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Maternal investment and habitat selection by Dall's sheep

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University of Alaska Fairbanks, 1991
MATERNAL INVESTMENT AND HABITAT SELECTION
BY DALL'S SHEEP

A
THESIS

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of the University of Alaska Fairbanks
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MASTER OF SCIENCE

By

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May 1991
MATERNAL INVESTMENT AND HABITAT SELECTION
BY DALL'S SHEEP

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ABSTRACT

Maternal behaviors and selection of habitat during lambing by Dall's sheep (*Ovis dalli*) were studied in Denali National Park and Preserve, Alaska, from April through July in 1988 and 1989. Climatic conditions in early spring differed between years; plant phenology was delayed by two weeks in 1989. Births were later and less synchronous in 1989. Females appeared to respond to variation in timing of births by modifying patterns of maternal investment; ewes nursed lambs for greater total time following parturition, but reduced total time spent nursing more rapidly in 1989. Selection of habitat characteristics varied with lambing chronology; terrain features related to avoidance of predators and sites with milder climatic conditions were selected during peak lambing. Variation between years in group sizes strongly influenced habitat selection. When corrected for variation in group size, no significant differences between years in selection of habitat were identified.
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Chapter 1:
INTERANNUAL VARIATION IN TIMING AND SYNCHRONY OF
PARTURITION IN DALL'S SHEEP

ABSTRACT

Timing and synchrony of parturition in Dall's sheep (Ovis dalli) were studied on Igloo Mountain, Denali National Park and Preserve, Alaska from April through July in 1988 and 1989. Median ± SD dates of birth were 18 May (+ 5.1 days) in 1988 and 27 May (+ 8.8 days) in 1989. Ninety percent of births occurred in a 27-day period in 1988 and in a 36-day period in 1989; interannual variation in timing and synchrony of parturition was pronounced. Mortality of young in this predator-rich environment, however, did not differ between years, suggesting climatic variability may contribute more than predation in constraining timing and synchrony of parturition in Dall's sheep.

INTRODUCTION

Much recent work has addressed factors affecting timing and synchrony of reproduction in North American mountain sheep (Ovis spp.). In a review of 30 North American populations, Bunnell (1982) concluded that initiation of lambing was delayed and synchrony of
lambing increased at higher latitudes. Thermal stress on neonates may constrain how early lambing can occur, but forage quality and availability probably contribute more in affecting the overall timing of births (Bunnell, 1980). Onset of lambing in mountain sheep is correlated with plant phenology relative to energetic and nutritional requirements of lactation (Berger, 1979a; Bunnell, 1982; Festa-Bianchet, 1988b; Thompson and Turner, 1982). Duration of lambing in northern populations ultimately is constrained by the need of lambs to attain sufficient body mass and reserves to survive harsh winter conditions (Bunnell, 1982; Festa-Bianchet, 1988b; Thompson and Turner, 1982). Populations at lower latitudes, not subjected to severe winters or strong seasonal pulses in growth, have relaxed selection upon timing of parturition, and hence, longer lambing seasons (Bunnell, 1982; Festa-Bianchet, 1988b; Geist, 1971). Predation on young also may influence degree of birth synchrony in ungulates (Estes, 1976).

I quantified timing and synchrony of lambing in a population of Dall’s sheep, and tested for differences in these variables between years. Further, the relative importance of predation in birth synchrony was evaluated.
METHODS

Study Area

This study was conducted in Denali National Park and Preserve, located on the north side of the Alaska Range in central Alaska (64° N, 150° W). Broad valleys separate the Alaska Range from a parallel series of rugged foothills to the north. Distribution of Dall's sheep is patchy throughout the park, with concentrations of animals along the north side of the range and in the parallel foothills (Murie, 1944; Murphy and Whitten, 1976; Whitten, 1975). Indices of numbers of sheep suggest population size has varied between 500 and 2,000 animals since 1947 (Murphy and Whitten, 1976; Singer et al., 1981). Murie (1944) estimated populations of > 5,000 animals in the early 1920's.

Field work was conducted on Igloo Mountain, a traditional lambing ground for a segment of Dall's sheep inhabiting the park (Murie, 1944). Igloo Mountain is located in the foothills and isolated by drainages on three sides, but connected to Sable Mountain by a low ridge. The study area is approximately 1,165 ha, ranging in elevation from 1,480 m at the summit to 885 m in creek bottoms. Matted alpine tundra dominated by Dryas spp., Carex spp., lichens, mosses and several forbs occurs at higher elevations; shrub birch (Betula glandulosa) and willows (Salix spp.) dominate at lower elevations, and white spruce (Picea glauca) forest occurs near valley bottoms. Plant nomenclature follows Hultén (1968).
The park contains unmanipulated populations of predators of Dall's sheep including wolves (*Canis lupus*), coyotes (*C. latrans*), grizzly bears (*Ursus arctos*), golden eagles (*Aquila chrysaetos*), wolverines (*Gulo gulo*), and lynxes (*Lynx canadensis*). Only bears, wolves and golden eagles are relatively common on the study area.

Denali Park has a continental mountain climate with short, cool summers and long, harsh winters. January is the coldest month with temperatures averaging -17 °C. The warmest month is July, averaging 12 °C. Snowfall averages 190 cm, but winds keep some areas free of snow throughout winter. Precipitation (mostly rain) differed between study years, with 1988 receiving 8.4 cm more during April-July than did 1989. Weather in mid-May, however, was more severe during 1989; a late storm covered the area with approximately 25 cm of new snow from 9-12 May.

**Data Collection**

The study area and surrounding mountains were surveyed from the air with a small, fixed-wing aircraft on 1 April in 1988 and 1989 to locate groups of sheep for ground-based observations. Thereafter, observations were made on foot 3 days per week in April to early May, and 6 days per week from early May through July, totaling 68 days in 1988 and 74 days in 1989. Dall's sheep were located initially with binoculars or the unaided eye, then approached to ≤ 100 m for observation. When possible, animals were categorized as lambs, yearlings, ewes (females ≥ 2 years-of-age), or rams (males ≥ 2 years-of-
age). Lambs < 48 h old were categorized as neonates. Small body size, wet appearance of the umbilicus, and unsteadiness in locomotion were used to identify neonates; mountain sheep lambs are able to negotiate precipitous terrain about 48 h after birth (Geist, 1971; Shackleton and Haywood, 1985). Yearling and 2-year-old males were sometimes difficult to distinguish from ewes, especially in thick winter pelage when genitalia and udders were not visible. To avoid incorrect identification, yearlings, "class I" rams (Geist, 1971), and ewes were classified as "ewe-like" individuals. Nonetheless, attempts were made to categorize animals to sex and age class when observations were made at close range, especially following the spring molt.

The entire study area was surveyed for sheep three to four times per week. Ratios of lambs:ewe-like individuals were recorded from April-July in 1988 and 1989. Complete surveys for sheep that included the entire study area were obtained 23 times after termination of lambing in 1988 and 15 times following lambing in 1989; only these data were used to examine survivorship of lambs through July.

**Statistical Analyses**

Direct observations and evidence of recent births were recorded too infrequently to allow quantification of the lambing period. Thus, timing of parturition was determined by calculating medians and standard deviations of the birthing periods by use of probit analysis (Caughley and Caughley, 1974; Finney, 1952). Counts of lambs and ewe-like animals were pooled on two to five consecutive days to include an adequate
number of ewe-like individuals (n ≥ 28) in each sampling period, and mean day was assigned for each pooled sample. Data points were weighted by number of ewe-like individuals in each sampling period (Caughley and Caughley, 1974). Distribution of births, as measured by changes in the lamb to ewe-like ratio, exhibited a positive skew in both years. Thus, data were log-transformed before fitting probit lines.

Probit analysis is useful for calculating the weighted median of a frequency distribution, but not appropriate for tests that require assumptions concerning the “tails” of the distribution (Finney, 1952). Thus, distributions of births were estimated by fitting polynomial regressions in a stepwise fashion to the cumulative percent births for each year. Partial F-tests (Zar, 1984: 337) were used as the criterion for including a parameter in regression equations, and an F-statistic was calculated to test for differences between years in the distributions of births (Zar, 1984: 347). SAS probit and GLM procedures were used for these analyses (SAS Institute Inc., 1985).

Lamb:ewe-like ratios were regressed (Zar, 1984: 263) against time after completion of the lambing period to examine survival of lambs through July in 1988 and 1989. Additionally, trends in number of ewe-like individuals and proportion of adult ewes in the ewe-like category were examined using the Spearman rank correlation (Zar, 1984: 318) to ensure that changes in the lamb:ewe-like ratios resulted from changes in numbers of lambs and not changes in numbers of adult ewes or ewe-
like individuals. The Mann-Whitney U-test was used to compare daily values of proportions of ewes in the ewe-like category between years (Zar, 1984:139). Only observations during which sex and age of all animals were noted were used for this latter analysis.

RESULTS

Start of lambing differed markedly between years. In 1988, the first lamb was observed on Igloo Mountain on 9 May. This also was the first day on which a lamb was sighted in the park (L. Adams, pers. comm.). In 1989, however, the first lamb was observed on Igloo Mountain on 22 May, and the first lamb seen elsewhere in the park was on 21 May (C. McIntyre, pers. comm.) In both years, number of lambs sighted quickly increased following these initial births. Probit analysis indicated that median date ± SD for births was 18 May (± 5.1 days) in 1988, the 10th day after onset of lambing. In 1989, the median date for births was 27 May (± 8.8 days), the 6th day after the start of lambing.

When considered from the onset of lambing such that day 1 was the first day that a lamb was observed in each year (Fig. 1, inset), polynomial regressions of percent births against time indicated that distributions of births differed significantly ($F = 3.11$, $d.f. = 4$, 16, $p < 0.05$) between years. These analyses do not consider interannual variation in the start of lambing, but only the difference in distributions of births once lambing began. Variation in the pattern of births is even more striking...
when disparity in onset of lambing is considered (Fig. 1). In 1988, 90% of births occurred in a 27-day period ending 4 June. In contrast, 90% of lambs were born within a 36-day period ending 26 June in 1989. Not only were births later in 1989, but also less synchronous.

Although predation was not observed during this study, predators were common on the study area. One pair of golden eagles nested on Igloo Mountain in both years, and were observed near Dall's sheep almost daily. Feces and tracks of wolves and bears were observed often. Bears (often females with cubs) were sighted on 9 occasions in 1988 and on 8 occasions in 1989. One lamb that died shortly after birth was scavenged by two bears in 1989. Two wolves were observed on the study area in 1989. One lamb was killed by wolves on a nearby mountain during July 1988 (C. Beyer, pers. comm.).

Ratios of lambs:ewe-like individuals (1988, 0.38:1, $\text{SD} = 0.08:1$; 1989, 0.42:1, $\text{SD} = 0.06:1$) did not decline significantly after completion of lambing in either year (1988, $r^2 = 0.07$, $df = 22$, $P > 0.200$; 1989, $r^2 = 0.14$, $df = 14$, $P > 0.150$); these regression slopes were not different between years (1988, $h = -0.0011$; 1989, $h = -0.0033$; $t = 1.9075$, $df = 34$, $P > 0.050$). Thus, although synchrony differed greatly between years, survival of lambs from termination of the birthing period through July did not do so.

Number of ewe-like individuals observed daily on the study area (1988, $\bar{X} = 28.7$, $\text{SD} = 7.9$, range = 16 - 46; 1989, $\bar{X} = 29.8$, $\text{SD} = 8.9$, range = 15 - 42) did not change significantly following lambing in either year (1988, $r_s = -0.30$, $df = 22$, $P > 0.100$; 1989, $r_s = 0.21$, $df = 13$).
Fig. 1. -- Cumulative percent of births determined from lamb:ewe-like ratios showing differences in timing, and synchrony (inset) of lambing for Dall's sheep in Denali National Park, Alaska in 1988 and 1989. Curves were estimated by use of polynomial regression through the origin (1988, $\hat{Y} = 9.47x - 0.529x^2 + 0.011x^3$; 1989, $\hat{Y} = 8.962x - 0.381x^2 + 0.005x^3$). Arrows indicate dates of births observed ($n = 3$) and inferred from presence of a neonate, placenta, or blood stains ($n = 19$).
Proportion of ewes in the ewe-like category (1988, $\bar{X} = 0.59$, $SD = 0.05$; 1989, $\bar{X} = 0.72$, $SD = 0.08$) also remained relatively constant from the start of lambing onward in each year (1988, $r_9 = -0.30$, $df = 22$, $P > 0.100$; 1989, $r_9 = 0.16$, $df = 9$, $P > 0.500$); however, these proportions differed significantly between years ($U = 5.51$, $P < 0.02$). These results indicate that variation in the lamb:ewe-like ratios within each year resulted primarily from changes in numbers of lambs rather than changes in numbers of adult ewes or ewe-like individuals.

**DISCUSSION**

Parturition in mammals is timed to coincide with environmental and social conditions favorable for survival of young (Ims, 1990; Millar, 1977; Thompson and Turner, 1982). Resource availability during gestation and lactation influences timing of reproduction in mammals (Millar, 1977). Ultimately, duration of gestation is constrained physiologically in most mammals; timing of mating results from selection acting primarily upon timing of birth (but see Kiltie, 1982 for a review of intraspecific variation in mammalian gestation lengths).

Median dates of birth observed in this study (18 May in 1988, 27 May in 1989) include the range of dates reported for other northern populations of mountain sheep. Median dates of birth for a bighorn ($Q$. *canadensis*) population in Canada at approximately 51° N latitude, were 26 May in 1984 and 1985, and 23 May in 1986 (Festa-Bianchet, 1988b).
Median dates of lambing for Dall's sheep in Kluane Park, Canada at approximately 60° N latitude, were 19 May and 18 May for 1971 and 1972, respectively (Bunnell, 1980). Reports of parturition in Dall's sheep in Alaska suggest that lambing begins later than in Kluane Park (Hoefs and Cowan, 1979). Nichols (1978) reported 24 May as an overall mean date of lambing for three populations of Dall's sheep on the Kenai Peninsula (60° N) during 4 years.

Interannual variation in distribution of births observed in the Denali population was large; onset of lambing periods occurred 13 days apart, and dates by which 90% of lambs were born occurred 21 days apart. Most comparable data for Dall's sheep populations indicate less variation in lambing among years. Onset of lambing by Dall's sheep in Kluane Park varied by only 3 days between 1971 and 1972 (Bunnell, 1980). Of three populations of Dall's sheep studied by Nichols (1978) over 4 years, one exhibited nearly identical dates of peak lambing in all years, whereas peak dates of lambing in the two other populations were more variable (9 and 11 days). A slightly longer lambing period, and hence, greater interannual variation would be expected at more southerly latitudes (Bunnell, 1982; Festa-Bianchet, 1988b). Yet, my data showed even greater disparity in onset and equivalent differences in median dates of lambing (9 days) between two years at approximately 4° higher latitude.

Synchronous birthing seasons are common among ungulates (Bowyer, in press; Rutberg, 1987). Synchronous births in strongly
seasonal environments may result from limited time available for offspring development, and from the need for young to attain sufficient body mass to survive resource scarcity in winter (Bunnell, 1980; Festa-Bianchet, 1988b).

Females of prey species that concentrate births may "swamp" predators with vulnerable young, thereby reducing the probability of predation on individual neonates (Estes, 1976). Prey species that aggregate following parturition may gain additional benefits from group living (Hamilton, 1971). Female mountain sheep, however, usually become solitary 1-2 days before birth, and remain isolated with neonates for 1-2 days following parturition (Geist, 1971; Schaller, 1977; Shackelton and Haywood, 1985). Benefits from reduced predation related to grouping following birth would not occur until after this period.

Festa-Bianchet (1988b) postulated that mortality of late-born lambs should be greater within the first few days of life than for early-born individuals because young would be most vulnerable to predators during that time. If selection for birth synchrony resulted from strong selection upon timing of birth because of harsh climatic conditions, however, late-born lambs should suffer increased mortality during their first winter relative to those born closer to the peak of lambing. Festa-Bianchet (1988b) reported that late-born bighorn lambs did not experience greater mortality within the first few days, but did suffer greater losses than early-born lambs to five months, and at one year-of-age. He concluded
predation on young contributed little to explaining degree of birth synchrony in northern populations of bighorn sheep.

If predation strongly affected degree of birth synchrony in this population of Dall's sheep, then lambs born during the less-synchronous period in 1989 should suffer greater mortality through July than those born in 1988; however, this was not the case. No significant difference in lamb mortality between 1988 and 1989 supports the hypothesis that synchrony of parturition is affected more strongly by climate than by predation on young, even in a predator-rich environment. Indeed, Estes (1976) postulated that the "strategy" of swamping predators may be less important for species adapted to precipitous terrain where females with young can find sanctuary from predators.

Late-born lambs face two problems with respect to forage availability. Ewes must produce milk from forage of lower protein content; late-born lambs suckle for shorter durations and receive less milk from 1 month-of-age onward (Berger, 1979a; Festa-Bianchet, 1988b; Horejsi, 1976). Additionally, lambs born later have less access to high quality forage than earlier-born animals.

Several nonexclusive hypotheses may explain interannual variation in timing of parturition. Greater density on winter range has been correlated with an increase in proportion of late-born lambs in bighorn sheep (Festa-Bianchet, 1988b). Density of other ungulates also is known to influence timing of parturition probably through nutrition and body condition of females (McCullough, 1979; Ozoga and Verme, 1982;
Skogland, 1985). Mean date of conception estimated from reproductive tracts of white-tailed deer (*Odocoileus virginianus*) occurred five days earlier following reduction of the population size (McCullough, 1979). Similar shifts in parturition were reported for red deer (*Cervus elaphus*) (Clutton-Brock et al., 1987).

Among bighorn sheep, younger females tend to give birth later than adults (Festa-Bianchet, 1988a). Later conception for younger females also has been demonstrated in other ungulates (Clutton-Brock et al., 1982; McCullough, 1979). Lower reserves of body fat in young female ungulates probably causes delayed ovulation and conception (Bunnell and Olsen, 1981; Festa-Bianchet, 1988a; McCullough, 1979; Mitchell and Lincoln, 1973; Skogland, 1985). Proportion of ewes in the ewe-like category was higher in 1989. If this variation resulted from recruitment of young ewes in the second year, then a shift in age structure of adult females may have contributed to the observed variation in timing of births observed during this study.

Weather patterns may influence distribution of births in several ways. Heavy snow in autumn may interfere with movements to traditional rutting grounds thereby effecting timing of mating and parturition. Because sheep tend to remain on relatively snow-free slopes in winter and early spring (Geist, 1971), snow depth and hardness may influence amounts of forage available to ewes during the last third of gestation, resulting in lower rates of fetal growth and longer gestation periods (Kiltie, 1982; Skogland, 1984; Verme, 1965). Skogland (1984)
reported that fetal growth was depressed 26% in a resource-limited population of wild reindeer (Rangifer tarandus); peak calving was 9 days later than for a nearby population at lower density (Skogland, 1984). Verme (1965, 1969) demonstrated that female white-tailed deer on low planes of nutrition had longer gestation periods and produced smaller offspring.

Lastly, weather and plant phenology at time of parturition affect lamb survivorship. Because energetic costs of lactation are substantially larger than those of gestation (Millar, 1977), selection should favor individuals that could retain fetuses for a short period until forage necessary to meet lactational demands is available, and until climatic conditions are suitable for neonate survival. Size of young at birth might constrain how long females could postpone parturition because of potential problems in delivery of overly large lambs. Perhaps this occurred with the later lambing season of Dall's sheep on Igloo Mountain following substantial snowfall in May 1989. Although this mechanism of "fine tuning" of fetal growth has not been documented, it might be favored by selection in northern populations in years when late spring storms create inhospitable conditions for young and limit availability of forage for short periods of time. Clearly, fetal size may limit how long parturition could be prolonged due to problems with delivery of overly large lambs. Potential factors regulating timing of birth in wild ungulates have been explored, but a comprehensive
understanding of interactions among these factors is far from complete, and is deserving of further research.
Chapter 2:

INTERANNUAL PLASTICITY IN MATERNAL INVESTMENT

BY DALL'S SHEEP

ABSTRACT

Effects of environmental variation and timing of births on patterns of nursing and weaning behaviors were examined in Dall's sheep in Alaska. Indices of plant productivity, growing season, and diet quality (fecal crude protein) suggest that later plant phenology resulted in a shorter growing season in 1989. Timing of parturition was approximately two weeks later and less synchronous in 1989 than in 1988. Females responded to variation in timing of births and forage availability by modifying patterns of maternal investment; females nursed lambs for a greater total time (duration x rate) following parturition, but reduced total time spent nursing more rapidly in 1989. Ewes exhibited behaviors associated with weaning more often during early lactation in 1989 when parturition was delayed. These data suggest that (1) even in far northern latitudes where the period in which to rear young is extremely limited, females exhibited plasticity in patterns of maternal investment to compensate for variation in environmental conditions and timing of births, and (2) ability to modify patterns of maternal investment in response to immediate ecological conditions may...
be important even in highly predictable environments with only slight or occasional annual variation.

**INTRODUCTION**

How life-history patterns of animals are influenced by environmental heterogeneity is of considerable interest (Boyce and Daley, 1980; Carlisle, 1982; Fretwell, 1972). In severe, but highly predictable environments such as the Arctic and sub-Arctic, plasticity of behavioral responses to variation in proximal ecological conditions may be limited (Levins, 1968). Reproductive patterns of mammals living in seasonal environments usually are timed so that young are born when the climate is relatively hospitable and resources are available to support costs of lactation and growth (Ims, 1990; Millar, 1977; Pond, 1977; Rutberg, 1987; but see Bowyer, in press). Parturition in North American mountain sheep (*Ovis* spp.) inhabiting northern latitudes coincides with increases in forage quality associated with advancing plant phenology during spring (Bunnell, 1980, 1982; Geist, 1971; Festa-Bianchet, 1988a).

Patterns of maternal behavior should be affected by varying environmental conditions (Carlisle, 1983; Lee, 1984; Lott, 1984). Indeed, Berger (1979a) demonstrated differences in nursing behavior and timing of weaning between northern and desert populations of bighorn sheep (*O. canadensis*). He hypothesized that females exhibited variation in weaning "strategies" based upon proximate ecological conditions.
Horejsi (1976) observed interannual variation in suckling behaviors of bighorn lambs, and speculated that timing of parturition relative to plant phenology may have been responsible.

The need for lambs to attain sufficient body mass and reserves to survive harsh winter conditions is an important factor regulating timing of birth in northern populations of mountain sheep (Bunnell, 1980; Geist, 1971; Thompson and Turner, 1982). For instance, Festa-Bianchet (1988a, 1988b) reported that late-born lambs suffered higher rates of winter mortality. Because of the short growing season at northern latitudes, lambs born later in spring suckle from ewes feeding on forage of declining quality, and have access to high quality forage for a shorter time than do individuals born earlier (Berger, 1979a; Festa-Bianchet, 1988b; Horejsi, 1976). The extent to which this pattern applies to sheep populations at extreme northern latitudes is unknown, but given this narrow “window” of suitable environmental conditions, maternal investment should be intense.

Females might follow several “strategies” for partitioning investment in offspring in response to late births and a shortened season for growth: (1) abandon neonates and conserve resources for subsequent reproduction; (2) invest more heavily in late-born lambs and forego reproduction in the next year; or (3) invest more heavily following parturition, but terminate that investment more quickly in an attempt to successfully raise offspring in consecutive years. Factors regulating reproductive timing and synchrony have received considerable attention.
(Ims, 1990), but life-history consequences of variation in timing of births are less well understood.

I studied patterns of nursing and weaning behaviors in a population of Dall's sheep in central Alaska during two consecutive years in which length of growing season and plant productivity differed markedly. In addition, timing and synchrony of births differed between years. Onset of lambing occurred 13 days later in 1989 than in 1988; late spring snowstorms delayed plant phenology by approximately two weeks in 1989. Ninety percent of lambs were born in a 26-day period beginning 9 May 1988. The same proportion of births occurred in a 35-day period beginning 22 May in 1989 (Rachlow and Bowyer, in press; chapter 1). Hence, time available for growth of lambs and replenishment of female body reserves also differed between years.

METHODS

Study Area

Field work was conducted in Denali National Park and Preserve, in the central Alaska Range (64° N, 150° W), USA. Dall's sheep inhabit these mountains as well as a parallel range of rugged foothills to the north (Murie, 1944; Murphy and Whitten, 1976). Observations were made on Igloo Mountain and the surrounding area, which has been a traditional lambing ground for Dall's sheep for many years (Murie,
1944). The study area encompasses approximately 1,165 ha ranging in elevation from 885 m to 1480 m at the summit of Igloo Mountain.

White spruce (Picea glauca), shrub birch (Betula glandulosa), and willows (Salix spp.) are common at lower elevations. Matted alpine tundra dominated by Dryas spp., lichens, mosses, graminoids, and forbs occurs at higher elevations interspersed with rock, talus, and scree slopes. Climate in Denali Park is typical of continental mountainous regions at high latitude. Summers are short and cool; winters are long and severe. Average monthly temperatures range from -17 °C in January to 12 °C in July. Yearly snowfall averages 190 cm, but some windswept areas remain relatively free of snow throughout winter.

**Data Collection**

Behavioral observations were made three days per week in April and early May, and six days per week from May through July, totalling 68 days in 1988 and 74 days in 1989. Observations typically were made between 09:00 and 21:00 h Alaska Standard Time. I collected data on activity by scan-sampling focal groups at 15-min intervals (Altmann, 1974); groups consisted of ewes (females > 2 yrs), lambs, often yearlings, and sometimes juvenile males. Nursing behaviors were recorded using *ad libitum* sampling (Altmann, 1974); when possible, length of suckling bouts were timed to the nearest second, and the individual (lamb or ewe) responsible for termination of the event was noted.

Fresh fecal pellets were collected from ewes following observation periods, and analyzed for fecal crude protein content using standard
macro-Kjeldahl procedures (Horwitz, 1975). This index to diet quality may be problematic where herbivores ingest large amounts of forage high in protein-complexing phenolics (Mould and Robbins, 1981; Robbins et al., 1987), but provides a reliable indicator of large changes in dietary quality for many species (Hodgman and Bowyer, 1986; Leslie and Starkey, 1985; Renecker and Hudson, 1985) including mountain sheep (Hebert, 1973; Seip and Bunnell, 1985; Wehausen, 1980).

**Definitions and Statistical Analyses**

Terminology for maternal behaviors follows Cowie et al. (1951); nursing refers to behavior performed by the ewe with the intention of passing milk to the young; suckling is behavior of the lamb for the purpose of obtaining milk. A “successful” suckle was recorded when the lamb appeared to be in contact with the ewe’s udder for ≥ 5 sec.; this was assumed to be sufficient time to initiate milk ejection or “let-down” (Cowie, 1984; Fraser, 1968; Horejsi, 1976). A suckle was considered “unsuccessful” if duration was < 5 sec. Rate of successful suckling was summarized on an acts-per-active-hour basis (e.g. Bowyer and Kitchen, 1987) for lambs. This measure differs from that used in other studies of suckling behavior (Berger, 1979a; Horejsi, 1976; Shackleton and Haywood, 1985) for two reasons. First, lambs were never observed to suckle while bedded, even immediately following birth, and acts-per-active-hour corrects for variation among observation periods in the proportion of time during which lambs were active. Second, animals in this population were not individually marked, and the presence of
nonreproductive ewes and juvenile males (which are sometimes difficult to distinguish from ewes) in focal groups could bias activity data of ewes, and thus, deflate estimates of suckling rates per lamb.

Total time spent suckling was indexed by multiplying weekly means for duration of successful suckling bouts by weekly means for rate (acts-per-active-hour) of suckling. This measure has been used previously as an index to the amount of milk obtained by lambs (Berger, 1979a; Fletcher, 1971; Horejsi, 1976).

Weighted regression analysis (Neter et al., 1985:167) was used to analyze weekly means of rate and duration of suckles by year. An E-statistic was calculated to examine trends in suckling behaviors through July. Analysis of covariance weighted by number of successful suckles was used to test for significant differences in slopes of the regression lines between years (SAS Institute Inc., 1985). Differences in proportions of suckles terminated by ewes and proportions of unsuccessful suckling bouts were compared between years using the Z-test (Zar, 1984:396); these proportions were calculated for three-week intervals (early-, mid-, and late-lactation) standardized from onset of parturition in each year.
RESULTS

Environmental Variation Between Years

Weather at onset of lambing was markedly different between 1988 and 1989. Late-spring snowstorms covered the study area with approximately 25 cm of new snow in mid-May in 1989, and spring plant growth was delayed in that year. In 1988, however, patches of vegetation on gentler slopes were free of snow by early-May. Percent crude protein in the feces (1988, $\bar{X} = 15.5\%$, $SD = 0.71$, $n = 51$; 1989, $\bar{X} = 12.8\%$, $SD = 0.77$, $n = 41$) exhibited a similar pattern in both years, but fecal crude protein appeared to increase and reach a peak later in 1989, presumably due to delayed plant phenology (Fig. 2).

Timing and synchrony of parturition also differed substantially between 1988 and 1989 (Rachlow and Bowyer, in press; chapter 1); onset of lambing occurred 13 days later in 1989 than in 1988. Ninety percent of lambs were born in a 26-day period beginning on 9 May in 1988. The same proportion of births occurred in a 35-day period beginning on 22 May in 1989.

Indices of length of growing season and plant productivity were used to evaluate relative availability of forage between years. Length of growing season estimated by amount of time between the last spring and the first autumn freeze was approximately twice as long in 1988 as in 1989 (79 days versus 33 days). Number of degree-days above freezing is correlated with plant productivity in tundra ecosystems, and
Fig. 2. -- Means (± SE) of percent fecal crude protein for Dall's sheep females summed across 2-week intervals in 1988 (□) and 1989 (■). Numbers above the means indicate sample sizes. Arrows indicate onset of parturition in each year.
degree-days > 5 °C provides a reliable index to length of growing season and plant productivity in arctic ecosystems (Chapin, 1983; Weigolaski et al., 1981). This index also indicated a shorter growing season and lower productivity in 1989; number of degree days >5 °C were 576 and 496 in 1988 and 1989, respectively.

The delay in increase of fecal crude protein in 1989 corresponded with a two-week delay in onset of parturition (Rachlow and Bowyer, in press; chapter 1); the result being a shortened interval in which to raise lambs in that year. Assuming this delay was related to later plant phenology in 1989 resulting from late-spring snow, several predictions about the timing of maternal behavior follow: (1) ewes should provide more milk to lambs early in lactation during 1989 to compensate for later births in that year; (2) ewes should decrease amount of milk provided to lambs more rapidly during the shorter growing season; and (3) ewes should exhibit behaviors associated with weaning earlier and more frequently during lactation in 1989 due to a more constrained time period for weaning lambs.

**Suckling Duration and Rate**

Durations of successful suckling bouts (1988, $\bar{X} = 20.1$ sec, $SD = 18.7$; 1989, $\bar{X} = 23.0$, $SD = 15.9$) declined following onset of lambing in both study years (1988, $F = 5.06$, $df = 1,9$, $P = 0.051$; 1989, $F = 37.51$, $df = 1, 7$, $P < 0.001$) (Fig. 3). Analysis of covariance (ANCOVA) indicated that no significant difference in rate of decline (slope) existed between years.
Fig. 3.--Comparison of suckling behavior of Dall's sheep lambs in Alaska during 1988 (○) and 1989 (●). Regression slopes of weekly means of duration of suckling bouts from onset of births did not differ significantly between years ($P = 0.849$). Sample sizes for weekly means range from 8 to 64 suckles.
(\(F = 0.04, df = 1, 16, P = 0.849\)) when compared from onset of lambing.

Although durations of successful suckling bouts were similar in both study years, rate (acts/active hr/lamb) of suckling varied (1988, \(\bar{X} = 0.033 \text{ a} \cdot \text{ah}^{-1} \cdot 1^{-1}\); 1989, \(\bar{X} = 0.020 \text{ a} \cdot \text{ah}^{-1} \cdot 1^{-1}\)) (Fig. 4). A negative trend was only significant in 1989 (1988, \(F = 0.17, df = 1, 9, P = 0.692; 1989, F = 111.32, df = 1, 7, P < 0.001\)); and the decline in rate of suckling was significantly more rapid in 1989 than in 1988 (1988, \(F = 14.03, df = 1, 16, P = 0.002\)). Thus, durations of nursing bouts were comparable in 1988 and 1989, but ewes nursed lambs at a higher rate following parturition in the second year.

Precise data on weaning dates were unavailable, but total time spent suckling (duration x rate), which decreased significantly following onset of lambing in each year (1988, \(F = 8.31, df = 1, 9, P = 0.018; 1989, F = 159.87, df = 1, 7, P < 0.001\)) (Fig. 5) provides information about rates of weaning. ANCOVA indicated a significant difference in the decline of total time spent suckling between years (\(F = 43.52, df = 1, 16, P < 0.001\)); total suckling time decreased more rapidly in the second year (1988, \(h = -0.2983; 1989, h = -1.3322\)). Ewes nursed lambs for more total time following onset of lambing in 1989. Yet, by the end of July, total suckling times were comparable in both years. Although observed differences between years in amount of milk provided cannot be assessed, the time course of nursing varied significantly between years. In 1989, ewes spent more time nursing early in lactation, but also reduced maternal care more quickly.
Fig. 4.—Comparison of suckling behavior of Dall's sheep lambs in Alaska during 1988 (□) and 1989 (■). Regression slopes of weekly means of rate of suckling bouts from onset of births differed significantly between years ($P = 0.026$). Sample sizes for weekly means of rate of suckling range from 4 to 89 suckles.
Fig. 5.—Comparison of total time (rate x duration) spent suckling per hour by Dall's sheep lambs in Alaska during 1988 (▲) and 1989 (△). Lambs suckled for longer total times per hour following birth in 1989. The decline in total time spent suckling was significantly more rapid in that year than in 1989 (P < 0.001). Sample sizes range from 4 to 89 for weekly means of rate and duration of suckling bouts.
Behaviors Associated with Weaning

Behaviors associated with weaning also differed markedly between years. Proportion of suckles terminated by ewes was greater during early lactation in 1989 than in 1988 (Fig. 6). Differences were not significant during mid-lactation, and after six weeks, females terminated all suckling bouts for which individuals (ewes or lambs) ending the event were observed. The proportion of unsuccessful suckling bouts increased following onset of lambing in 1988. In 1989, however, the proportion of unsuccessful suckling bouts was relatively high at onset of lambing and remained so throughout my study (Fig. 6). Differences between years were significant only in early and mid-lactation. Thus, during early lactation in 1989, females terminated and denied suckles to lambs more frequently than in 1988.

DISCUSSION

Dall’s sheep occur at higher latitudes than other North American mountain sheep, and hence, experience a severely restricted growing season and long, severe winters; a trade-off between investing in current versus future offspring should be especially important under such circumstances. Evans (1990) noted that a cost must be incurred by the female before an argument can be made for parental investment versus parental input. Hebert (1973) demonstrated that winter forage quality was below that required for maintenance for bighorn sheep in Canada,
Weaning Behaviors

Fig. 6. -- Interannual variation in proportion of suckles terminated by ewes and proportion of suckles that were unsuccessful (≤ 5 sec) during early, mid, and late lactation for Dall's sheep lambs in 1988 (□) and 1989 (■). Proportions were tested with the Z-test, and P-values are presented above yearly comparisons. Sample sizes used to calculate proportions in each three-week period of lactation are indicated above bars.

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and that snow cover influenced level of nutrition, ostensibly by limiting forage availability. Low levels of fecal crude protein in April suggest that Dall's sheep ewes still experience poor nutritional conditions at that time (Fig. 2). Other northern ungulates such as female reindeer (*Rangifer tarandus*) and muskoxen (*Ovibos moschatus*) may mobilize fat and protein reserves for early milk production (White et al., 1981; White et al., 1989). Early lactation in Dall's sheep undoubtedly represents a considerable investment by females because high-quality forage is not available for about two weeks following parturition (Fig. 2); maternal females must rely on endogenous reserves to meet demands of early lactation.

Milk intake by young has been correlated with growth in several species of ungulates (Carl and Robbins, 1988; Robbins and Moen, 1975; Sadleir, 1980; White and Luick, 1984) including sheep (Fletcher, 1971). Amount of milk consumed by young ungulates has been directly related to amount of time spent suckling (Ewebank, 1967; White and Luick, 1984). Although total time spent suckling is an imperfect measure of milk consumption, this index is useful for yearly comparisons of amount of milk furnished to young. Total time spent suckling in this study was approximately twice as great following births, and decreased more rapidly in 1989 than in 1988. Weaning is a gradual process, controlled largely by the ewe (Berger, 1979a, 1979b; Geist, 1971; Horejsi, 1976); both proportion of suckles terminated by ewes and proportion of unsuccessful suckles indicate a more active weaning process in 1989 relative to 1988.
Ewes were terminating significantly more suckles in 1989 (Fig. 6) at a time when diet quality was increasing (Fig. 2). Changes in plant phenology, and hence, diet quality as indexed by fecal crude protein were later in 1989 than during 1988. Onset of harsh winter conditions, however, did not differ between years. Thus, length of time available for growth of lambs, weaning, and acquisition of body reserves for ewes was shorter in the second study year.

Differences observed between 1988 and 1989 in patterns of nursing may have been influenced by additional factors. If ewes nursed male lambs differently than females, variation in sex ratio at birth could have contributed to interannual variation in nursing behaviors, but field data on mountain sheep do not support this view (Festa-Bianchet, 1988a, 1988b). Additionally, differential investment by sex may be confounding if male and female lambs are not equally visible (Green and Berger, 1990). Such a bias is unlikely due to openness of the terrain. Lastly, if maternal behaviors vary with age and experience, then age structure of maternal ewes could influence nursing and weaning behaviors. Although data on ages of adult females are not available, we have no information suggesting that age structure of breeding ewes shifted dramatically between 1988 and 1989.

Females might follow one of at least three "strategies" when faced with a shortened interval in which to provision young and regain body reserves for subsequent reproduction. First, females could terminate investment by aborting or abandoning offspring (Festa-Bianchet, 1988a).
This behavior wastes maternal resources already invested during gestation. Moreover, once a lamb is brought to term, presence of the neonate may be a strong stimulus eliciting maternal care (Festa-Bianchet, 1988a). Nonetheless, some female ungulates may terminate investment at that late time (Langenau and Lerg, 1976).

Second, a female may choose to invest a greater amount of energy in current offspring and forego reproduction in the following year. Alternate-year reproduction has been documented for one population of Dall's sheep (Heimer, 1978; Heimer and Watson; 1982) in Alaska as well as for other ungulates (Clutton-Brock et al., 1982; Bowyer, in press).

Lastly, females may attempt to raise offspring in consecutive seasons despite the shortened growing period; consequently, a greater amount of resources would be invested in current offspring, but that investment would be terminated earlier so that females could reach reproductive condition in the next breeding season. Lamb:ewe ratios in Denali Park range between 0.40:1 and 0.64:1, suggesting that not all females reproduce each year (Rachlow and Bowyer, in press; chapter 1; Murphy et al., 1990); Whatever “strategy” ewes adopted, clear differences existed in patterns of maternal investment in years with markedly different environmental conditions and onsets of lambing.

Plasticity in weaning behaviors in response to environmental conditions has been proposed for ungulates (Berger, 1979g; White and Luick, 1984). Early weaning in a population of mule deer (Odocoileus hemionus) has been related to declining forage quality and availability.
Early weaning also has been documented for muskoxen under conditions of nutritional stress (Jingfors, 1980; White and Luick, 1984); late-born muskoxen calves also suckled for longer durations in early lactation than did earlier-born calves (Jingfors, 1980). This study documents a similar pattern in Dall’s sheep, and I hypothesize that such behavior is an adaptation to cope with a limited time period during which to successfully rear young in a harsh arctic environment.

Patterns of weaning evolve under selection for a balance between probability of offspring survival and future reproductive success of females (Berger, 1979a; Clutton-Brock, 1984; Trivers, 1974). In unpredictable environments, where a pattern achieving this balance may vary greatly among reproductive efforts, a degree of behavioral flexibility is adaptive (Lee, 1984; Levins, 1968). Although Dall’s sheep inhabit far northern latitudes with an extremely short period in which to rear young, females responded to proximal variation in resource availability by altering their pattern of investment in offspring, specifically, nursing time and behaviors associated with weaning. Ability to modify patterns of parental investment based on ecological conditions should be adaptive even when conditions are highly predictable, as in the Arctic and sub-Arctic, and when they vary only occasionally.
Chapter 3:
Selection of Lambing Habitat by Dall's Sheep

ABSTRACT

Use and selection of habitat by Dall’s sheep during lambing were investigated in Denali National Park and Preserve. Discriminant function analysis was used to identify characteristics of the habitat useful in discriminating between randomly located sites and those used by sheep. Selection of habitat features varied with lambing chronology; sites with milder climatic conditions and areas closer to escape terrain were selected strongly during peak-lambing. Variation in size of maternal groups between years was correlated with differences in habitat use, but when corrected for variation in group size, no significant differences in habitat selection were observed between years.

INTRODUCTION

Behavior and habitat selection by female ungulates is influenced by reproductive state as well as local ecological conditions (Berger, in press; Clutton-Brock et al. 1982; Festa-Bianchet, 1988c). Gestation and especially lactation increases nutritional and energetic demands on females (Oftedal, 1985; Sadleir, 1980). Additionally, maternal females
may be constrained in selection of habitat due to vulnerability of young to predation (Berger, in press; Geist, 1971).

Dall's sheep, which occur throughout rugged mountain ranges in western Canada and Alaska (Rausch, 1950), are the northern most species of mountain sheep in North America. Severity of the arctic and sub-arctic environments may pose unique constraints on selection of habitat by Dall's sheep; growth and development of young, and replenishment of female body reserves must occur in a shortened time period at higher latitudes.

Considerable information exists about habitat selection by bighorn sheep (*O. canadensis*) (Festa-Bianchet, 1986; Geist and Petocz, 1977; Gionfriddo and Krausman, 1986; Hebert, 1973; Krausman and Leopold, 1986; Witham, 1983), and recent studies (Fairbanks et al. 1987; Wakelyn, 1987) have examined habitat components selected on summer and winter ranges. Data for selection of habitat used by mountain sheep females during lambing, however, are comparatively scant.

Habitat use by Dall's sheep outside the lambing period has been described (Burles and Hoefs, 1984; Hoefs and Bayer, 1984; Whitten, 1975), but habitat characteristics selected during the period of lambing have not been quantified. Use of higher elevations, more rugged terrain, and steeper slopes by female mountain sheep during lambing has been noted (Geist, 1971; Murie, 1944; Fitzman, 1970), but the relative contribution of these features to selection of habitat by ewes remains uncertain. Estimates of availability of habitat components during lambing for
comparison with measures of habitat use are necessary to address questions regarding selection of habitat by ewes (Petrides, 1975).

Several factors probably interact to affect selection of habitat for lambing by mountain sheep. Studies on both domestic and wild sheep have documented that substantial mortality of neonates occurred from exposure and hypothermia (Alexander, 1961; Wehausen et al. 1987). Predation on neonates on lambing grounds has been implicated as a major cause of mortality (up to 75%) for a population of bighorn sheep (Hass, 1989). Energetic requirements of female mammals shift with onset of lactation (Millar, 1977), and habitat selection may vary in response to such changes in reproductive state (Berger, in press; Bowyer, 1986; Lott, 1984). Likewise, habitat requirements of young might vary with age as vulnerability to predation changes, and as young begin foraging (Geist, 1971).

Herein, I test for differences in habitat selection by female Dall’s sheep before lambing, during its peak, and following the season of births. I hypothesize that females should use sites more sheltered from harsh climatic conditions, and closer to escape terrain during the peak period of lambing, reflecting vulnerability of young lambs to hypothermia and predation. Other researchers have suggested that a “trade-off” between forage quantity and distance to escape terrain is often made by mountain sheep (Berger, in press; Risenhoover and Bailey, 1985; Warrick and Krausman, 1987). If a positive correlation exists between forage abundance and distance to escape terrain, then I predict that females
should use areas with lower forage abundance during peak lambing. During post-lambing, however, ewes should select areas with a greater abundance of forage because of the high nutritional demands of lactation (Millar, 1977; Sadlier, 1980). Further, escape terrain should be less important during post-lambing when lambs are less vulnerable to predation.

Timing of births and subsequent patterns of maternal investment by Dall's sheep in Denali differed markedly between 1988 and 1989. Births were later and less synchronous in the second year (Rachlow and Bowyer, in press; chapter 1). Following parturition in 1989, total time spent suckling per hour was greater than twice the time in 1988, but milk intake was reduced more rapidly in 1989 (chapter 2). Berger (in press) documented shifts in foraging behavior and habitat use relative to reproductive status of female bighorn. I hypothesize that females in this study should compensate for increased energetic demands of early lactation in the second year by: (1) foraging in areas of greater forage availability; or (2) increasing total time spent foraging in 1989 relative to 1988.

**METHODS**

**Study Area**

Igloo Mountain and the surrounding area (approximately 1165 ha) in Denali National Park and Preserve was chosen as the site for this
study based on its habitat characteristics and traditional use by Dall's sheep (Murie, 1944). Igloo Mountain is separated from nearby mountains by drainages on 3 sides, and connected by a low ridge to Sable Mountain to the south (Fig. 7). Elevation ranges from 1,450 m at the summit to 885 m in river valleys. Topography varies from steep, rocky slopes at higher elevations to gently rolling hills at lower elevations.

A wide range of habitats is available to sheep in this area. White spruce (Picea glauca) forest occurs in valley bottoms, and shrub birch (Betula glandulosa) and willows (Salix spp.) are abundant at lower elevations, especially along drainages. Matted alpine tundra dominated by Dryas spp., graminoids, lichens, mosses, and forbs occurs above tree line at approximately 950 m.

Predators of Dall's sheep common on the study area are grizzly bears (Ursus arctos), wolves (Canis lupus), and golden eagles (Aquila chrysaetos). Other predators of Dall's sheep in Denali Park include wolverines (Gulo gulo), lynxes (Lynx canadensis), and coyotes (C. latrans).

Sampling Procedures

Observations of Dall's sheep were made from April through July in 1988 and 1989. Field work was conducted three days per week in April and early May, and six days per week thereafter, for a total of 68 days in 1988 and 74 days in 1989. Groups of females, often accompanied by yearlings, young males (≤ 3 years-of-age), or lambs were located initially
Fig. 7. — Map of Igloo Mountain in Denali Park, Alaska. Macro-site zones for sampling of Dall’s sheep habitat are identified with numbers (n=21). Zones were delineated using elevation and aspect, and each zone was characterized for habitat macro-measurements (1 cm=.25 km).
using binoculars, and then approached on foot to < 100 m for observation. Data on activity were collected using scan-samples of focal groups at 15-min intervals (Altmann, 1974), totalling 155 h of observation in 1988 and 235 h in 1989. Percent of time active (standing versus bedded) and percent of active time spent feeding were examined using activity data on females chosen at random from focal groups. This procedure minimizes dependence between samples of activity because observations were made ≥ 1 h apart. Size of the focal group also was monitored during observation periods. Groups were defined as animals ≤ 100 m from another individual that exhibited similar activity and movement patterns.

Sites used by sheep were identified by randomly choosing an adult female (≥ 2 years-of-age) in the focal group at ≥ 1 h intervals. Location and activity of that individual also were recorded. Locations of selected individuals were plotted on an infra-red aerial photograph (approximately 12 cm = 1 km) and sketches were made to aid in relocation of the exact sites. Care was taken not to disturb sheep during periods of observation and habitat sampling; sampling was discontinued if animals exhibited alarm behaviors. Sites used by sheep usually were sampled after sheep had left the area, but if sheep remained near selected sites, those were sampled on the following day. When possible, all groups of females with lambs within the study area were located and sampled on each day of observation. Randomly chosen sites also were
located on the infra-red aerial photograph, and sampled in the same manner as sites used by sheep.

Measurements of habitat variables (Table 1) were made at two scales: (1) plots of 1-m² ("micro-sites") were sampled at locations used by sheep and at randomly located sites; (2) "macro-sites" were determined by subdividing the study area into 19 zones based on elevation and aspect (Fig. 7). Each micro-site was located within one of these zones, and assigned the values for macro-habitat measurements associated with that zone.

Habitat characteristics sampled at micro-sites included vegetative, climatic, and physiogeographic variables (Table 1). A point frame (Kershaw, 1964:15) was used to sample percent vegetative cover by species (n = 40 "pin hits" per plot); these data subsequently were summed by forage class (graminoids, forbs, browse, Dryas, or mosses and lichens) for statistical analyses. Species seldom eaten by Dall's sheep in Denali Park (e.g. Betula, Juniperus, Ledum, etc.) (Whitten, 1975) were categorized as "other."

Climatic variables measured in this study included wind speed, wind direction, temperature, and snow cover. Wind speed was measured using a wind meter, and direction was determined with a compass. Measurements were taken for greatest sustained wind speeds, or for maximum gusts when wind speed was variable. A thermometer was used to record ambient temperature to the nearest 1°C, and values for wind chill were calculated from wind speed and temperature.
Table 1.-- Means (± SD) of raw data for components of Dall’s sheep habitat measured in Denali National Park and Preserve. Total sample sizes for sites used by sheep and for randomly located sites are given for 1988 and 1989 combined. Variables transformed for analyses are indicated by superscripts.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Sites Used by Sheep</th>
<th>Random Sites</th>
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<tbody>
<tr>
<td></td>
<td>(\bar{X})</td>
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<tr>
<td>Distance to escape (m) (^a)</td>
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<td>Elevation (m)</td>
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<td>Micro-brokenness (cm) (^a)</td>
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<tr>
<td>Micro-slope (degrees) (^b)</td>
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<tr>
<td>% cover browse (^c)</td>
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<tr>
<td>% cover forbs (^a)</td>
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<tr>
<td>% cover <em>Dryas</em> (^a)</td>
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<td>% cover moss-lichen (^a)</td>
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<tr>
<td>% cover “other”</td>
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<tr>
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<tr>
<td>Macro-slope (degrees)</td>
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<tr>
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<td>Macro-site openness</td>
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<td>1.35</td>
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\(^a\) Data were log transformed for analyses.  
\(^b\) Data were square root transformed.  
\(^c\) Data were arcsine transformed.
measurements. Wind and temperature measurements were taken at the time of micro-site selection from the position of the observer (<0.100 m from sheep, and usually <0.50 m). Snow was recorded as present or absent on micro-sites.

Terrain features at micro-sites were recorded as follows: slope was measured using an abney level; aspect was determined with a compass; brokenness was indexed by laying a fine chain diagonally across each plot, measuring this "surface distance," and subtracting the distance calculated for a flat surface; elevation was determined from a topographic map (scale = 1:63). Directional measurements (aspect and wind direction) were coded as two values (Cartesian coordinates), sine and cosine of the angle, to allow analyses of these circular variables (Zar, 1984:426). Sine and cosine represent east-west and north-south differentiation, respectively.

Distance to escape terrain was estimated visually, and verified on an aerial photograph. Escape terrain was defined by Gionfriddo and Krausman (1986) as rockland with steep slopes or cliffs on which sheep could outrun predators. Wakelyn (1987) quantified slope as $>60^\circ$ and percent rock cover as $>60\%$ in defining escape cover for bighorn. I observed sheep disturbed by predators (bears) on several occasions during this study, and terrain to which sheep fled was noted. Steep slopes and canyons were used while fleeing from bears; scree slopes and hard rock outcrops also were used, and thus, included in the definition of escape terrain in this study.
Macro-scale measurements were obtained from a topographic map (scale = 1:63) and an infra-red aerial photograph. Macro-aspect of each zone was categorized as one of eight directions (N, NE, E, SE, S, SW, W, NW), and the central value (degrees) for each category was transformed into sine and cosine. Macro-slope (in degrees) was calculated by taking the inverse of the tangent of change in elevation divided by the distance over which the rise occurred (rise/run). Brokenness of terrain was indexed by subtracting straight-line distances across zones from those measured by following contour lines within each macro-site zone. Three values for brokenness were averaged for each zone. Lastly, openness of habitat (Hirth, 1977) in each zone was rated on a scale from 1-7 ranging from rock and scree slopes (1) to spruce forest (7) (Table 2); this measure reflects broad habitat types. Thus, each random and used site was characterized on small and large scales to examine habitat selection.

Statistical Analyses

Data were tested for normality, and transformations were required for several variables (Table 1) (Zar, 1983:238-242). Pearson correlation coefficients were examined to minimize multicollinearity among variables (Table 3); elevation and habitat openness were removed from further analyses because of multicollinearity (r ≥ 0.701) with other variables. Additionally, percent cover of the "other" vegetative class was deleted from analyses due to lack of independence with percent cover of forage categories.
Table 2. -- Classification of vegetation for an index of openness used to describe habitat for Dall's sheep on Igloo Mountain. Values are ranked from (1) open habitat to (7) closed habitat, forested habitat.

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<th>Vegetative type</th>
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<tr>
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<td>3</td>
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<td>Tundra-Willow</td>
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<tr>
<td>≥70 Willow</td>
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<tr>
<td>Willow-Spruce</td>
<td>6</td>
</tr>
<tr>
<td>≥70% Spruce</td>
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Table 3. — Correlation matrix for components of Dall's sheep habitat measured in Denali National Park and Preserve. Asterisks indicate significance levels for Pearson Correlation Coefficients: * P< 0.05 and ** P< 0.01.

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<tr>
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<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
<th>F</th>
<th>G</th>
<th>H</th>
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Periods of lambing chronology were defined based on timing of births in each year. Peak-lambing included those dates during which 90% of births occurred (Rachlow and Bowyer, in press; chapter 1), 9 May - 4 June in 1988, and 22 May - 26 June in 1989. Pre-lambing samples were collected before onset of lambing in each year, and post-lambing samples included those collected from completion of the peak-lambing period through July.

Discriminant function analysis (DFA) with stepwise inclusion of variables (Johnson and Wichern, 1988) was used to identify habitat components important in separating sites used by sheep from those sampled randomly. Selection of variables was based on maximization of Mahalanobis' distance between random and used sites (Dixon, 1983). DFA was used primarily for model building in these analyses, but only variables with significant ($P < 0.05$) $E$-values were included in DFA models. Appropriateness of the models was examined by jackknifing on a case-by-case basis; prior probabilities were based on sample sizes used to build each DFA model, and posterior probabilities were calculated by eliminating one case, applying DFA, and classifying the case withheld from analysis (Dixon, 1983). In addition, DFA was conducted on rank transformed data to check for violation of assumption of normality; similar models resulted from ranked data, suggesting that models were apt. DFA models of lambing periods (pre-, peak-, post-) within years were overparamatized, and hence, omitted from analyses.
Hypotheses regarding simultaneous selection of habitat components were tested using two-way multivariate analysis of variance (MANOVA) (Johnson and Wichern, 1988:249). Class variables were "use" and either "period" of lambing chronology (pre-, peak-, or post-) or "year" (1988 or 1989). Selection for or against habitat components was inferred from significant variation between sites used by sheep and random sites (use versus availability). Further, interactions between selection and period effects in the MANOVA were used to test hypotheses about variation in selection of habitat components relative to time of birth and nursing of lambs. Likewise, interactions between selection and year effects were used to test hypotheses regarding yearly differences in habitat selection. Differences in habitat selection by time interval were inferred from a significant interaction between use and either period or year. The Hotelling-Lawley trace was used to test for overall differences of multivariate models (SAS Institute, 1985). Two-way ANOVA's with a sequential Bonferroni test (Rice, 1989) were applied to univariate statistics to determine which variables contributed most to overall differences in selection. Lastly, sites used by sheep ≤ 48 h following birth were compared to sites used over the period of lambing for the population following similar procedures.

Multiple linear regression (MLR) with stepwise inclusion of variables was used to identify habitat variables related to distance to escape terrain and to group size (Bowyer et al., 1988; Neter et al., 1985). Residuals of regressions between group size and significantly related
variables were analyzed to examine their influence on habitat use while controlling for differences in group size.

Yearly trends in group size, percent of time that sheep were active, and percent of active time spent feeding were analyzed using the Mann-Whitney U-test (Zar, 1984:138). Variation among periods was examined with a Kruskal-Wallis test (Zar, 1984:176). Influence of group size on feeding behaviors was examined using simple linear regression. The Mann-Whitney U, and Kruskal-Wallis tests also were used to examine differences between years and among periods of lambing in elevation of sites used by sheep.

RESULTS

Habitat Selection Among Lambing Periods

Interannual variation in environmental conditions between study years was large, and is probably representative of the extremes of spring climatic conditions under which habitat selection by Dall's sheep has evolved. Such variation may influence the degree to which ewes make trade-offs between predation risk and forage abundance following parturition; requirements of neonates during peak lambing, however, should be largely unaltered by the difference in spring climatic conditions between years. Hence, I combined years in analyses examining differences among pre-, peak-, and post-lambing, and
consider the effects of interannual climatic variation in the following section.

Data on individual variation could not be obtained during this study. Number of sites used by sheep sampled during this study was 316, but only 279 (134 in 1988 and 145 in 1989) were used in multivariate analyses due to missing values for measurements of habitat variables. Mean numbers of individuals in the ewe-like category observed per day were 29 and 30 in 1988 and 1989 respectively. Thus, each individual contributed to habitat sampling of sites used by sheep an average of 4.6 times in 1988 and 4.8 times in 1989. Although this violates the assumption of independence among samples, the effect on statistical results is unknown. Nonetheless, reducing degrees of freedom even fivefold has little effect on P-values from MANOVAs, but aptness of these models needs to be tested on other populations.

Discriminant function analysis with years and lambing periods combined (full model) indicated that nine variables were useful in discriminating between random sites and those used by sheep (Table 4). Standardized canonical correlations indicated that macro-brokenness, percent cover of graminoids, and distance to escape terrain were influential variables in the DFA model. Sign and magnitude of the canonical correlation coefficients describe the way in which a variable relates to random sites versus those used by sheep. For example, distance to escape terrain is negatively related to sheep use and is
Table 4. -- Standardized Canonical Correlation Coefficients for habitat variables useful in discriminating between sites used by sheep and randomly located sites on Igloo Mountain when all data were considered (full model). Order of variables indicates the order in which each was added in stepwise DFA. Percent of sites classified correctly using this model was evaluated with a jackknifing procedure.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Full Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance to escape terrain</td>
<td>-0.742</td>
</tr>
<tr>
<td>% cover graminoids</td>
<td>0.310</td>
</tr>
<tr>
<td>% cover Dryas</td>
<td>0.361</td>
</tr>
<tr>
<td>Macro-aspect (E-W)</td>
<td>0.380</td>
</tr>
<tr>
<td>Macro-brokenness</td>
<td>0.459</td>
</tr>
<tr>
<td>Micro-slope</td>
<td>-0.363</td>
</tr>
<tr>
<td>Macro-slope</td>
<td>0.303</td>
</tr>
<tr>
<td>Macro-aspect (N-S)</td>
<td>-0.286</td>
</tr>
<tr>
<td>Snow presence</td>
<td>-0.178</td>
</tr>
<tr>
<td>% classified correctly</td>
<td>84.3</td>
</tr>
</tbody>
</table>
relatively important in discriminating between sites (Table 4); percent
cover of graminoids, however, is positively related to use of sites by sheep.

DFA within each period of lambing (pre-, peak-, post-) suggest
that similar variables were selected during each time interval with a few
notable exceptions (Table 5). Windchill, macro-brokenness, and browse
were useful in discriminating between random sites and those used by
sheep only during peak-lambing, whereas snow was important only
during pre-lambing. A two-way MANOVA, including all variables
\( (n = 11) \) that entered either the full (Table 4) or one of the within-period
models (Table 5), indicated that random sites and those used by sheep
differed overall when these variables were considered simultaneously
\( (F = 30.23, df = 11, 428, P < 0.001) \).

Ewes selected habitat features differently among time periods
(pre-, peak-, and post-lambing). A significant interaction between
selection of habitat and period of lambing in the two-way MANOVA
\( (F = 5.68, df = 11, 428, P < 0.001) \) suggested that changes in selection of
habitat were associated with the chronology of lambing. Variables
contributing most to difference in selection among periods were macro-
brokenness, percent cover of browse, and snow; these variables were
significant at joint confidence of 95% using a sequential Bonferonni test.

If distance to escape terrain is positively related to forage
abundance, then females must make "trade-offs" between forage
availability and vulnerability to predators. Significant positive
Table 5. -- Standardized Canonical Correlation Coefficients for DFA models built for each lambing period independently with years combined. Percent of sites correctly classified using each model was evaluated using a jackknifing procedure.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Pre-lambing Model</th>
<th>Peak-lambing Model</th>
<th>Post-lambing Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance to escape terrain</td>
<td>-0.766</td>
<td>-0.865</td>
<td>-0.857</td>
</tr>
<tr>
<td>% cover graminoids</td>
<td>0.482</td>
<td>0.423</td>
<td></td>
</tr>
<tr>
<td>% cover Dryas</td>
<td>0.516</td>
<td>0.248</td>
<td>0.623</td>
</tr>
<tr>
<td>Macro-aspect (E-W)</td>
<td>0.383</td>
<td>0.383</td>
<td>0.428</td>
</tr>
<tr>
<td>Macro-brokenness</td>
<td>0.679</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Micro-slope</td>
<td></td>
<td>0.352</td>
<td>0.428</td>
</tr>
<tr>
<td>Macro-slope</td>
<td></td>
<td></td>
<td>-0.648</td>
</tr>
<tr>
<td>Macro-aspect (N-S)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Snow presence</td>
<td>-0.387</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% cover browse</td>
<td></td>
<td>0.374</td>
<td></td>
</tr>
<tr>
<td>Wind chill</td>
<td></td>
<td>0.320</td>
<td></td>
</tr>
<tr>
<td>% classified correctly</td>
<td>81.9</td>
<td>89.6</td>
<td>82.9</td>
</tr>
</tbody>
</table>
correlations were observed between distance to escape terrain and percent cover of graminoids and of browse (Table 3). Additionally, stepwise MLR of habitat (independent) variables against distance to escape terrain (dependent variable) indicated that percent cover of browse, *Dryas*, and graminoids were all positively related to distance to escape terrain ($R^2 = 0.37, F = 42.54, P < 0.001$; $\hat{Y} = 0.63 + 0.91$ browse + 0.30 *Dryas* + 0.43 graminoids - 0.02 macro-slope). These data suggest that ewes must make a "trade-off" between forage abundance and distance to escape terrain in selection of habitat; areas with higher forage abundances tended to be further from escape terrain.

Constraints on habitat use reflecting vulnerability of lambs to predation and thermal stress should be most important to females with new-born young. Sites used by females with neonates (≤ 48 h of birth) differed from those used over the entire period of peak lambing for the population ($F = 2.31, df = 8, 108, P = 0.025$); distance to escape terrain, macro-aspect (east-west), and cover of browse differed most in use between sites used by females with neonates and all other peak-lambing sites. Sites used within 48 h of birth were closer to escape terrain, had greater cover of browse, and tended to be on east-facing slopes. Because these comparisons were made over the same time interval, availability should not differ greatly, and thus, differences in use reflect differences in selection. Sheep appeared to adjust habitat use during the time in which lambs were most vulnerable to predation.
Habitat Selection Between Years

Selection of habitat characteristics also varied between 1988 and 1989. DFA models were similar between years (Table 6), however, percent cover of forage classes (grass, Drwas, and browse) were useful in discriminating between random sites and those used by sheep only in 1989. Forage variables were strongly selected for in 1989, whereas terrain features (macro-brokenness and macro-slope) entered the DFA model only in 1988 (Table 6). All variables present in the full model (Table 4) were included in at least one of the yearly models, except percent cover of browse. Variables effective in discriminating between random and used sites in either year were used to test for differences in selection between years. An interaction between use and year in the two-way MANOVA indicated a significant difference in selection between years ($F = 3.12$, $df = 11, 429, P < 0.001$); selection of distance to escape terrain, macro-brokenness, and snow differed most between years, however, these differences were not jointly significant at 95% confidence when examined with the conservative sequential Bonferroni test.

Effects of Group Size on Habitat Selection

Group size of maternal bands also was related to selection of habitat by Dall's sheep. Stepwise MLR of all habitat (independent) variables that entered either the full or yearly DFA models on group size (dependent variable), indicated that distance to escape terrain and percent cover of Drwas were significantly related to group size ($R^2 = 0.06$, $F = 11.18, P < 0.001$; $Y = 5.30 + 2.01$ escape + 1.43 Drwas). Likewise, group
Table 6. -- Standardized Canonical Correlation Coefficients for DFA models built for 1988 and 1989 independently with lambing periods combined within each year. Percent of sites classified correctly was evaluated using a jackknifing procedure.

<table>
<thead>
<tr>
<th>Variable</th>
<th>1988 Model</th>
<th>1989 Model</th>
</tr>
</thead>
<tbody>
<tr>
<td>Distance to escape terrain</td>
<td>-0.421</td>
<td>-1.124</td>
</tr>
<tr>
<td>% cover graminoids</td>
<td>0.334</td>
<td>0.334</td>
</tr>
<tr>
<td>% cover Dryas</td>
<td>0.466</td>
<td>0.466</td>
</tr>
<tr>
<td>Macro-aspect (E-W)</td>
<td>0.701</td>
<td>0.277</td>
</tr>
<tr>
<td>Macro-brokenness</td>
<td>0.664</td>
<td>0.664</td>
</tr>
<tr>
<td>Micro-slope</td>
<td>-0.413</td>
<td>-0.312</td>
</tr>
<tr>
<td>Macro-slope</td>
<td>0.571</td>
<td>0.571</td>
</tr>
<tr>
<td>Macro-aspect (N-S)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Snow presence</td>
<td></td>
<td></td>
</tr>
<tr>
<td>% cover browse</td>
<td>0.242</td>
<td>0.242</td>
</tr>
<tr>
<td>% classified correctly</td>
<td>84.5</td>
<td>84.6</td>
</tr>
</tbody>
</table>
size varied significantly with distance to escape terrain in MLR's performed independently for 1988 ($R^2 = 0.08, F = 10.99, P < 0.002; \hat{Y} = 7.04 + 3.71$ escape) and 1989 ($R^2 = 0.07, F = 5.74, P = 0.004; \hat{Y} = 0.93 + 1.42$ escape + 0.16 macro-slope). *Dryas* did not enter the MLR model for either year independently, and macro-slope was significantly related to group size only in 1989.

Analyses of interannual variation in habitat selection must consider yearly differences in group sizes. Mean size of maternal bands of Dall's sheep (1988, $\bar{X} = 9.48$; 1989, $\bar{X} = 5.28$) was relatively constant within each year (1988, Kruskal-Wallis $X^2 = 2.84, df = 2, P = 0.243$; 1989, Kruskal-Wallis $X^2 = 2.22, df = 2, P = 0.330$). In 1988, however, mean group size was significantly larger than in 1989 ($U = 27.34, df = 1, P < 0.001$) (Fig. 8). Residuals from simple linear regressions between group size and habitat variables strongly influenced by group size (distance to escape terrain, *Dryas*, macro-slope) were analyzed to partial out the influence of group size on use of habitat. A two-way ANOVA performed on the residuals of the regression between group size and distance to escape terrain indicated no significant difference in selection of this feature existed between years when controlled for group size ($F = 0.98, df = 1, 308, P = 0.323$); however, differences in selection of this feature among lambing periods still were significant ($F = 9.50, df = 2, 308, P < 0.001$).

Controlling for group size produced similar results for use of macro-slope between years ($F = 0.19, df = 2, 298, P = 0.666$) and among
Fig. 8. -- Mean size (± SD) of maternal groups of Dall's sheep in Denali Park, Alaska during 1988 (口) and 1989 (■). Group sizes differed significantly between years during and following peak lambing (Pre-lambing: $U = 1.29, df = 1, P = 0.056$; Peak-lambing: $U = 8.19, df = 1, P < 0.001$; Post-lambing: $U = 16.90, df = 1, P < 0.001$). Samples size (number of groups) is indicated above bars.
lambing periods ($F = 4.34, df = 2, 298, P <0.002$). Although use of percent cover of *Dryas* was related to group size in the full MLR, analysis of residuals showed that no difference in use of *Dryas* occurred either between study years ($F = 2.11, df = 1, 307, P = 0.147$) or among lambing periods ($F = 1.07, df = 2, 307, P = 0.345$). Availability of escape terrain and macro-slope cannot differ between years or among periods, and availability of *Dryas* as estimated by cover on random plots, did not differ significantly either between years ($F = 2.43, df = 1, 187, P = 0.121$) or among lambing periods ($F = 0.06, df = 2, 187, P = 0.521$). Thus, since availability did not differ significantly, variation in use of these characteristics reflects variation in selection for them by sheep. Consequently, group size was a confounding variable in analyses of habitat selection between years, and when corrected for interannual variation in group size, selection for neither distance to escape terrain, nor of macro-slope varied significantly between 1988 and 1989.

**Effects of Group Size on Foraging**

Data on activity and foraging behaviors suggest that ewes spent more total time foraging in 1988. When percent of time spent active was summed across 1-2 week intervals, no significant differences were evident between years ($U = 0.10, df = 1, P = 0.757$) or among time periods (Kruskal-Wallis $X^2 = 4.10, df = 2, P = 0.129$). Percent of active time that ewes spent feeding, however, was significantly higher in 1988 ($U = 5.10, df = 1, P = 0.024$), but did not differ among time periods (Kruskal-Wallis $X^2 = 2.55, df = 2, P = 0.280$). Because ewes were active for comparable
proportions of time in both years, but spent a greater percent of active
time foraging in 1988, ewes appeared to spend more total time foraging in

Group size also influenced activity and feeding behaviors. Regressions of percent time active and percent active time spent feeding against group size with years combined, indicated that percent of time active increased significantly with group size ($b = 0.84, P = 0.026$). Percent of active time spent feeding, however, did not show a significant trend with group size ($b = 0.20, P = 0.440$). Ewes in larger groups, then, spent a greater total time (% active time x % active time spent foraging) feeding. This conclusion is supported by the results of yearly comparisons of foraging behavior; ewes spent more total time foraging in 1988 when groups were larger.

A high degree of correlation was exhibited among some habitat variables (Table 3). Although elevation was not allowed to enter multivariate analyses of lambing habitat because of problems with multicollinearity, sheep used elevation differently among lambing periods and between years. Sheep used sites at significantly lower elevations during pre- and peak-lambing in 1989 when snow melt was later relative to 1988 (pre: 1988, $\bar{X} = 1168$ m; 1989, $\bar{X} = 1156$ m; peak: 1988, $\bar{X} = 1181$ m; 1989, $\bar{X} = 1146$ m; $U = 2.27, P = 0.023$). In both years, elevation of sites used post-lambing was greater than that used in the earlier periods of lambing (post: 1988, $\bar{X} = 1226$ m; 1989, $\bar{X} = 1228$ m).
DISCUSSION

Distance to escape terrain was useful in discriminating between randomly located sites and sites used by sheep during all time periods of lambing and in both years. Terrain features constituting "escape terrain" have been consistently noted as essential components of sheep habitat (Geist, 1971; Krausman and Leopold, 1986; Tilton and Willard, 1977; Wakelyn, 1987). Berger (in press) associated relative levels of predation risk with habitat types for mountain sheep. He found that lambs in open or flat terrain were killed by predators more frequently than lambs occurring in steep or rugged terrain (71% versus 22% respectively). Considering the high densities of terrestrial predators of Dall's sheep in Denali Park (Murie, 1944), similar relative risks of predation probably are associated with these habitat types on Igloo Mountain.

Selection of habitat by female Dall's sheep varied with lambing chronology. Greater cover of vegetation (graminoids and Dryas), lower snow cover, and shorter distances to escape terrain were selected by sheep prior to lambing. Sample sizes were comparatively small during pre-lambing, and results of habitat selection during that period should be interpreted with caution because DFA on such sample sizes may be subject to biases (Williams et al., 1990). During peak lambing, however, terrain features associated with predator avoidance (macro-brokenness and macro-slope) were strongly selected for use by maternal females. In
addition, areas sheltered from climatic extremes (higher windchills) were selected for only during the peak period of lambing. Post-lambing features selected by ewes included steeper macro-slopes, but gentler micro-slopes. This probably reflects use of high altitude benches consisting of meadows with gentler slopes interspersed with broken, steep terrain. Such areas provide forage in close proximity to escape terrain. Igloo Mountain possesses a particularly large high-altitude meadow with an east-facing aspect that was used commonly by sheep during peak- and post-lambing. Murie (1944) refers to this area as the "nursery" on Igloo Mountain. Heavy use of this meadow by sheep is reflected in the selection for east-facing macro-aspect during peak- and post-lambing in both study years. Such meadows may be a key habitat characteristic in defining suitable lambing areas and is worthy of investigation in other areas.

Lambs are most vulnerable to predation for several days following birth (Geist, 1971). Sites used by females with neonates showed even stronger selection for proximity to escape terrain than those used during the entire period of peak lambing for the population. In addition, sites used within 48 h of birth were characterized by greater cover of browse. Percent cover of browse exhibited a significant positive correlation with windchill (Table 3), and ewes may have been seeking sheltered sites for neonates or visual cover from predators during that critical time.

Variation between years in size of maternal bands was a confounding factor in analyses of habitat selection. Maternal bands were
approximately twice as large in 1988 as in 1989. Other researchers have documented correlations between group sizes and distance from escape cover or terrain in mountain sheep (Berger, in press; Risenhoover and Bailey, 1984; Warrick and Krausman, 1987). Selection of distance to escape terrain contributed strongly to between-year variation in selection of habitat. Yet, when use of habitat was corrected for group size, no significant differences between years were noted. Likewise, use of macro-slope, which varied significantly between years, did not do so when adjusted for interannual differences in group size. Thus, use of habitat did not differ significantly between years when corrected for variation in size of maternal groups.

Although elevation was not entered into models of sheep habitat in this study due to multicollinearity (Table 3), it is undoubtedly useful in describing habitat used by mountain sheep on Igloo Mountain. A suite of habitat features measured on both micro- and macro-scales varied with elevation (Table 3). Selection for elevation is probably a result of selection for habitat components that vary along an elevational gradient such as forage availability, phenology, and openness of habitat. Interannual variation of snow cover in early-spring and of plant phenology was correlated with elevational shifts in use of habitat by sheep. Use of lower elevations was associated with heavy spring snows in 1989. Although selection of snow cover differed significantly between years, sheep used sites with less snow cover than randomly located sites in both study years. Magnitude of selection (distance between means for random sites
and sites used by sheep) was greater in the second year, however, due to an increase in snow cover on random sites. Thus, after adjusting for group size, most differences in habitat selection between years in this study are explicable in terms of a shift to lower elevations during pre-and peak-lambing in 1989 when spring snows were heavier.

Although group size influenced use of distance to escape terrain and macro-slope between years, group sizes did not differ markedly among time periods within each year (Fig. 8). Thus, significant interactions between habitat selection and lambing periods indicate differential selection by females in association with lambing chronology. Selection for windchill was significant only during peak-lambing, supporting the hypothesis that females would select sites sheltered from harsh climatic conditions during that time when neonates are susceptible to thermal stress. Distance to escape terrain was strongly selected for during all periods of lambing, but magnitude of the standardized canonical correlation coefficient for escape terrain was greatest during peak-lambing. Williams (1983), however, cautioned that such interpretations may be misleading.

Abundance of forage in the summer diet of Dall's sheep in Denali Park (Murie, 1944; Whitten, 1975) was positively correlated with distance to escape terrain. Thus, feeding in areas with greater forage abundance might involve moving farther from escape terrain and hence, foraging in a more risky fashion (Berger, in press; Risenhoover and Bailey, 1985). \textit{Dryas} was the only forage class selected during post-lambing (Table 5);
although graminoids are important summer forage (Murie, 1944; Whitten, 1974), this forage class was not useful in discriminating between random sites and sites used by sheep during the post-lambing period as predicted, perhaps because the distribution of graminoids tends to be more widespread. Distance to escape terrain also was strongly selected during post-lambing, even though lambs are much less vulnerable to predation during this time (Geist, 1971). Thus, the hypothesis that ewes would seek more abundant forage during the post-lambing period at the cost of feeding farther from escape terrain was not supported. Later plant phenology at the higher altitudes used by sheep during post-lambing may provide adequate forage in proximity to escape terrain, making a trade-off between forage abundance and distance to escape terrain less necessary at that time. Also, lambs may still be vulnerable to predators constraining selection of habitat by ewes even in late summer.

Timing of births and patterns of maternal investment differed substantially between 1988 and 1989 (Rachlow and Bowyer, in press; chapters 1 and 2). Because of increased investment following parturition and later births in the second year, females were expected to compensate by feeding in areas of higher forage abundance, or by increasing total time spent foraging. When data were adjusted for interannual differences in group size, however, selection for forage abundance did not differ significantly between years, and total time spent foraging appeared to be higher in 1988. These data do not support the hypothesis that ewes
should compensate for later births and higher milk output during early lactation in 1989.

Even though marked differences in maternal investment during early lactation occurred between 1988 and 1989, ewes did not appear to alter either selection of habitat or feeding behavior in response to yearly variation. The strong influence of group size on use of terrain features associated with avoidance of predators reflects the importance of predation risk in selection of habitat by mountain sheep, and suggests that such risk may override needs for increased forage, even in 1989 when ewes invested heavily in lambs.
LITERATURE CITED


Rachlow, J. L., and R. T. Boywer. In press. Interannual variation in timing and synchrony of parturition in Dall’s sheep.


