insect harassment})} - 1$; $R^2_a = 0.05$, $P = 0.006$, $df = 162$). Although group size and insect harassment had very similar influences on distance moved, insect harassment had a greater effect, because both its standardized coefficient and coefficient of partial determination were greater than those of group size (Table 10). Within Greenland, there were no significant relationships between distance moved and the variables investigated (Table 10).

In Alaska, distance moved was positively influenced by feeding-site area and insect harassment in an exponential relationship (distance moved = 3.74 feeding-site area$^{0.36}$ $e^{(2.09 \text{ insect harassment})} - 1$; $R^2_a = 0.33$, $P \leq 0.0001$, $df = 65$). Clearly, insect harassment dominated this relationship, accounting for 87.5% of the total variance in distance moved explained by the model (Table 10).

On the calving range at Caribou River, distance of group movement also was positively related to insect harassment and feeding-site area in an

Table 10. Standardized regression coefficients and coefficients of partial determination (r^2) for variables predictive of distance moved by foraging caribou in Alaska (1992) and West Greenland (1993).

Area	Range Density	Range Patchiness	Feeding Site Area	Feeding Site Patchiness	Feeding Site Density	Group Size	Insect Harassment
ALL SITES	NS	NS	NS	NS	NS	0.171* $r^2 = 0.029$	0.186* $r^2 = 0.033$
GREENLAND	-	-	NS	NS	NS	NS	NS
ALASKA	NS	NS	0.232* $r^2 = 0.044$	NS	NS	NS	0.457*** $r^2 = 0.308$

continued

Table 10. Continued.

Area	Range Density	Range Patchiness	Feeding Site Area	Feeding Site Patchiness	Feeding Site Density	Group Size	Insect Harassment
CARIBOU RIVER	-	-	0.402** $r^2 = 0.076$	NS	NS	NS	0.368** $r^2 = 0.299$
BLACK HILL	-	-	-0.457* $r^2 = 0.143$	NS	NS	NS	0.863** $r^2 = 0.367$

* $P \leq 0.05$
** $P \leq 0.01$
*** $P \leq 0.0001$
NS = $P > 0.05$

exponential function (distance moved = $1.67\ e^{(2.94\ \text{insect harassment} + 0.785\ \text{feeding-site area})} - 1$; $R^2_a = 0.23$, $P = 0.001$, $df = 46$). In this instance, though, it is not so clear which of the two variables exerted greater influence on distance moved, because feeding-site area had a greater standardized coefficient in the final model, while insect harassment explained substantially more of the variance in distance moved (Table 10).

For the calving range on Black Hill, distance of group movement was linearly related to insect harassment and feeding-site area, but in this instance feeding-site area had a negative influence (distance moved = 282.3 + 186.9 insect harassment - 68.9 feeding-site area; $R^2_a = 0.45$, $P = 0.003$, $df = 16$). Insect harassment had the stronger influence on distance moved in this instance, accounting for nearly 72% of the total variance explained by the model (Table 10).

2.5.6 Factors Influencing Frequency of Group Movement

Interpretation of the results from this analysis are most accurately described as factors influencing whether a group moves during a 15-minute foraging bout. Results are presented as odds ratios (the factor by which the probability of movement increases or decreases with a 1 unit increase in the independent variable) and McFadden's Rho^2, an approximation of linear regression's R^2, which usually takes on a lower value than would R^2 (Steinberg & Colla 1991).

For combined data, insect harassment was the only variable significantly influencing whether groups moved while foraging (Table 11). According to the model, a one-unit increase in insect harassment increases the probability of group movement by a factor of 1.45 ($P = 0.02$, $n = 165$). In Greenland, group movement was similarly influenced by insect harassment, a one-unit increase in harassment nearly doubling the probability of movement ($P = 0.05$, $n = 97$) (Table 11). In Alaska, the probability of group movement was strongly positively influenced by insect harassment, a one-unit increase in which increases the probability of movement by a factor of 14.57 ($P = 0.001$, $n = 68$) (Table 11).

On the Caribou River calving range, the probability of group movement was not predicted by any of the variables investigated, but it is worth considering that feeding-site patchiness was marginally significant ($P = 0.06$, $n = 49$) in a negative association (Table 11). On Black Hill, the probability of group movement during a foraging bout was strongly positively influenced by insect harassment ($P = 0.02$, $n = 19$) (Table 11).

Table 11. Odds ratios and McFadden's *Rho*^{2} values for variables influencing the probability that a group of caribou will move during a 15-minute foraging bout in Alaska (1992) and West Greenland (1993).

Area	Insect Harassment	Feeding Site Patchiness
ALL SITES	1.45* *Rho*^{2} = 0.030	NS
GREENLAND	1.87* *Rho*^{2} = 0.044	NS
ALASKA	14.57** *Rho*^{2} = 0.122	NS
CARIBOU RIVER	NS	-0.85 *Rho*^{2} = 0.035 $P = 0.06$
BLACK HILL	10.87* *Rho*^{2} = 0.220	NS

* $P \leq 0.05$; ** $P \leq 0.001$; NS = $P > 0.05$

2.6 Discussion

2.6.1 The Influences of Environmental Factors

Predation Risk

Skogland (1989*b*) compared group sizes of wild reindeer in Norway (Rangifer tarandus tarandus) with those on Svalbard Island (R.t. platyrhyncus), and concluded that predation risk was not an important influence on group size above a certain "predator-safe threshold" (i.e., that predation risk was important in determining minimum, but not maximum, group sizes). Other studies have suggested that for ungulates, the period of highest vulnerability to predation is during and immediately following parturition (Lent 1974; Estes 1976; Jarman & Jarman 1979; Carl & Robbins 1988), and that it is during this period that ungulates should be expected to exhibit adaptations that reduce risk of predation on neonates (Geist 1974; 1981). During the time of calving, caribou group sizes are actually at their lowest (Lent 1966; Bergerud *et al.* 1984), and caribou have been classified as having a "follower" (Lent 1974) or a "hider-follower" (Geist 1981) strategy for reducing predation on neonates.

Our results indicate no conclusive influence of predation risk on intraseasonal social dynamics of caribou. Because our quantification of predation risk was limited to numbers of predators observed daily, it may not reflect actual risk to caribou, because predators were not always observed near caribou.

Additionally, our observations combined various species of predators, each of which might pose a different level or type of risk to the herbivore (Berger 1991). The lowest group sizes in the Alaskan sites, those on Caribou River, however, were larger than those in Greenland (Table 5). This may indicate that caribou foraging under the risk of predation forage in larger groups than caribou free from the risk of predation.

Insect harassment

Undoubtedly, harassment by insects can strongly influence the foraging behavior of ungulates (Fancy 1983; Downes *et al.* 1986; Rutberg 1987). Unlike large African ungulates, most of which possess relatively long tails which they use in warding off insects (Siegfried 1990), caribou possess only a short tail and are generally attacked about the head and forequarters where a tail would be ineffective in warding off insects. Thus, some of the behavioral responses of caribou to increasing seasonal harassment by mosquitos include formation of large groups (Roby 1978), migration to coastal areas (Skoog 1968; Nixon 1991), and migration to wind-blown ridgetops devoid of vegetation (Nixon 1991), all of which reduce foraging time and efficiency (Downes *et al.* 1986).

Based on these observations, we expected similar behavioral responses to daily changes in mosquito harassment. Thus, we predicted that caribou under increasing harassment by mosquitos would form larger groups, occur at higher densities in feeding sites, stand closer together, and to move further and more frequently than when they were not under insect harassment. In Alaska, mosquito harassment did cause caribou to form large groups (Table 7), occur at higher feeding-site densities (Table 8), move over greater distances (Table 10), and move more frequently (Table 11). When data from Alaska and Greenland were combined, the effects of harassment by mosquitos included increases in group size (Table 7) and frequency of movement (Table 11) and a decrease in feeding-site density (i.e., dispersal) (Table 8). Thus, mosquito harassment imposed the effects on group size and movement we expected across all sites, but its effects on density and spacing of animals with the Greenlandic data included were unexpected.

Dispersal under mosquito harassment is not a typical response by barren-ground caribou (see Skogland 1989*b*), but has been observed in forest-dwelling reindeer in Finland (Helle 1980; Helle & Aspi 1983). We suggest that this unique response by the West Greenland caribou is due to the influence of the distribution of vegetation within the feeding sites. As will be discussed later, our results suggest that clumping or congregating within feeding sites during daily increases in mosquito harassment are only possible if the forage base is sufficiently homogeneous and abundant to promote close proximity of conspecifics. Thus, harassment by mosquitos elicited increases in group size and density within feeding sites in Alaska, where both ranges and feeding sites were more homogeneous, and where feeding sites were larger, than in Greenland. Consequently, we propose that the immediate response of caribou to mosquito harassment (whether to congregate or disperse) depends on the structure and distribution of forage within feeding sites as well as level of harassment.

Range Patchiness

Temporal heterogeneity of vegetation profoundly influences group size and movements of herbivores. Seasonal changes in foraging group size and migratory behavior of wildebeest (Connochaetes taurinus), zebra (Equus quagga), and African buffalo (Syncerus caffer) have been associated with seasonal changes in the distribution and availability of forage according to rainfall (Vesey-FitzGerald 1960; Bell 1971; Sinclair 1977; Jarman & Jarman 1979; Maddock 1979; McNaughton 1979*b*). In the Arctic, changes in group sizes of caribou have been similarly attributed to changes in forage availability. Increases in group size with the progression of summer are believed to be a response to increasing species abundance and biomass of forage coincident with phenological progression of vegetation (Skogland 1989*b*). Conversely, decreases in group size from summer into winter are thought to be a result of increasing patchiness of vegetation due to senescence of summer-growing species and variable snow cover (Skogland *1984, 1989b*; Tyler & Øritsland 1989;

Biddlecomb 1992).

Considering the important influence of seasonal changes in range patchiness on group size and movements of ungulates, we predicted that intraseasonal differences in patchiness of ranges would explain some of the variability in sociality of caribou on different ranges. Thus, we expected that aggregation of caribou within feeding sites would be influenced negatively by increasing range patchiness. Specifically, we predicted that both group size and density of caribou within feeding sites during summer would decrease with increasing range patchiness. Our data confirmed the predicted influences of range patchiness on group size and density of caribou in feeding sites only within Alaska (Tables 7 and 8). Conversely, when data from Alaska and Greenland were analyzed together, a strong positive effect of range patchiness on feeding site density became apparent (Table 8). Indeed, for combined data, range patchiness had the greatest influence on feeding site density. This relationship clearly was driven by inclusion in the model of data from Greenland, where range patchiness was more than twice as great as in Alaska (Table 6). These results suggest that when landscape and vegetation patterns combine to produce an extremely heterogeneous distribution of resources between feeding sites, social herbivores forage at high densities within feeding sites.

Feeding-Site Patchiness

Just as large scale, range-wide heterogeneity of forage distribution influences gregariousness among ungulates, there is considerable evidence suggesting that heterogeneity within feeding sites poses consequences for herbivore sociality and foraging behavior. For instance, browsers are typically asocial feeders because the patchy distribution of their forage, from plant to plant, does not facilitate gregariousness (Damuth 1981), but rather, in some instances, territoriality and intolerance of the proximity of conspecifics (Geist 1974; Jarman & Jarman 1979). On the other hand, grazers are typically social (Geist 1974; Jarman & Jarman 1979), at least in part because the homogeneous and wide-spread nature of their forage promotes tolerance of conspecifics (Jarman 1974; Damuth 1981; Sinclair 1983) rather than territoriality (Geist 1974). Studies focusing on single species of herbivore have similarly concluded that sizes of feeding groups are lower in sites with greater concealment cover and patchy distributions of forage, and larger in sites with homogeneous distributions of forage (Chadwick 1977; Hirth 1977; Monoghan & Metcalfe 1985; Owen-Smith 1988).

The distribution of forage within feeding sites also has effects on the distribution of animals within feeding sites. For example, theoretical studies have concluded that when forage is patchily distributed within feeding sites, it should be adaptive for herbivores to aggregate locally in feeding sites, or to "clump", where the patches occur, to enhance feeding efficiency and reduce searching time by exploiting the efforts of conspecifics (Noy-Meir 1975; Caraco & Giraldeau 1991). Support from field studies for this hypothesis is variable. Clumping behavior has been observed in empirical studies of caribou in response to highly localized availability of newly emergent forage at the beginning of the plant growth season (Skogland 1989*b*). Just the opposite has been observed for African buffalo, however, which have been observed spacing out as forage patchiness increased and patch size decreased during the dry season (Sinclair 1977).

Patchiness of vegetation within feeding sites also influences movement patterns of herbivores, and this has been a topic of considerable focus in optimal foraging theory (OFT). In separate reviews of OFT, Pyke *et al.* (1977) and Senft *et al.* (1987) concluded that a scattered, irregular distribution of resources should compel foragers to move frequently within feeding sites. Consistent with this, wildebeest travel frequently and over great distances between high quality patches of forage created by local rainstorms (Sinclair 1977). Similarly, individual caribou move frequently and at high speeds between scarce, highly nutritious plants early in the growing season, apparently in competition with conspecifics (see Skogland 1989*b*, P. 52).

Based on these theoretical suggestions and the empirical evidence, we predicted several influences of feeding-site patchiness on caribou sociality. As patchiness within feeding sites increased, we expected the following responses by caribou within the range of patch size values on our study sites: decreasing group size, decreasing density, changing average individual distance (as caribou distribution became more clumped), increasing distance of group movement, and increasing frequency of group movement.

The predicted effects of feeding-site patchiness on group size and density of caribou within feeding sites were strongly supported for combined data as well as for data from each range individually (Tables 7 and 8). The exception was Black Hill, where there was no effect of feeding-site patchiness on density of animals within a feeding site. Interestingly, Black Hill had the most homogeneous feeding sites, indicating that a wide range of patchiness values is necessary for these effects to become manifest.

Clumping as a response to increasing feeding-site patchiness was only observed within Alaska. In this instance, mean individual distance within groups decreased with patchiness (Table 9). If this response were true clumping behavior, it must have been the result of groups fragmenting into sub-groups, which then became widely spaced within patchy feeding sites.

The predicted influence of feeding-site patchiness on distance and frequency of group movement was not clearly supported. Although patchiness did not influence distance of movement in any of the models, it marginally influenced frequency of movement in feeding sites on the Caribou River range (Table 11). That frequency of movement decreased with increasing patchiness on the Caribou River range was unexpected and difficult to explain. But it is worth noting that patchiness within feeding sites on Caribou River was only about one-third as great as in Greenlandic feeding sites (Table 6). Other data have shown that forage density was greater within feeding sites in the Alaskan study areas than it was in the Greenland study area (Post & Klein, unpublished). This suggests that feeding-site patchiness can have dual effects on movement, depending on the nature of forage within the patches. Thus, when forage is patchy as well as sparse within the patches, movement to other patches may be adaptive. Alternatively, when forage is patchy, but densely packed within the patches, residence within patches may be adaptive.

Feeding-Site Area

Increased vulnerability to predators in open environments is believed to have been a major motivating factor for the evolution of gregariousness among ungulates as they moved from forests to exploit grasslands during the Miocene (Estes 1974; Hirth 1977; Vaughan 1978). The same idea has been used to explain why extant ungulate species form larger groups when they emerge from forests or dense cover into open areas (Geist 1974; Hirth 1977; Molvar & Bowyer 1994). Applying the same principle to the sizes of feeding sites, we expected caribou under the threat of predation to form larger groups, stand closer together, and move over greater distances in larger feeding sites, where they might experience a greater sense of vulnerability and also, possibly, because groups are more restless than individuals. Alternatively, we expected caribou free of the threat of predation not to exhibit these behavioral responses to increasing feeding site area.

Feeding-site area had a strong positive influence on group size only on Black Hill (Table 7), where the largest groups occurred (Table 5). Thus, the tendency of a highly social herbivore to forage in large groups is obviously facilitated on ranges where feeding sites are large and homogeneous, as on Black Hill (Table 6). The negative relationships between feeding site area and feeding-site density seen in Greenland, Alaska, and Caribou River likely result from the opposing influences of range- and feeding-site patchiness, which keep sizes of groups down or constant even when they forage in larger sites.

As predicted, individual distance decreased with increasing feeding-site area in Alaska, while increasing in Greenland (Table 9). The effect of feeding site area on individual distance in Alaska, however, was relatively minor and may have been a side effect of large groups occurring in large feeding sites (Table 7).

The expected influence of feeding-site area on distance of movement in Alaska was observed only for combined Alaskan data and data from Caribou River. Unexpectedly, on Black Hill, distance of movement was negatively associated with feeding-site area. Again, this result may have been confounded by forage density within feeding sites on Black Hill. Analysis of additional data indicates that density of forage can be as much as an order of magnitude greater on Black Hill than on Caribou River (Post & Klein, unpublished). Certainly, high-density forage together with a low degree of patchiness in feeding sites could influence groups on Black Hill to adopt a more resident foraging strategy.

2.6.2 The Influences of Social Factors

Range-Wide Density of Animals

The main effects of range-wide density of caribou on their ecology are manifest in demographic and morphological responses. Generally, as range density of any particular herd increases to a level at which resources become depleted due to overgrazing, reproductive success declines (Skogland 1985*a*), body size drops (Skogland 1983), and body condition declines (Klein 1968). The eventual result is typically a population crash (Klein 1968; Skogland 1985*a*). Moreover, in continental populations of Rangifer, an increase in range-wide density of conspecifics typically leads to expansion of the range area (Messier *et al.* 1988). Comparatively little has been written about the effects of range-wide density of caribou on their sociality, although Reimers (1983) has suggested that low group sizes at high densities may be an adaptive response to overgrazing of winter ranges.

We observed that group size was strongly positively influenced by density of caribou on their ranges, suggesting that in summer, caribou tend to form larger groups as density increases (Table 7). That this relationship is absent during winter for wild reindeer in Norway and Svalbard (Skogland 1989*b*) indicates an important difference between the interactions of range density and forage conditions during winter and summer. Apparently, during winter, caribou forage in groups of sizes related to the availability, and perhaps patchiness, of lichens, but independent of range-wide density of animals (Skogland 1989*b*). Conversely, during summer, forage is abundant enough that group size varies with range density.

Group Size

Not surprisingly, individual distance within feeding sites decreased with increasing group size (Table 10), but not for all instances. Group size affected how close together caribou stood while foraging only at the highest levels of feeding-site density observed (Table 5). Group size exerted a relatively strong positive influence on feeding-site density, but only for combined data (Table 8).

We predicted that caribou would move farther as the size of the feeding group increased, both because social facilitation causes a greater tendency to move (Curatolo 1975; Duqette & Klein 1987) and because we expected that larger groups might deplete available forage more quickly than smaller groups (Krebs & Davies 1987). Our data confirmed this prediction (Table 10), but the influence was relatively weak in comparison to the overriding influences of insect harassment on movement (Tables 10 and 11).

Feeding-Site Density

The only influence that density of caribou within feeding sites had on sociality was for individual distance. As with group size, increasing density of caribou within feeding sites caused individuals to stand closer together, and in Alaska, this was the predominant influence on individual distance (Table 9). Ostensibly, group size and density within feeding sites interact to produce the most widespread influences on individual distance within aggregations of foraging caribou.

2.7 Conclusions

Sociality in large herbivores has been and is influenced by many selective pressures, including predation and environmental factors such as resource distribution and insect harassment. In this study, predation risk was not shown to have any concrete influence on short-term social dynamics of foraging caribou.

Instead, the single most influential factor affecting daily variation in caribou social dynamics was resource distribution, both on landscape and local levels. Indeed, range patchiness and feeding site patchiness, together or separately, exerted the greatest influence on the greatest number of aspects of caribou sociality investigated. These results indicate that while minimizing predation risk is certainly important to the survival of individual caribou, the ability to respond to variation in resource distribution patterns and maximize foraging efficiency is of more immediate relevance to survival in a rapidly changing environment with a short summer foraging season.

CHAPTER 3

RELATIONSHIPS BETWEEN GRAMINOID GROWTH FORM AND LEVELS OF GRAZING BY CARIBOU (Rangifer tarandus) IN ALASKA[3]

3.1 Abstract

Herbivores and their forage interact in many ways, in some instances to the benefit or detriment of herbivore and vegetation. Studies of wildebeest (Connochaetes taurinus) in Africa and snow geese (Chen caerulescens) in the Arctic have suggested that these grazers enhance graminoid production in certain sites by repeatedly using them. Other studies have concluded that herbivores are sensitive to local variation in forage quality and quantity, and preferentially use those sites that are intrinsically more productive. In this study, caribou (Rangifer tarandus) were observed foraging at different densities on two adjacent Alaskan ranges, within which particular feeding sites contained predictably high, medium, or low densities of caribou. Vegetation from one high- and one low-use site on each of the high- and low-density ranges was sampled and tested for responses to clipping, with the objectives of determining which forage characteristics influence usage by grazers and whether the productivity and nature of graminoid responses to clipping were related to grazing history.

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[3] Post E.S. & Klein D.R. Relationships Between Graminoid Growth Form and Levels of Grazing by Caribou (Rangifer tarandus) in Alaska. Submitted to *Oecologia*.

Forage biomass density (g/m^3), shoot density (#/m^2), stand densities of nutrients and minerals (g/m^3), and forage concentrations of nutrients and minerals (g/100g tissue) correlated positively with use of sites by caribou. Productivity and responses to clipping were independent of previous use by grazers, but consistent within ranges. These results indicate that caribou are highly sensitive to local variation in forage quality and quantity, preferentially use those sites with higer returns of nutrients and minerals, and have the potential to enhance graminoid growth on sites that are inherently more productive.

3.2 Introduction

Grazing is a dynamic process in which both the grazer and the vegetation are affected, the results of which can alter ecosystem structure and function (Naiman 1988; McNaughton *et al.* 1988; 1989). At moderate levels, grazing stimulates aboveground productivity of graminoids across a range of ecosystems, including arid North American grasslands (Holland *et al.* 1992; Frank & McNaughton 1993), savanna grasslands of East Africa (McNaughton 1985), sub-Arctic coastal salt marsh (Hik & Jeffries 1990), Arctic tundra (Archer & Tieszen 1980), and tropical Asian savanna (Pandey & Singh 1992). At high densities of herbivores or grazing intensity, however, the soil layer can become compacted and vegetation trampled or overgrazed, finally dying back (Lock 1972).

Associated with the influence of grazing on productivity of graminoids are effects on the chemical and physical structure of the grazed sward. For instance, grazed plants often have higher nutrient and mineral concentrations (g/100g tissue) than nongrazed plants (Chapin 1980; McKendrick *et al.* 1980; Bryant *et al.* 1983; Polley & Detling 1990). This can result either through herbivore fertilization of soils by urine and dung deposition (Ruess & McNaughton 1987; Day & Detling 1990; Holland & Detling 1990), or through increased mineral uptake and nutrient investment in leaf regrowth by graminoids following defoliation (Chapin 1980). Grazing in high-latitude ecosystems can further enhance productivity by removing competitors for light and nutrients, increasing solar radiation to soil and remaining plants (Bryant *et al.* 1983; Chapin 1983). Furthermore, grazed plants have different patterns of growth and biomass allocation than nongrazed or lightly grazed plants. For example, grazing coupled with fertilization may increase the leaf:shoot ratio (Ruess & McNaughton 1984), production of tillers (Oesterheld & McNaughton 1988; Georgiadis *et al.* 1989; Jaramillo & Detling 1992), and biomass concentration of forage (McNaughton 1983; 1984). These responses of graminoids to grazing are dependent not only upon a certain level of herbivory and fertilization, but also upon the vegetation being in a state of stress (usually nutrient limitation) beforehand, which is relieved or alleviated by the combined effects of tissue removal and fertilization (Grime 1977; Belsky 1986; Oesterheld &

McNaughton 1991).

Graminoid responses to herbivory can be seen at three temporal scales: immediate responses, occuring within individual plants just days after being grazed; short-term alterations of plant growth form over weeks and years (Holland *et al.* 1992); and long-term, successional and evolutionary responses that result in changes in plant community composition or morphology of plant species (McNaughton 1979a; Jaramillo & Detling 1992). The concept of the grazing lawn described by McNaughton (1984) from East African savannas is an example of long-term evolutionary responses of graminoids to herbivory. The grazing lawn ecotype is an embodiment of the responses described previously of graminoids to grazing. The dynamics of herbivore-graminoid interactions in grazing lawns mediated by large mammals have not been quantified outside of Africa, where conditions for development of grazing lawns were supposed to be prevalent because of a long coevolutionary history of ungulates and grasses (McNaughton 1979; 1985). Nonetheless, Thing (1984) described qualitatively how browsing by caribou (Rangifer tarandus) in West Greenland caused the die-back of shrubs, opening local areas to graminoid swards, which were then grazed and maintained in herbaceous growth. Furthermore, clipping experiments and comparisons of grazed and ungrazed Arctic meadows have illustrated the potential of Arctic graminoids to respond positively to grazing by muskoxen

(Ovibos moschatus) and caribou (Henry & Svoboda 1989; Ouellet *et al.* 1994).

Because Arctic soils typically are nutrient limited (McKendrick *et al.* 1980), we predict that grazing and fertilization by social grazers can produce grazing lawns in the Arctic. Indeed, the foraging activities of lesser snow geese (Chen caerulescens) in a sub-Arctic salt marsh were shown to maintain the vegetation in a productive, rapidly growing state, which may be considered a grazing lawn (Cargill & Jeffries 1984; Hik & Jeffries 1990). In other studies of foraging dynamics of herbivores, associations have been demonstrated between ungulate group sizes or use of sites and productivity of graminoid swards on those sites for white-tailed deer (Odocoileus virginianus) (Etchberger *et al.* 1988), elk (Cervus elaphus) (Hobbs & Swift 1988; Frank and McNaughton 1992), and bison (Bison bison) (Frank & McNaughton 1992) in North America; red deer (C. elaphus) in Scotland (Clutton-Brock *et al.* 1982); and thar (Hemitragus jemlahicus) in Nepal (Bauer 1990). The purposes of this study were: (1) to determine whether sub-Arctic graminoid meadows grazed at different intensities by caribou, a highly social grazer, differed in their physical and chemical characteristics; (2) to determine which aspects of graminoid growth form and concentrations (g/100g tissue) and stand densities (g/m^3) of nutrients and minerals correlated with use by caribou; and (3) to determine, experimentally, whether graminoid productivity and response to clipping were related to previous levels of use by caribou, as predicted by grazing lawn theory.

3.3 Methods

3.3.1 Study site

Research was conducted on the Southern Alaska Peninsula Caribou Herd (SAPCH). Ranges used by the SAPCH, and the groups composing this herd, have been described in Chapter 1.

3.3.2 Collection and analysis of forage samples

Preliminary field work began during summer, 1991, and included terrestrial and aerial surveys of the Black Hill and Caribou River calving ranges. During these surveys, caribou groups were characterized and recorded on maps (scale 1:63,360). After two surveys each in May, June, and July, it became apparent that calving and post-calving congregations of caribou on both ranges were using certain sedge meadows more often than others, and that some meadows usually contained large groups while others usually contained small ones.

In 1992, two sedge meadows were selected on each range: within each range, one site was selected that had been used in 1991 by large groups and one that had been used by small groups. To quantify graminoid productivity and response to clipping, 10 wire exclosures (0.25m^2) were randomly located in each of the four sites in early June 1992. Each site was dominated by a single species of sedge, Carex nesophila, and exclosure-microsites contained no signs of recent grazing or visible traces of feces. At the end of June, sedges were clipped at the moss layer and collected. All exclosures were harvested within 36 hours. Any exclosures that showed signs of having been grazed or disturbed by caribou were excluded from samples. At the time of clipping, sedges at all sites were in a similar flowering stage of phenology. All exclosures were harvested again 2 weeks later, without the addition of feces, urine, or other fertilizers in the interim.

While in the field, samples were dried over a heater and stored in paper bags. In the laboratory, samples received the following treatment: clipped plant material from each exclosure was dried to a constant weight at 60°C for 24 h, shoots were counted and measured to the nearest 1 mm, and samples subsequently weighed to the nearest 1 mg using a Mettler balance.

Graminoid quantity and growth form were described in three ways: biomass (g/m^2), biomass density (g/m^3), and shoot density (shoots/m^2). Biomass density is a quantification of volumetric biomass, incorporating both vertical and horizontal components of biomass distribution, and was calculated for each exclosure by sorting individual sedge plants into height classes and weighing each height class. The total mass of each height class within an exclosure was converted to g/m^3, and these were summed to give a total mass in g/m^3 for each exclosure. Shoot density represents the spatial distribution of graminoids within sites and was calculated by multiplying by four the number of shoots counted from each exclosure. Concentrations (g/100g tissue) of nitrogen, phosphorous, magnesium, sodium, calcium, and potassium were quantified at The Habitat Lab, Washington State University, Pullman, WA. Finally, stand densities (g/m^3) of nitrogen and macrominerals were derived by converting their concentrations to $g_{mineral}$/sample and then to $g_{mineral}/m^3$ for each sample. Forage quality was defined as stand nitrogen density (McNaughton 1984).

3.3.3 Caribou Group Sizes and Indices of Use

Exclosure sites were monitored for use by caribou during June and early July 1992. Feeding sites were visited once daily while working in either of the two calving ranges. When caribou were observed, groups were characterized according to numbers of adults and calves, and sexes of adults. In all instances, only female caribou and calves were observed, and only adults were considered in calculations of group size, because we could not determine with certainty whether calves were grazing.

A use index was calculated for each site, because group size or density of herbivores in a site are not necessarily accurate indicators of the degree of use of a site. For instance, a site may sustain the same degree of use if visited serially for several days by a single animal or once by a group of animals. Therefore, a time component is necessary to reflect the actual degree of use. We derived a use index for each site by converting group sizes to densities and then calculating the average density of animals within each site per day of observation (# caribou/km^2/day).

We used *t*-tests to assess differences between two-sample cases, using pooled variances for samples with similar variances and separate variances for samples with disparate variances, according to Zar (1984). Correlations across all four sites were tested using Pearson product-moment correlation coefficients, with Bonferroni adjustments for multiple pairwise comparisons (SYSTAT, Inc. 1992). *F*-tests were used to assess differences between regression coefficients between clipping events within sites. All analyses were performed using SYSTAT version 5.0 for Windows (SYSTAT, Inc. 1992), and results were considered significant at $P \leq 0.05$.

3.4 Results

3.4.1 Differences Between High and Low Use Sites

Range-wide density of caribou was greater on Black Hill (2.11 caribou/km^2) than on Caribou River (0.53 caribou/km^2), and sizes of summer feeding groups were significantly larger on Black Hill (mean = 273 ± 471) than on Caribou River (mean = 12 ± 27) (Table 5). Within Black Hill, groups were significantly larger on the high-use site than on the low-use site ($t = -3.76$, $P = 0.03$, $df = 3.1$) (Table

12). Similarly, the average daily density of caribou (use index) was substantially greater on the high-use site than on the low-use site (Table 12). On Caribou River, foraging groups were significantly larger on the high-use site than on the low-use site (t = -3.78, P = 0.001, df = 24.5), and the average daily density of caribou was greater on the high-use site than on the low-use site (Table 12).

Graminoid biomass on Black Hill was more than twice as great in the high-use site as in the low-use site (t = -4.30, P = 0.002, df = 9.4) (Table 13). The same trend was apparent on Caribou River, where forage biomass on the high-use site exceeded that on the low-use site by nearly a factor of two (t = -4.42, P < 0.0001, df = 18) (Table 13).

Patterns of graminoid growth on high- and low-use sites paralleled closely differences in biomass between sites on both ranges (Table 13). On Black Hill, shoot density of graminoids was significantly greater on the high-use site than on the low-use site (t = -4.42, P = 0.001, df = 13.5). Additionally, biomass density was greater on the high-use site than on the low-use site (t = -5.21, P < 0.0001, df = 13.6). Similarly, shoot density on Caribou River was significantly greater on the high-use site than on the low-use site (t = -4.48, P < 0.0001, df = 15.9), and mean biomass density was greater on the high-use site than on the low-use site (t = -3.66, P = 0.002, df = 17.2) (Table 13).

Concentrations of macrominerals in sedges were largely similar between

Table 12. Caribou group sizes and indices of use in high- and low-use feeding sites on the adjacent Black Hill and Caribou River ranges, Alaska, 1992. Values are means ± 1 SD based on sample sizes in parentheses.

Site	Mean Group Size (n = # of groups)	Usage Index* (n = # of days)
BLACK HILL HIGH-USE	108 ± 52 (n = 4)	41 ± 71 (n = 13)
BLACK HILL LOW-USE	10 ± 5 (n = 3)	6 ± 13 (n = 13)
CARIBOU RIVER HIGH-USE	14 ± 16 (n = 25)	11 ± 22 (n = 24)
CARIBOU RIVER LOW-USE	1.3 ± 0.6 (n = 3)	0.3 ± 1.0 (n = 24)

* calculated as the average daily density of caribou within the site (#/km^2/day)

Table 13. Graminoid physical characteristics in high- and low-use caribou foraging sites on Black Hill and Caribou River, Alaska, 1992. Values are means ± 1 SD based on sample sizes given in parentheses.

Feeding Site	Biomass (g/m^2)	Shoot Density ($\#/m^2$)	Biomass Density (g/m^3)
BLACK HILL HIGH-USE (8)	27 ± 10	1833 ± 443	443 ± 88
	**	**	***
BLACK HILL LOW-USE (9)	11 ± 4.4	964 ± 358	239 ± 72
CARIBOU RIVER HIGH-USE (10)	26 ± 5.3	1286 ± 182	303 ± 50
	***	***	**
CARIBOU RIVER LOW-USE (10)	16 ± 4.8	878 ± 211	212 ± 61

** $P < 0.005$, *** $P < 0.0005$; within categories, between high and low use sites high- and low-use sites on both ranges (Table 14). On Black Hill, high- and low-use sites differed only in that sodium concentration was greater in sedges on the low-use site (Table 14). On Caribou River, phosphorous and sodium occurred at higher concentrations in graminoids on the high-use site than on the low-use site (Table 14). Graminoid nitrogen concentration (g_N/100g tissue) did not differ between high- and low-use sites on Black Hill ($P = 0.8$) or Caribou River ($P = 0.2$) (Table 14).

Stand densities of macrominerals differed between high- and low-use sites on both ranges (Table 15). On Black Hill, densities of phosphorous, magnesium, sodium, calcium and potassium were all greater, and indeed in some cases more than twice as great, in sedge samples from the high-use site than those from the low-use site (P: $P < 0.0001$, $df = 11.6$; Mg: $P < 0.0001$, $df = 15$; Na: $P = 0.048$, $df = 15$; Ca: $P < 0.0001$, $df = 15$; K: $P < 0.0001$, $df = 11.3$). A similar association between usage and stand densities of minerals existed on Caribou River, where all minerals occurred at higher densities in graminoids on the high-use site than on the low-use site (P: $P < 0.0001$, $df = 18$; Mg: $P = 0.002$, $df = 18$; Na: $P < 0.0001$, $df = 17.4$; Ca: $P = 0.001$, $df = 18$; K: $P < 0.0001$, $df = 17.7$) (Table 15).

Differences in forage quality, as indicated by stand nitrogen density (g_N/m^3) (McNaughton 1984) were pronounced between high-and low-use sites on both ranges (Table 15). On Black Hill, graminoid nitrogen density was approximately

Table 14. Graminoid mineral and nitrogen concentrations (g/100g tissue) in high- and low-use caribou foraging sites on Black Hill and Caribou River, Alaska, 1992. Values are means ± 1 SD based on sample sizes given in parentheses.

Feeding Site	P	Mg	Na	Ca	K	N
BLACK HILL HIGH	0.40 ± 0.09	0.14 ± 0.01	0.05 ± 0.01	0.19 ± 0.01	2.4 ± 0.2	3.0 ± 0.2
(5)			*			
BLACK HILL LOW	0.31 ± 0.04	0.14 ± 0.01	0.08 ± 0.02	0.19 ± 0.01	1.8 ± 0.1	3.0 ± 0.1
(5)						
CARIBOU RIVER HIGH	0.31 ± 0.03	0.14 ± 0.01	0.08 ± 0.01	0.22 ± 0.03	2.0 ± 0.2	3.0 ± 0.1
(5)	*		**			
CARIBOU RIVER LOW	0.26 ± 0.02	0.14 ± 0.01	0.06 ± 0.01	0.21 ± 0.01	1.8 ± 0.1	3.1 ± 0.2
(5)						

* *P* < 0.05; ** *P* < 0.005; within categories, between high- and low-use sites

Table 15. Graminoid mineral and nitrogen densities (g/m^3) in high- and low-use caribou foraging sites on Black Hill and Caribou River, Alaska, 1992. Values are means ± 1 SD based on sample sizes given in parentheses.

Feeding Site	P	Mg	Na	Ca	K	N
BLACK HILL HIGH	1.77 ± 0.35	0.62 ± 0.12	0.24 ± 0.05	0.84 ± 0.17	10.7 ± 2.13	13 ± 2.6
(8)	***	***	*	***	***	***
BLACK HILL LOW	0.74 ± 0.22	0.33 ± 0.10	0.18 ± 0.06	0.45 ± 0.14	4.3 ± 1.30	7.2 ± 2.2
(9)						
CARIBOU RIVER HIGH	0.94 ± 0.15	0.42 ± 0.07	0.25 ± 0.04	0.67 ± 0.11	6.1 ± 1.0	9.1 ± 1.5
(10)	***	**	***	**	***	**
CARIBOU RIVER LOW	0.55 ± 0.16	0.30 ± 0.09	0.12 ± 0.03	0.45 ± 0.13	3.9 ± 1.13	6.4 ± 1.8
(10)						

* $P < 0.05$; ** $P < 0.005$; *** $P < 0.0005$; within categories, between high- and low-use sites

twice as great in the high-use site than in the low-use site ($t = -5.27$, $P < 0.0001$, $df = 15$). On Caribou River, graminoid nitrogen density differed in the same manner between the high-and low-use sites ($t = -3.66$, $P = 0.002$, $df = 18$) (Table 15).

3.4.2 Correlations Across Sites

Degree of use of graminoid meadows by foraging caribou was most highly correlated with phosphorous concentration ($r = 0.97$; $P < 0.0001$) and density ($r = 0.90$, P P 0.0001) and potassium concentration ($r = 0.98$, $P < 0.0001$) and density ($r = 0.88$, $P < 0.0001$). Stand densities of nitrogen, magnesium, and calcium were also highly correlated with use of feeding sites by caribou (N: $r = 0.79$, $P < 0.0001$; Mg: $r = 0.79$, $P < 0.0001$; Ca: $r = 0.71$, $P < 0.0001$). Of the aspects of graminoid growth form investigated, both biomass density and shoot density were highly correlated with use by caribou (biomass density: $r = 0.79$, $P < 0.0001$; shoot density: $r = 0.76$, $P < 0.0001$), whereas graminoid biomass was not ($r = 0.55$, $P = 0.07$).

3.4.3 Graminoid Productivity and Response to Clipping

Productivity and responses of graminoids to clipping were comparable within Black Hill and Caribou River, but did not reflect the historical foraging regimes of the individual sites (Figure 9). On Black Hill, graminoids on both the high- and low-use sites displayed at least compensatory growth in response to

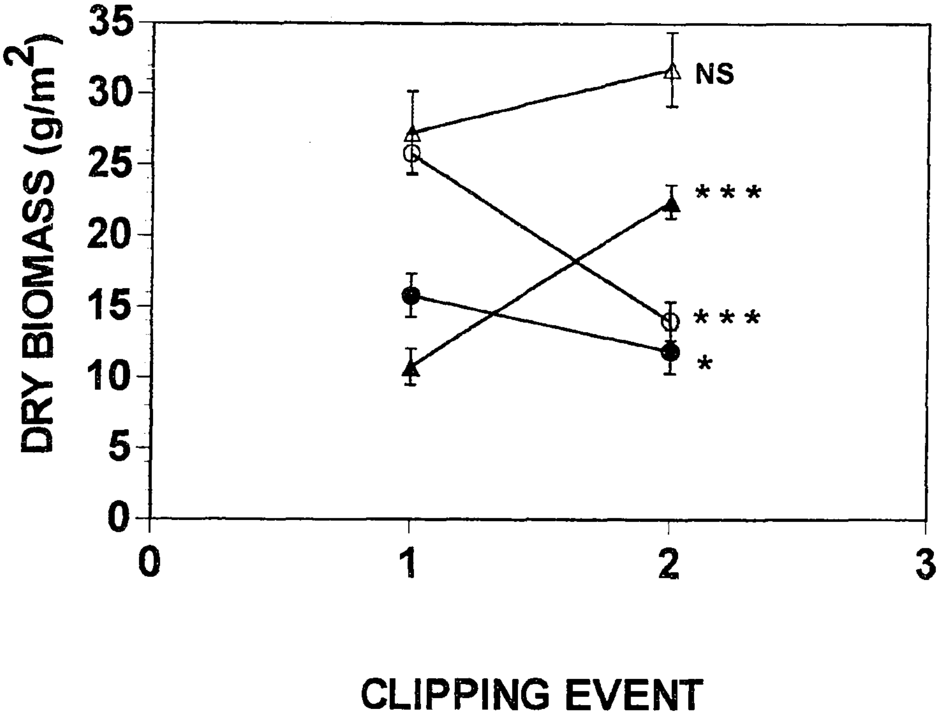

Figure 9. Available above-ground biomass (dry) within exclosures at first and second clipping events in high- and low-use caribou feeding sites on Black Hill and Caribou River, Alaska, 1992. Open triangle: Black Hill high (n = 8); solid triangle: Black Hill low (n = 9); open circle: Caribou River high (n = 10); solid circle: Caribou River low (n = 10). * $P = 0.06$, *** $P < 0.0005$, NS = not significant, based on *t* - tests.

clipping. Although the difference in above-ground biomass before and after clipping was not significant on the high-use site (mean before = 27 ± 10 g/m^2, mean after = 32 ± 6.6 g/m^2; $t = -1.10$, $P = 0.30$, $df = 11.6$), above-ground biomass more than doubled in response to clipping on the low-use site (mean before = 11 ± 4.4 g/m^2, mean after = 23 ± 3.2 g/m^2; $t = -6.67$, $P < 0.0001$, $df = 17$). Both the high- and low-use sites on Caribou River, however, displayed undercompensation in response to clipping. Regrowth on the high-use site was merely one-half of the original standing crop (mean before = 26 ± 5.3 g/m^2, mean after = 14 ± 3.2 g/m^2; $t = 6.04$, $P < 0.0001$, $df = 18$), whereas on the low-use site, graminoid production after clipping fell only slightly short of the biomass originally present (mean before = 16 ± 4.8 g/m^2, mean after = 12 ± 5.0 g/m^2; $t = 1.80$, $P = 0.09$, $df = 18$).

Linear regressions between biomass density and shoot density within sites reveal the nature of the relationship between graminoid volumetric and spatial growth forms. Such regressions demonstrate, for example, how much volumetric biomass increases with a one-unit increase in shoot density for feeding sites under varying levels of use by herbivores. Moreover, $\hat{Y}$-intercept values from such regressions indicate what may be considered the theoretical minimum biomass density value for each site, and whether this minimum is influenced by clipping. In high- and low-use feeding sites on both Black Hill and Caribou River, graminoid biomass density and shoot density were positively linearly related before clipping (Black Hill high: $r^2 = 0.60$, $P = 0.02$; Black Hill low: $r^2 = 0.64$, $P = 0.01$; Caribou River high: $r^2 = 0.41$, $P = 0.05$; Caribou River low: $r^2 = 0.81$, $P = 0.001$) (Figure 10).

After clipping, the theoretical minimum density of biomass increased on both the high- and low-use sites on Black Hill, as demonstrated by elevation of the $\hat{Y}$-intercept value (high-use: constant = 161 ± 96 g/m^3 before clipping, constant = 338 ± 90 g/m^3 after clipping, $F = 3.90$, $P = 0.09$; low-use: constant = 84 ± 47 g/m^3 before clipping, constant = 295 ± 71 g/m^3 after clipping, $F = 20.2$, $P = 0.003$) (Figure 11). On Caribou River, clipping had no significant effect on the theoretical minimum biomass density in either of the high- or low-use sites (high-use: constant = 80 ± 96 g/m^3 before clipping, constant = 27 ± 35 g/m^3 after clipping, $F = 2.37$, $P = 0.17$; low-use: constant = -27 ± 45 g/m^3 before clipping, constant = -30 ± 29 g/m^3 after clipping, $F = 0.003$, $P = 0.96$) (Figure 12).

3.5 Discussion

3.5.1 Forage Influences on Herbivore Behavior

Herbivores display sensitivity to variation in forage quality across wide ranges of spatial scales (Klein 1970; Westoby 1974; Fryxell 1991; Molvar *et al.* 1993). In an experiment with captive red deer inside an enclosure, Langvatn and Hanley (1993) demonstrated that these grazers were able to discriminate

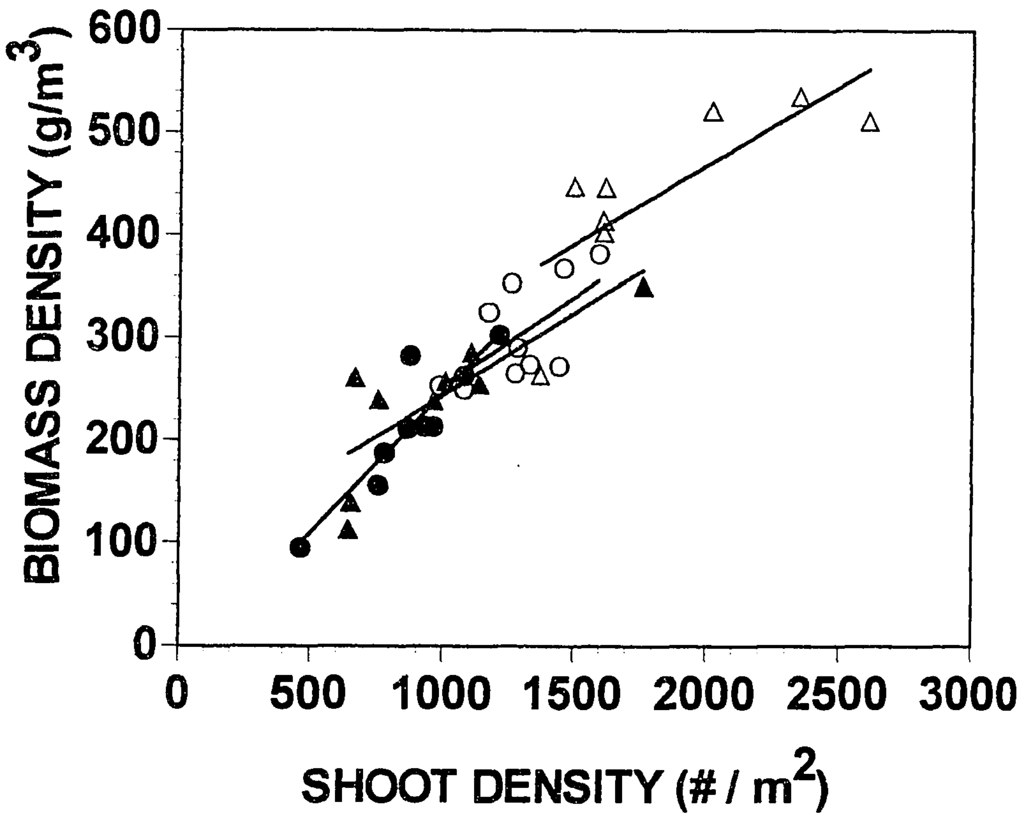

Figure 10. Linear regressions between graminoid dry biomass density (g/m^3) and shoot density (# / m^2) within exclosures in high- and low-use caribou feeding sites on Black Hill and Caribou River calving ranges, Alaska, 1992. Open triangle: Black Hill high-use ($R^2 = 0.60$, $P = 0.02$); solid circle: Black Hill low-use ($R^2 = 0.64$, $P = 0.01$); solid triangle: Caribou River high-use ($R^2 = 0.41$, $P = 0.05$); open circle: Caribou River low-use ($R^2 = 0.81$, $P = 0.001$).

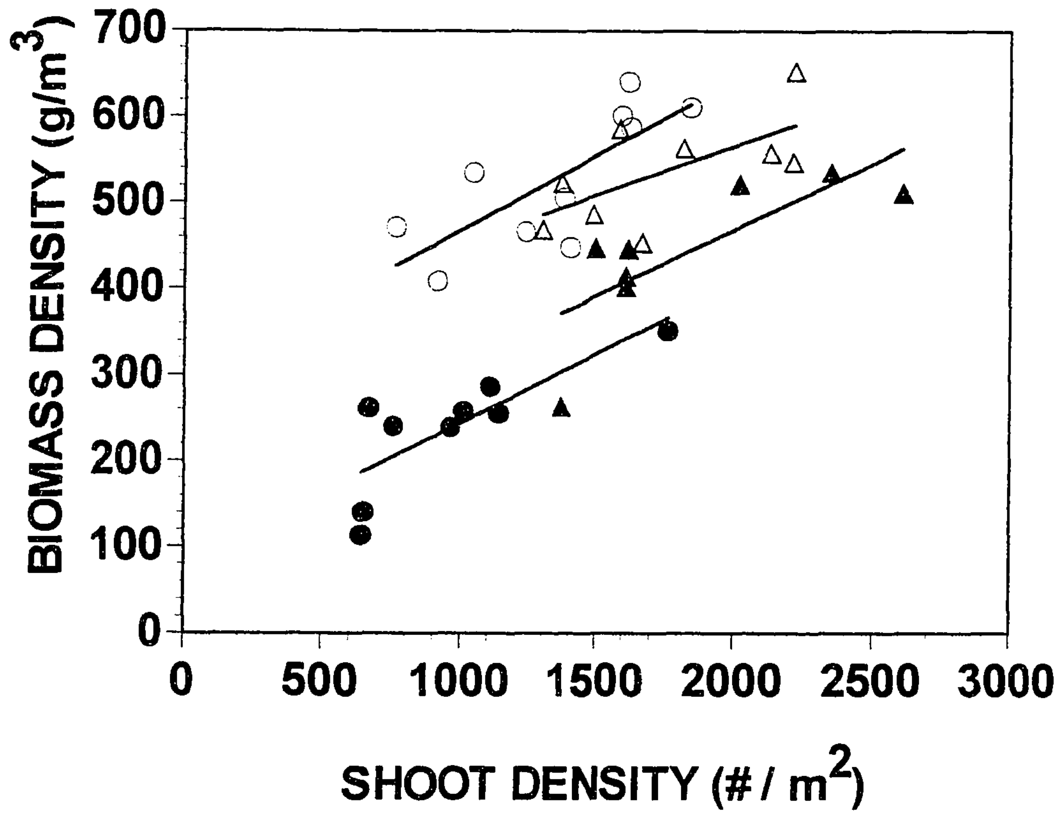

Figure 11. Productivity of graminoids after clipping in high- and low-use caribou feeding sites on Black Hill, Alaska, 1992, indexed by a change in the relationship between biomass density (g/m^3) and shoot density (# / m^2). Solid triangle: high-use, first clipping (constant = 160.7 ± 95.8 g/m^3); open triangle: high-use, second clipping (constant = 337.9 ± 89.8 g/m^3; *F* = 3.90, *P* = 0.09); solid circle: low-use, first clipping (constant = 84.0 ± 46.8 g/m^3); open circle: low-use, second clipping (constant = 294.5 ± 71.3 g/m^3; *F* = 20.2, *P* = 0.003).

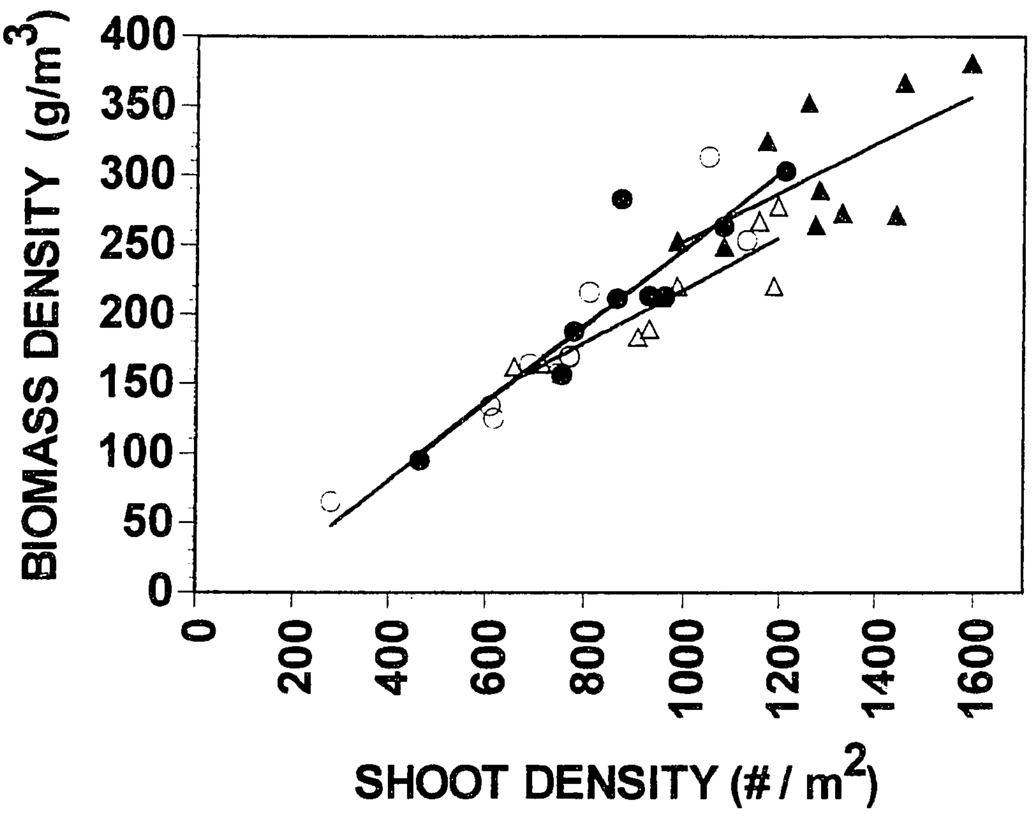

Figure 12. Productivity of graminoids after clipping in high- and low-use caribou feeding sites on Caribou River, Alaska, 1992, indexed by a change in the relationship between biomass density (g/m³) and shoot density (# / m²). Solid triangle: high-use, first clipping (constant = 80.1 ± 96.4 g/m³); open triangle: high-use, second clipping (constant = 26.9 ± 34.5 g/m³; $F = 2.37$, $P = 0.17$); solid circle: low-use, first clipping (constant = -27.2 ± 45.1 g/m³); open circle: low-use,second clipping (constant = -29.5 + 28.7 g/m³; $F = 0.003$, $P = 0.96$).

between patches of grass on the basis of their quantity and quality. Implications from their study can be applied to investigate other possible levels of discrimination by large mammalian herbivores, including where to feed within ranges (Langvatn & Hanley 1993). Belovsky (1978; 1986), used linear programming models to establish that a wide range of herbivores (from insects to large mammals) display a strategy of energy maximization in their choices of where to forage and which types of forage to consume. This agrees with results of other studies that have shown that foraging efforts of large mammalian herbivores are greatest on sites with the highest returns of energy and nutrients (White & Trudell 1980*b*; White 1983; McNaughton 1985; Etchberger *et al.* 1988; Bauer 1990; Albon & Langvatn 1992; Frank & McNaughton 1992; Klein & Bay 1994).

Herbivore sensitivity to local variation in forage quantity and quality thus produces patterns of distribution of herbivores over landscapes, and this in turn can cycle back on vegetation. This is apparent from results of studies focusing on the multiple effects of grazing on forage condition that have shown grasses and sedges tend to be more productive, grow more densely, and contain higher concentrations of nutrients when moderately grazed than when lightly grazed or ungrazed (*sensu* McNaughton 1983; 1984; Hik & Jeffries 1990; Pandey & Singh 1992). Variation in group sizes and average daily densities of caribou across feeding sites in this study may be interpreted as an indication of the influences of forage structure and quality on forager behavior, according to a simple line of reasoning: if a social herbivore is social while foraging, there must be a sufficient forage base to support, or allow for, this sociality. This idea was presented slightly differently by McNaughton (1985) as herbivores adjusting their densities according to productivities of grasslands.

Within Black Hill and Caribou River, densities of caribou were higher on the sites with greater biomass, biomass density and shoot density (Table 13), and higher forage nutrient and mineral densities and concentrations (Table 13, Table 14). Variation in densities of foraging groups across sites from both ranges indicates the ecosystem level influences of variable forage structure and distribution on caribou sociality. While factors such as predation risk and socialization of calves may promote formation of groups (Lent 1966; Bøving 1994.; Post *et al.* unpublished), these results indicate that formation of increasingly larger groups by an herbivore with high social tendencies was facilitated on feeding sites with relatively higher returns of forage, nutrition and minerals per unit foraging effort.

3.5.2 Herbivore Influences on Structure and Quality of Vegetation

In this study, the four feeding sites examined were presumed to have had different grazing histories, based upon observations of patterns of use of the sites that were consistent over two summers as well as upon range-wide densities of caribou that were widely disparate between Black Hill and Caribou River (Post *et al.* unpublished). Across these sites, forage characteristics correlated with usage of the sites by caribou in the following order, from highest to lowest: densities and concentrations of phosphorous and potassium; densities of nitrogen and magnesium; biomass density and shoot density; and, finally, density of calcium.

Although our data indicate that site use by caribou increased with forage density and quality, it is not clear in this instance whether increasing levels of grazing by caribou have produced richer, denser swards than would be present in the absence of grazing. The formation of grazing lawns depends upon compensatory plant growth in response to herbivory (McNaughton 1983) and fertilization (Ruess & McNaughton 1984; Georgiadis *et al.* 1989). Maintenance of the grazing lawn as such depends upon return of grazers to the site (McNaughton 1984). Considering that large herbivores are able to distinguish between graminoid patches of variable quantity and quality (Langvatn & Hanley 1993), and that physiological and energetic needs influence the foraging strategies of a wide range of herbivores (including mammalian grazers) (Belovsky 1986), it is plausible that the foraging effort of grazers on intrinsically productive graminoid swards can lead to development of grazing lawns through positive feedback mechanisms (McNaughton 1985).

Hence, our clipping experiment was aimed at determining to what extent caribou might have influenced the structure of graminoid swards in which they grazed. If both high-use sites had displayed compensatory or greater biomass production after clipping, while both low-use sites displayed undercompensation, we might conclude that previous grazing pressure had enhanced sward productivity and the ability of graminoids on the sites to respond to defoliation (*sensu* McNaughton 1984; Henry & Svoboda 1989). Instead, both Black Hill sites responded positively to clipping (Figures 9 and 11), whereas those on Caribou River did not (Figures 9 and 12), independent of previous levels of use by caribou. We conclude, therefore, that the Black Hill sites are inherently more productive and able to respond to grazing, and that this may have originally attracted greater numbers of caribou to that range. Indeed, the Black Hill sites bordered a watercourse, while the Caribou River sites were in flat, saturated meadows with little apparent drainage or sub-surface water flow, which are important influences on productivity of arctic sedges (Chapin *et al.* 1988). Thus, given this landscape variation in ecosystem function, and, possibly, geomorphological differences across the Southern Alaska Peninsula, herbivores on the most productive sites are likely exerting positive influences on plant growth and nutrient cycling processes where they feed (Ruess & Seagle 1994).

The high correlation of forage phosphorous density and concentration with caribou site use coincides with Chapin's (1980) assertion that Carex responds to defoliation with an increased rate of phosphate absorption via the root system and a subsequent increase in phosphorous concentration in regrown tissues. That the plants sampled in this study had not been grazed during the year of sampling indicates that sites with different grazing histories can carry this legacy into the next growing season. Similarly, in semi-arid grasslands, the effects of tissue removal by herbivores can be detected in remaining tissues months afterward (Caldwell *et al.* 1981), while tundra soils may be altered for years by fertilization by mammalian herbivores (McKendrick *et al.* 1980).

The high correlations between site use and graminoid densities of phosphorous, potassium, and nitrogen as well as phosphorous concentration may be indicative of caribou tracking forage quality on the basis of phenology, because younger plant tissues tend to have higher concentrations of these elements (Chapin 1980; Albon & Langvatn 1992). Although phenology can differ between Black Hill and Caribou River by up to eight days, depending on site and exposure (Post & Klein unpublished), we attempted to control for plant age by collecting samples when all four sites were in the same phenological stage. Indeed, post-hoc comparisons between the two low-use sites on Black Hill and Caribou River revealed no differences in forage mineral densities ($P > 0.05$ in all cases). Increasing caribou use of feeding sites with higher concentrations and densities of forage minerals also may indicate a response by caribou to a seasonal mineral shortage at the time of calving and lactation (White 1979). Phosphorous, magnesium, and sodium are particularly important for lactating cows and growing calves, and the need for these minerals has been linked to the seasonal migrations of some African ungulates (McNaughton 1990).

The high correlations of biomass density and shoot density with caribou use of sites coincide with the reported influences of ungulates on grasses and sedges in other ecosystems. The increase in shoot density with site use reported here is analogous to increased tillering rates of African (Oesterheld & McNaughton 1988; Georgiadis *et al.* 1989) and arid North American (Jaramillo & Detling 1992) grasses following defoliation.

Finally, the correlation between increasing density of nitrogen in forage with usage by caribou can be ascribed to several processes. For example, other studies have shown that herbivory increases soil microbial activity, either by reducing the plant's carbon input to its roots (Holland & Detling 1990), or through fecal and urinary nitrogen inputs (Ruess & McNaughton 1987), both of which result in increased soil nitrogen mineralization and increased nitrogen uptake by the plant. In turn, caribou may use sites with high forage nitrogen concentrations more intensely as a strategy of maximizing nutrient intake as predicted by Belovsky's (1986) model. Indeed, a study of foraging selectivity by reindeer

(Rangifer tarandus) in Arctic Alaska and their subsequent weight gain and productivity showed that small variation in forage quality can have magnified effects on herbivore productivity (White 1983). Similarly, a study of red deer foraging and productivity showed that small-scale differences in forage quality can have profound effects on their reproductive success (Iason *et al.* 1986). Thus, caribou observed in this study may be displaying sensitivity to local variation in forage quantity and quality across potential feeding sites; concentrating more heavily in the better sites; enhancing the productivity, nutrient and mineral content of the forage in turn; and maximizing energy intake in the process.

3.6 Conclusions

Caribou respond to variation in quantity, quality and growth-form of graminoid forage across landscapes and within local ranges by concentrating in those sites with highest returns of energy and nutrients per unit foraging effort. In turn, caribou may enhance the productivity and nutrient content of graminoid forage in sites that possess characteristics favorable for nutrient cycling. These results place the foraging ecology of a social, arctic, mammalian herbivore in the context of grazing theory developed from studies of wildebeest in East Africa.

CONCLUDING REMARKS

Despite early contentions that mainland populations of caribou in North America were limited by natural and human predation (Bergerud 1974), data presented in this thesis indicate that a depredated population of caribou inhabiting the mainland can indeed become limited by food availability, lending further support to an emerging body of evidence along these lines (Messier *et al.* 1988; Couturier *et al.* 1990). Thus, the conditions that might have led to overgrazing of winter lichen resources on the Southern Alaska Peninsula during the SAPCH's recent peak are of considerable interest. Because of the rugged mountains around Port Moller on the eastern extent and Isanotski Strait on the western extent of the SAPCH range, this caribou population may be unable to expand its range as caribou density increases. There is some indication that the SAPCH may be functionally insular, as regular or large-scale migrations of caribou out of the Southern Alaska Peninsula have not been recorded; some few animals, however, have been observed crossing between Unimak Island and the mainland as well as high up in the mountains around Port Moller. As an insular population, the SAPCH would probably be more likely to overgraze its lichen ranges during population highs. Furthermore, lichen beds on the Southern Alaska Peninsula may be inherently susceptible to overgrazing because the relatively mild and snow-free winters in the area leave lichens readily accessible throughout the year.

Considering that vegetation begins to green-up much later on the Black Hill range than it does on Caribou River, and that the availability of forage per caribou is greater on Caribou River (because density of caribou is higher on Black Hill), why some caribou are calving on Black Hill is not immediately clear. Possible explanations lie in results presented in Chapters 2 and 3. Large, homogeneous meadows such as those found on Black Hill are conducive to formation of large foraging groups, and calves in such groups may escape the risk of predation better than those in smaller groups. Moreover, calves and adults may be able to devote more time to foraging while in large groups such as those commonly observed on Black Hill, because the amount of time spent by individuals in searching for both food and predators tends to decrease with group size (Focardi & Paveri-Fontana 1992). Another benefit to calving on Black Hill lies in exploitation of the highly productive and nutritious forage occurring there. As demonstrated in Chapter 3, forage on Black Hill is more productive and can be twice as dense as, and contain much greater concentrations of nutrients than, forage on Caribou River. For a particular volume of bite, therefore, caribou on Black Hill can consume greater amounts of biomass and nutrients than can caribou on Caribou River. Within the Caribou River subpopulation, however, lower caribou density apparently alleviates intraspecific competition, because females inhabiting Caribou River are able to forage more selectively than those on Black Hill (Figure 6).

Finally, a point of interest raised in this thesis bears further consideration. Why are there apparently two subpopulations within the Southern Alaska Peninsula Caribou Herd, and why does one migrate while the other does not? Of course, it is possible that these populations are not distinct, but is clear that there are two separate sets of seasonal ranges, and that females calving on one of the ranges consistently produce greater proportions of calves. For migration to be adaptive, there must be some benefit derived from it (Tyler & Øritsland 1989). One potential benefit for caribou migrating from Black Hill into Cold Bay for winter may be some level of release from predation by wolves (Fryxell *et al.* 1988), because wolves may be less inclined to hunt near the village. Another benefit may be access to greater lichen reserves, because, as indicated by range sampling, lichens are more abundant around Cold Bay than on Black Hill. Finally, understanding why the Caribou River group does not migrate requires considering what they gain by not migrating. By remaining resident on the Caribou River range, caribou have access to vascular plant forage, as well as lichens, throughout winter. Furthermore, they have access to highly nutritious forage as early as green-up commences, which can be 1 month prior to calving.

Although the points discussed here do not provide concrete answers to the puzzling phenomena which constitute a study of caribou ecology, they should, at least, provoke interest for further research in this fascinating field.

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