

CHAPTER 24

Dall's and Stone's Sheep

R. Terry Bowyer, David M. Leslie, Jr., and Janet L. Rachlow

INTRODUCTION

Dall's sheep inhabit rugged and precipitous mountain ranges in Alaska and western Canada, and are the northernmost species of mountain sheep in the New World (1) (Figure 24-1). The severity and variability of arctic and subarctic environments have placed unique constraints on the ecology, behavior, and evolution of these mountain ungulates. Dall's sheep and Stone's sheep were named for W. H. Dall and A. J. Stone, respectively (2). Following Bowyer and Leslie, we use Dall's sheep as the common name for the species and use subspecific designations as appropriate (1).



(a)



(b)

Figure 24-1 (a) Dall's sheep are the northernmost member of their genus in the New World. (b) Their stocky body conformation is well adapted for inhabiting extremely rugged and precipitous terrain. (Photographs by J. L. Rachlow.)

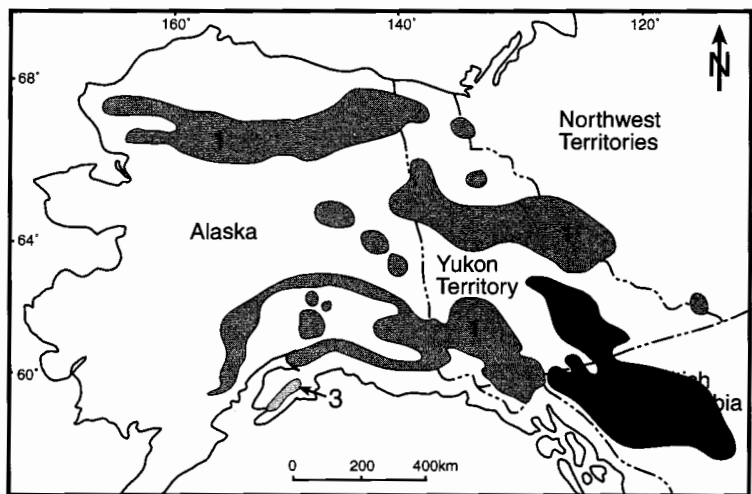


Figure 24–2 Distribution of Dall's sheep: (1) *Ovis dalli dalli*, (2) *O. d. stonei*, and (3) *O. d. kenaiensis*. (From Ref. 1.)

flare more widely than those of females (11). Horns of male Dall's sheep also flare more widely (88 centimeters tip to tip) than do those of bighorn sheep (66 centimeters). Horns of snow sheep are smaller but similar in shape to those of Dall's sheep. Dall's sheep exhibit two distinct color morphs: *O. d. dalli* and *O. d. kenaiensis* are white (or off-white), whereas Stone's sheep is much darker and possesses a rump patch and other markings more typical of bighorn sheep and snow sheep (1). Some *O. d. dalli* may possess a black tail, and Fannin's morph, which is intermediate in coloration between Dall's sheep and Stone's sheep occurs occasionally, where the ranges of the subspecies are close (41, 42) (Figure 24–2).

The distribution of mountain sheep in the New World has been influenced, in part, by the activities of humans; however, Dall's sheep have been little affected compared with bighorn sheep (43, 44, 45, 46, 47). This difference most likely reflects the harsh, remote locations inhabited by Dall's sheep and the relative lack of human developments, including grazing of livestock, at far northern latitudes. Indeed, the Dall's sheep ranges through rugged and steep mountain ranges in Alaska, Northwest Territories, Yukon, and British Columbia from 69°40' to 59°30'N latitude.

The northernmost subspecies is *O. d. dalli*, but these animals occur in Alaska as well as the Yukon, Northwest Territories, and British Columbia (Figure 24–2). *Ovis d. kenaiensis* is confined to the Kenai Peninsula in Alaska, whereas *O. d. stonei* is distributed the farthest southward with populations occurring in British Columbia and the Yukon. In the southern part of its distribution, Dall's sheep may be restricted to isolated patches of alpine habitat, but the contiguous areas inhabited by Dall's sheep generally are larger than those occupied by bighorn sheep (48, 49, 1). Hoefs reported about 13,000 Stone's sheep and 9,000 Dall's sheep from the Yukon, but now suggests a total estimate of 22,000 animals (personal communication) (50). I. Hatter (Wildlife Branch, British Columbia Environment personal communication) estimates about 14,000 Stone's sheep and 500 Dall's sheep from British Columbia. Hoefs suggested a population of about 7,000 Dall's sheep from the Northwest Territories, but A. Veitch (personal communication) believes there are at least 14,000 animals (50). Hoefs estimated 72,650 Dall's sheep occurred in Alaska including 1,500 *O. d. kenaiensis* (50). Valdez and Krausman estimated a total of 113,750 Dall's sheep (99,750 in Alaska and 14,500 in Canada) (51). Despite some variation in population estimates and the need for more quantitative survey methods, there were probably more than 110,000 Dall's sheep in 1998. Dall's sheep are the most abundant wild sheep in the world and still occupy about 90% of their former distribution (50). More detailed information on taxonomy and distribution of Dall's sheep is available in several other reviews (2, 39, 52, 1, 51a).

The ecology and behavior of mountain sheep should be viewed in an evolutionary perspective to understand how these ungulates have adapted to the harsh environments they occupy. This understanding has far-reaching consequences for the conservation and management of Dall's sheep. As with the evolution of *Ovis*, ideas for how these mountain ungulates became adapted to the landscapes they inhabit are clouded. Two related ideas, in particular, that have contributed to our existing view of mountain sheep need closer examination.

The first of these is the glaciation hypothesis proposed by Geist and its role in the evolution of mountain sheep (11). In general, this hypothesis suggested that sheep evolving at the face of retreating glaciers were subjected to differing selective forces than those inhabiting glacial refugia. Consequently, sheep from glaciated areas should possess larger horns and rump patches than those that evolved in refugia. In addition, Geist proposed that glaciation, in Asia and the New World, led to a pattern of colonization (and evolution) that placed aoudad-like ancestors at the base of an evolutionary tree leading to New World mountain sheep (i.e., the argali cline) (11). Geist further refined his ideas concerning glaciation by formulating his dispersal theory, which attempted to explain rapid evolution of sheep in relation to withdrawal of the glaciers (53). Geist postulated that abundant forage at the face of retreating glaciers would promote increased body size, larger horns, rump patches, increased productivity, and early maturation in mountain sheep (53). These conditions, then, promoted the evolution of neoteny in sheep. This brief overview does not do justice to the entire scope of ideas proposed by Geist but is sufficient to examine their relevance to mountain sheep (11, 53).

Schaller raised serious questions concerning the pattern of evolution for mountain sheep proposed by Geist, especially whether the aoudad was closely related or ancestral to modern-day mountain sheep (25, 11). Indeed, modern genetic techniques indicate that the phylogenetic relationships proposed by Geist were not correct and that morphological similarities he used as support for his hypotheses likely were the result of convergent evolution (11, 54). Of course, Geist did not have access to this information at the time he formulated his hypotheses (11, 53). Nonetheless, the aoudad is not closely related to mountain sheep and, consequently, the argali cline should now be set aside as an explanation for the evolution of mountain sheep (54).

There is little doubt that Geist was correct in assuming that glaciation helped shape the evolution and distribution of mountain sheep (11, 53). Likewise, retreating glaciers unquestionably altered the landscape and the habitats available to sheep. How much new habitat would have been created relative to the ability of nearby populations of sheep to reproduce and expand, however, is the critical question. Glaciers that withdrew at a rate of even several meters each year would likely have adjacent populations of sheep that capitalized on the production of new forage. The dispersal distances of caprids and ovids far outdistance any new habitat created by receding glaciers (25, 47). Similarly, the reproductive potential of mountain sheep would have rapidly filled vacant habitats and made the long periods necessary for the evolution of characteristics postulated by Geist unlikely (2, 11). Given the new information on phylogenetic relationships, dispersal, and population dynamics, there is no longer a need to hypothesize neoteny to explain why male sheep attain sizes larger than females; sexual dimorphism is best explained by degree of polygyny in ungulates (55, 56, 57, 58). Schaller criticized Geist's hypotheses for giving too much attention to social selection and too little to natural selection. Indeed, neither the glaciation nor dispersal hypotheses will explain the evolution of sexual dimorphism or rump patches in ruminants; both of these characteristics are widespread in species that do not have close phylogenetic ties and did not evolve in areas subject to heavy glaciation (25, 11). Moreover, Dall's sheep undoubtedly were exposed to retreating glaciers in the mountainous areas of Beringia, yet sheep in interior Alaska lack a rump patch.

More parsimonious hypotheses now exist to explain the evolution of rump patches, sexual dimorphism, and the evolution of horn-like structures (59, 60, 55, 56,

58, 61, 62, 63). We concur with Schaller that the evolution of life history traits of mountain sheep needs to be viewed in a broad perspective that includes a multitude of factors such as steepness and ruggedness of terrain, snow depth and other aspects of climate, predation, and phylogenetic constraints (25). An approach that emphasizes the role of natural selection in understanding adaptation offers the best explanation for the life-history characteristics of mountain sheep, which include age at first reproduction, litter size, longevity, and many other aspects we discuss later (64).

DIET SELECTION IN RELATION TO HABITAT

Studies on the diet of Dall's sheep are not numerous, but there is general agreement that these ungulates feed mostly on graminoids (7, 65, 2, 66, 67, 68, 69, 70). Nonetheless, Hoefs and Cowan recorded 110 different plant species in the diet of these herbivores (66). In the southwest Yukon, Canada, Hoefs and Cowan noted that reedgrass was the most common grass in the diet of sheep, whereas fescue was eaten most often in Alaska, (66, 2, 70). Other important genera of grasses eaten by Dall's sheep include brome grass, bluegrass, and wheatgrass. The occurrence of sedges and rushes in the diet of Dall's sheep may increase with north latitude: Hoefs and Cowan reported about 18% of this forage eaten by sheep in the southern Yukon, Nichols noted about 25% from the Kenai Peninsula, and Hansen indicated about 30% from the Brooks Range (66, 2, 70). These northern-most populations appear to consume the common sedge most often.

Dall's sheep also eat a variety of forbs, especially during late spring and summer, including saxifrage, cinquefoil, willow-herb, pussytoes, and many others (66, 70). Browse consumed by Dall's sheep was principally sagebrush in the southern part of their range and willow, dryas, and blueberry in the north (66, 70). Sheep sometimes move to lower elevations in early spring to obtain browse and do so again in early autumn when frost curtails growth in forbs and graminoids at higher elevations; note the peaks in use of browse by Dall's sheep during those periods (Figure 24-3). These sheep also consume limited amounts of lichens and moss.

Hansen reported strong selection (use greater than availability) for grasses during all seasons, selection for forbs in spring and summer, and for sedges in winter; browse was avoided (use less than availability) throughout the year in the Brooks Range, Alaska (70). Hansen cautioned, however, that interannual patterns of

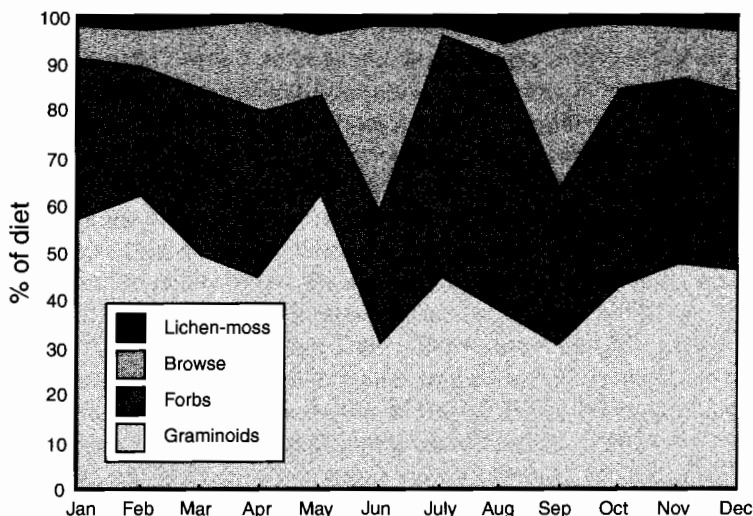


Figure 24-3 The year-round diet of Dall's sheep, Kluane, Yukon, Canada. (Modified from Ref. 66.)

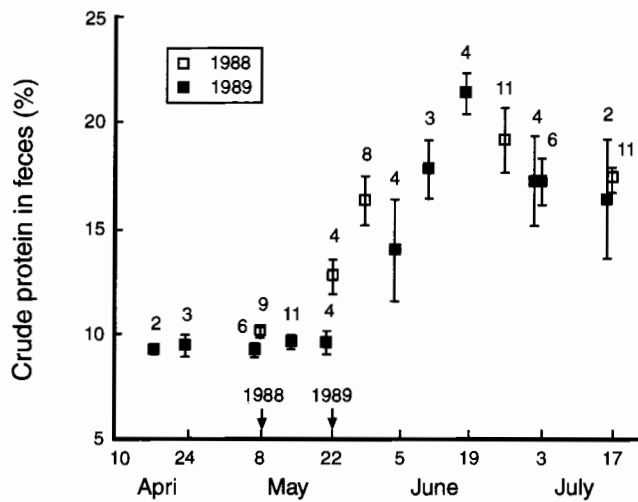


Figure 24-4 Mean (\pm SE) percent crude protein in the feces of female Dall's sheep in interior Alaska, USA. Sample sizes are provided above means; arrows indicate onset of lambing in 1988 and 1989. (From Ref. 73.)

diet selection could be affected by 10 to 15 centimeters of snow cover. Likewise, Rachlow and Bowyer noted that a cool summer that limited growth of forage resulted in differences in selection of habitat by Dall's sheep in interior Alaska (71). Mineral licks also can be important seasonally to Dall's sheep (6, 72, 7, 11).

Diet quality, as indexed by fecal crude protein, increased rapidly during early spring, peaked in June, and then began declining by July (Figure 24-4). Hansen reported a continued decline in fecal crude protein to pre-spring levels by October and that levels remained low throughout winter (70). This same general pattern was evident for digestible nitrogen, digestible energy, and *in vitro* dry matter digestibility of sheep forages (70). The growing season in arctic and subarctic environments is extremely reduced. The number of days between the last freeze in spring and the first freeze in autumn was 79 days in 1988 but only 33 days in 1989 for Dall's sheep in interior Alaska (73). Likewise, degree days greater than 5°C, an index to the length of the growing season in arctic plants, were 576 and 486, respectively, for these same 2 years (74, 73). The cool, short growing season in 1989 resulted in a marked decrease in grasses and dryas available to Dall's sheep (71). Thus, Dall's sheep must acquire the resources necessary to meet their need for reproduction and to cope with harsh winter conditions in a narrow window that may vary markedly between years (73). In addition, forage generally was more plentiful as distance from steep, precipitous terrain preferred by Dall's sheep increases (75, 71). Hence, diet selection was affected by risk of predation in these mountain ungulates (71).

REPRODUCTIVE STRATEGY

Dall's sheep are thought to have an estrous cycle of about 17 days (76). Photoperiod is likely an important cue in timing of reproduction, and the presence of an adult male and physical condition of the female are proximal stimuli that also affect onset of estrus, which is thought to last for 1 day (11, 2). Timing reproduction so that young can be provisioned successfully regulates when parturition occurs in ungulates (77, 78, 73, 79). Dall's sheep are monestrous with rut typically occurring in November and December (11, 80). One young weighing 3 to 4 kilograms normally is born after about 171 days of gestation; twins are rare (81, 80, 82). There is increasing evidence that adjustment in gestation length may be under proximal control of the female in Dall's sheep and other ungulates (78, 83, 79). For instance, Dall's sheep in interior Alaska

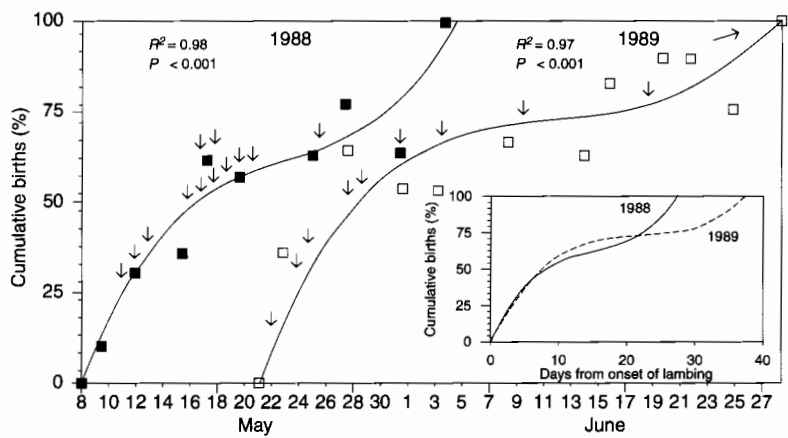


Figure 24-5 Cumulative percent of births determined from young to female female-like ratios showing differences in timing and synchrony (inset) of lambing in interior Alaska 1988 and 1989. Arrows indicate date of birth observed or inferred. (From Ref. 78.)

delayed onset of lambing by 14 days when a spring storm deposited 25 centimeters of fresh snow during the peak lambing period of the previous year (Figure 24-5) (78). There is a trend for date of parturition to be earlier for populations of mountain sheep with increasing north latitude (84, 85). Nonetheless, marked interannual differences in the date of birth can occur. Rachlow and Bowyer reported that median date of birth in a normal year was 18 May, but was 27 May in the year with the late snowstorm. Synchrony of births also differed in these 2 disparate years (78). Evidence that birth synchrony in Dall's sheep is related to predation is lacking; instead, synchronous births result from a limited time in which offspring can develop to a sufficient size in spring and summer to withstand harsh conditions in winter (78).

Reproduction has not been reported for lambs, but young yearlings may become pregnant in highly productive populations (80). Females usually do not begin reproducing, however, until 30 months of age (11). Indeed, young : adult ratios at birth for Dall's sheep in interior Alaska varied from 0.4:1 to 0.6:1 indicating not all adult females reproduced each year, a pattern reported for other arctic ungulates (86, 78, 87). Males can become sexually mature at 18 months, but because of the polygynous mating system they seldom gain an opportunity to breed until 5 to 7 years old (11).

Fetal sex ratios, although skewed slightly toward males in free-ranging populations, do not depart significantly from parity (11, 80). Captive females kept on a high nutritional plain, however, produced proportionally more daughters than sons (88). Thus, nutritional condition of the female likely affects the rate of reproduction and the sex of her offspring.

Females seek steep, rugged terrain where they seclude themselves from other sheep for 1 to 2 days to give birth (89, 78, 73, 71). Neonates are exceptionally precocial and have been observed standing within 30 minutes following parturition; young have been observed traveling with their mothers within 24 hours of birth (89). Weaning generally is completed within 3 to 5 months (36).

In a cool summer with reduced availability of forage, females markedly curtailed the amount of time they spent nursing young (Figure 24-6). These females also attempted to compensate for a reduction in forage biomass by spending more time nursing young early in 1989 (73). Such differences in maternal care between years also were reflected in the proportion of unsuccessful suckles initiated by young and the proportion of suckling bouts terminated by adult females. Although the presence of a neonate may be a strong maternal stimulus, the amount of maternal care delivered clearly is under control of the adult female (73). Moreover, differences in maternal investment between years did not simply track environmental conditions, but represented a female strategy for coping with a harsh, unpredictable environment (73).

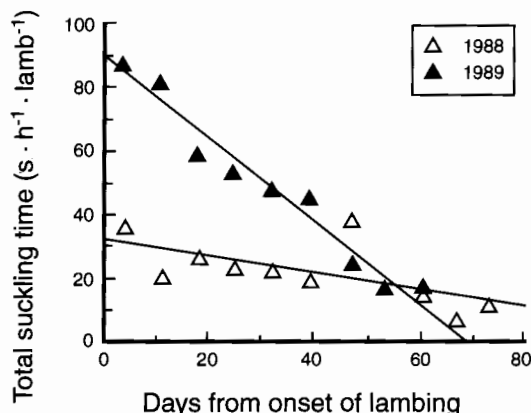


Figure 24-6 Comparison of total time spent suckling per active hour by young during poor (1989) and normal (1988) summers in interior Alaska, USA. Note that female Dall's sheep attempted to compensate by nursing longer in 1989 but also weaned lambs more quickly in that poor year. (From Ref. 73.)

Growth of well-provisioned young is rapid; body mass may attain 27 to 30 kilograms by 9 months of age (36). Indeed, milk of Dall's sheep is rich in protein (70%), and composed of about 12% fat by 10 days postpartum (90, 91). Losses of young may be 40% to 50% during their first winter, and the nutrition obtained during their first short summer of life may be crucial to their overwinter survival (2, 73). In addition to affecting survival, poor nutrition may cause females to forego reproduction in subsequent years and can slow growth of horns in males for 5 years following birth (78, 73, 92).

Males ultimately attain greater (about 40%) body mass than do females, and sustain growth for a longer period of time (6 years in males, 4 years in females) (36). Rates of growth (kilograms body mass/month) for the first 5 years have been estimated at 0.49 for males and 0.48 for females (85).

Maximum longevity of Dall's sheep in the wild appears to be about 14 years for males, and 19 years for females, although there is a slight tendency to underestimate the age of females by counting horn annuli (7, 92, 2, 93). Simply examining life expectancy for populations without considering other aspects of their demography, however, can lead to misinterpretation of data and the dynamics of populations (86).

Like other arctic ungulates, Dall's sheep have a suite of adaptations that help them cope with a severe climate. They possess an undercoat of fine wool, and long, hollow guard hairs that provide insulation against the long, cold winters (20, 11). The winter pelage of Dall's sheep may exceed 5 centimeters and is shed in a single molt that occurs from March through July; mature males molt earlier than females, young, or animals in poor physical condition (2, 11, 20). Another adaptation of these sheep relates to the concentrations of fatty acids in the marrow of leg bones, especially the radius. These fatty acids decrease in concentration distally, which likely helps to reduce heat loss via thermal conduction; hair covering the legs is comparatively short and probably does not provide sufficient insulation to prevent heat loss in winter (94).

Hematology and blood chemistry of Dall's sheep are similar to those reported for bighorn sheep (95, 96, 97, 35). Such data, however, may vary with sex, age, physical condition, season, handling, and numerous other factors (35, 98). Although some blood variables may correlate with physical condition, direct comparisons between populations using these values should be made with appropriate caution (98).

BEHAVIOR

Dall's sheep are an extremely gregarious species that exhibit a high degree of polygyny, with large, dominant males mating most often (11). Dall's sheep possess a

tending-bond mating system, in which a dominant male guards, tends, and courts an estrous female (99, 11). Once the male has copulated with a receptive female, he soon leaves in search of additional mates. Competition among males for mates has led to the evolution of marked dimorphism in body mass and size of horns between the sexes (1).

Rutting groups of Dall's sheep were composed of as many as 21 sheep, with an overall mean of 3.7 for 166 groups; however, group size declined for both males and females by midwinter (11). The mean size of 139 maternal bands ranged from about 4 to 10 individuals from prelambling through postlambling in spring and early summer (71). Group size is related to foraging efficiency with larger groups spending more of their active time feeding than smaller ones, and spending less time in vigilance or alarm behaviors than smaller groups (75, 71). Likewise, group size increases with increasing distance to escape terrain, ostensibly an adaptation to lower the risk of predation (100, 75, 71).

The sexes of Dall's sheep spatially segregate from one another during spring and summer (71). The causes of sexual segregation in bighorn sheep have been more thoroughly studied than in Dall's sheep, but the explanation is likely similar (101). Females are confined to steep, rugged terrain where they and their neonates can reduce the risk of predation, but where forage is less abundant and of lower quality than on areas inhabited by males. Larger males are less susceptible to predation than females with young, forage in areas with more predators, and obtain the forage required to attain large body size necessary to be effective in combat for mates. The hypothesis that this behavior resulted from males avoiding competition with potential mates and offspring (102) is no longer considered viable for most populations of mountain sheep (101).

The sexes begin to associate as rut approaches. By that time males already have formed groups and begun to sort out dominance interactions with relatively low-intensity behaviors that include foreleg kicks, horn displays, and more rarely jump-threats and clashes (11). Males also mount one another in dominance interactions, but the notion that dominant males treat all subordinates as if they were females may not be correct (11). For instance, dominant males seldom direct courtship behaviors such as tongue flicks toward subordinate males or lick their perianal region, and do not flehmen in response to smaller males or their urine. Dominance mounting is simply a common form of aggression among ungulates.

Aggressive interactions during rut are vigorous and tend to lack ritualization. Such behaviors include low-stretch postures, vigorous kicking, jump-threats, and forceful clashing of horns. The skulls of males have undergone pneumatization to help absorb such forceful horn clashes (11). Males often display their horns, which serve as indicators of social rank (11). Aggressive interactions determine which males mate, and such behavior between males over estrous females can be fierce; large males may strike opponents in the side of the body with their horns and even push rivals off cliffs (11). Vigorous rutting activities by these large males exhaust their energy reserves, and survivorship drops markedly in older age classes of males (11).

Geist provided excellent descriptions of courtship behaviors in mountain sheep (11). Dominant males approach females in a low-stretch posture while flicking their tongues. Males ascertain the reproductive status of females by licking the perianal region of the female or lapping urine from the ground where a female has urinated. Males then flehmen to determine if the female is in estrus and receptive (103). Courting males may be distracted by females inducing them to investigate an area where a female has urinated, and then moving away while the male flehmens (11). Estrous females sometimes elicit courtship from a male by butting and rubbing against him (11). Males may kick a female with a stiff foreleg during courtship, ostensibly to determine if she is willing to stand for mounting. Copulation cannot occur if a female moves forward, which prevents the male from mating successfully (11). Males may tend females for 2 to 3 days prior to copulation (11). As rut concludes, large males become less gregarious, and aggressive behaviors occur less frequently (11). Some smaller

males may continue to direct courtship behaviors toward females, but females typically are not receptive to such advances (11). No evidence of territoriality in Dall's sheep or bighorn sheep exists.

POPULATION DYNAMICS

Densities of Dall's sheep normally range between one and two animals per square kilometer; densities on winter range usually are higher than on summer range (66, 104). Densities of three to six sheep per square kilometer have been reported from Kluane Park, Yukon, and Dry Creek, Alaska (66). Comparisons of densities among populations, however, can reflect differences in habitat quality only if populations are at the carrying capacity (K) of their respective habitats.

Hoefs and Cowan believed that the adult sex ratio for Dall's sheep did not differ from parity (66). Their data, however, were gathered in spring when spatial segregation of the sexes can complicate sampling designs. Murphy and Whitten provided the best and most unbiased estimate of the adult sex ratio for an un hunted population: 66 adult males to 100 adult females (86). Adult sex ratios as low as 13 males to 100 females have been reported for a hunted population, although hunting alone probably was not the only explanation for that skewed ratio (66). A sex ratio favoring adult females is typical of polygynous ungulates and likely results from increased mortality of males engaging in strenuous rutting activities (11, 105, 77).

Several life table approaches have been used to examine the survivorship of male and female Dall's sheep (66, 7, 104). Time-specific life tables, however, do not provide accurate descriptions of the dynamics of Dall's sheep or other large mammals through time because population parameters such as survival and fecundity are fixed at the time of the sample and cannot reflect the changing dynamics of the population (106). Death-series life tables (i.e., reconstructed from ages of skulls) presented by Murie and Hoefs and Cowan are likewise problematical (7, 66). These tables assume a stable-age distribution, and Murphy and Whitten clearly demonstrated that this was not the case for data presented by Murie, because the partial survivorship curves varied markedly among cohorts (106, 86, 7). The restrictive assumptions of life tables and their inability to cope with density dependence reduce their usefulness for modeling the dynamics of populations of Dall's sheep (106).

Another concept that has limited the understanding of population dynamics of mountain sheep is the notion of "population quality" (11, 66). Population of sheep that evolved at the ~~fore~~ ^{fore} of retreating glaciers were hypothesized to be more productive than those that evolved in glacial refugia (11). Although it is possible that some populations may be genetically superior to others, this has not been demonstrated for Dall's sheep. Small, bottle-necked or isolated populations might differ from others genetically, but "low-quality" populations have been postulated for areas in Alaska where this is not likely (66). Populations of Dall's sheep in interior Alaska exhibited little genetic variability based on allozymes (107).

More importantly, the concept of "population quality" as applied to Dall's sheep has no theoretical underpinnings in population ecology; indeed, this concept completely ignores density-dependent mechanisms or weather-related effects on productivity, survivorship, behavior, and other population parameters. In addition, no mechanism has been proposed to explain what makes some populations "high quality" or others "low quality," except the area (e.g., glaciated or refugia) in which they presumably evolved, which ignores millennia of evolution since the end of the Pleistocene.

What then regulates population dynamics of Dall's sheep? These mountain ungulates occupy habitats at high elevations that are subjected to extreme climatic conditions during winter, which can be highly variable among years (79). Moreover, summers are short and forage likewise may vary in abundance and quality among years (73, 71). Murphy and Whitten reported a strong inverse relationship between snowfall in the previous winter, and the ratio of young to females the following spring (Figure 24-7) (86).

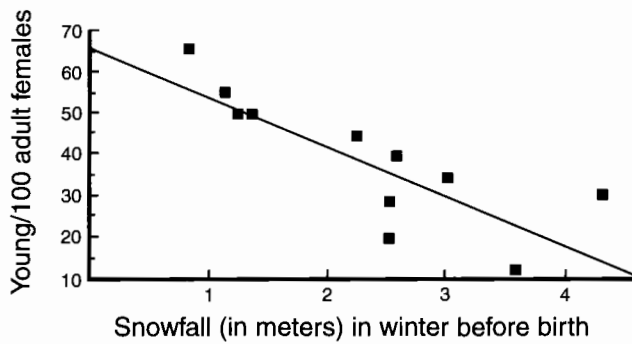


Figure 24-7 Relationship between young to female ratios and total snowfall during the previous winter before births, interior Alaska, USA. (From Ref. 86.)

Rachlow and Bowyer demonstrated that females curtailed investment in offspring more rapidly in a cool summer with lower quality and availability of forage than a normal year (73). Weather clearly affects both productivity and behavior in Dall's sheep.

Both Nichols and Murphy and Whitten argued that density-dependent mechanisms also were important in regulating populations of Dall's sheep; population density affects the per capita availability of forage to individuals (2, 86). Forage available in winter likely affects overwinter survival and perhaps the ability of pregnant females to carry a fetus to term (2, 108). Similarly, forage in spring and summer influences maternal provisioning of young and the likelihood of future reproduction by females (73, 71). Because young invest more resources in body growth than in fat deposition than do older age classes, undernourished young are less likely to survive harsh winter conditions, and overwinter mortality among young can be 40% to 50% (2).

Thus, both weather and density dependence interact to effect the dynamics of Dall's sheep populations. Maximal rates of increase in unhunted populations are probably between 11% and 18% (2). The year-round ability of habitat to support the needs of the sexes of Dall's sheep relative to the number of animals influences the per capita forage available to individuals and, thereby, their body size, age at first reproduction, fecundity, survivorship, and many aspects of their social behavior. This is one reason why comparing densities of sheep among populations may be inappropriate; the carrying capacity of the range in relation to the number of animals influences per capita availability of forage and, hence, productivity for the population. Variation in habitat quality makes comparisons of absolute density among populations meaningless for assessing density-dependent processes. These life-history traits also are strongly influenced by climatic conditions, which interact with population density to regulate populations of this mountain ungulate. Note the high variability in young to female ratios for a single population of Dall's sheep through time (Figure 24-7). The concept of "population quality" is not sufficient to understand this process.

We offer a simple conceptual model to illustrate our point and to help clarify interactions between density-dependent and density-independent phenomena in regulating populations of Dall's sheep (Figure 24-8). Although our model is focused on overwinter mortality, the same general ideas hold for other life-history characteristics (e.g., fecundity, age at first reproduction) related to population demography.

First, consider a population that is well below the carrying capacity (K) of the habitat (Figure 24-8a); such a circumstance might occur in a newly colonizing population from a reintroduction, from catastrophic mortality during a severe winter, or from an overharvest of females. Intraspecific competition in such populations is lax, and per capita availability of forage is high. Individuals reach a high nutritional plain, and body condition, including fat reserves, is excellent; reproductive rate and survivorship would be high (109). Winters of mild to moderate severity would have little effect on the overwinter survivorship of these individuals because they are well

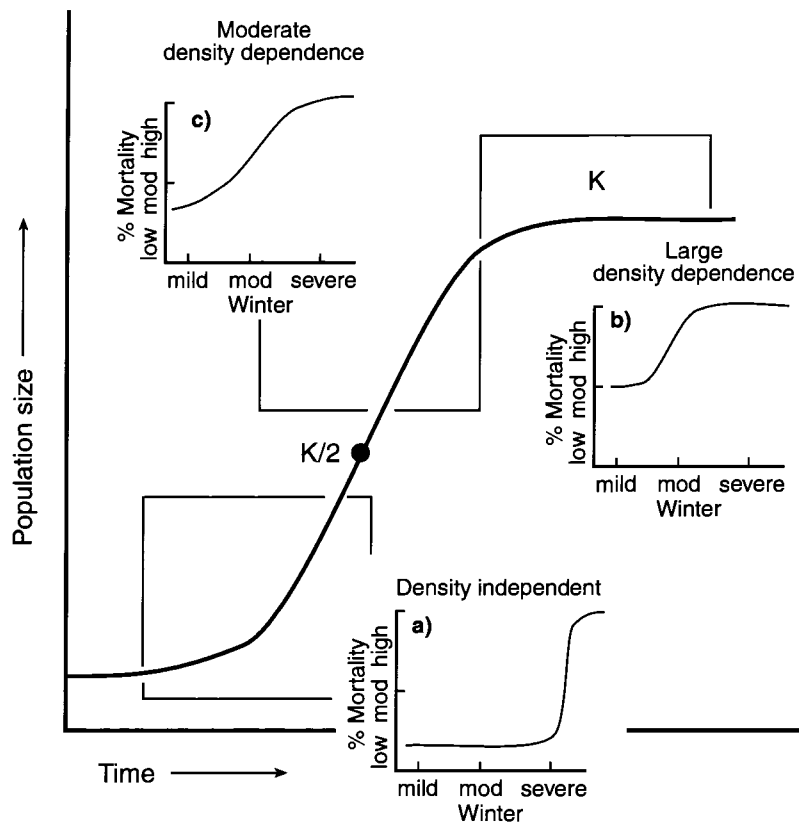


Figure 24-8 A conceptual model showing the relationships between population density, winter severity, and rate of mortality. Representative curves are provided for (a) density independent, (b) large, and (c) moderate density-dependent effects interacting with winter severity. The lines around the inset graphs show the area on the growth curve to which each inset corresponds. Note that the shape of the population-growth curve need not be symmetrical for the proposed relationships to hold.

buffered against such events by substantial body reserves. A sufficiently severe winter, however, might cause high rates of mortality even among animals in excellent physical condition.

Now consider the opposite extreme: a population at or near the K of the habitat (Figure 24-8b). Under this circumstance, intraspecific competition for forage is intense and, consequently, the average physical condition of individuals is poor. These animals have limited body reserves to withstand winter conditions, and even a mild winter is capable of causing some mortality. Moderate winter severity can produce high rates of death because these animals are poorly buffered against climatic extremes.

Finally, consider a population between $K/2$ and K (Figure 24-8c). Animals in this population would be in better physical condition than those at K , but in poorer condition than those at low density because of moderate levels of intraspecific competition for resources. Under those conditions, overwinter mortality would be higher than at low density, but lower than at high density. Indeed, this interaction between population density and winter severity produces a near-linear relationship between winter severity and overwinter rate of mortality (Figure 24-8c). Such linear relationships have been used to infer density-independent regulation of ungulate populations, but other interpretations are possible. Correlation should not be used to infer cause and effect, especially in population ecology (110). As an ungulate population approaches K and body reserves are diminished, climatic variables are likely to

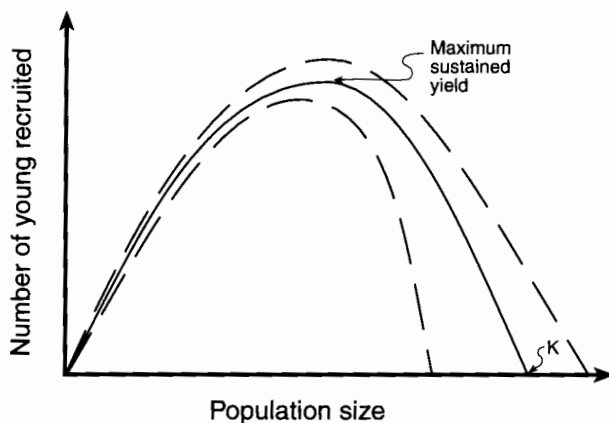


Figure 24-9 Conceptual relationship between the number of young successfully recruited into a population and population size (or density). The solid line shows the long-term mean, and the dashed lines indicate the effects of variable climatic conditions. Variability in recruitment becomes more pronounced at large population size because animals are in poor physical condition and more easily affected by climatic variability.

become increasingly important in predicting population parameters, even where such a population exhibits strong density dependence. Climate plays a more important role as populations approach K (Figure 24-9) because physical condition of individuals can be affected more easily by climatic variability. Moreover, our model indicates that individuals in good condition may survive all but the most severe winters, whereas animals in poor condition may succumb even during winters of mild or moderate severity (Figure 24-8), a conclusion that has been reached for other northern ungulates (111).

Predation also might affect the population dynamics of Dall's sheep. These mountain ungulates inhabit steep, rugged terrain that they readily negotiate to elude, avoid, and outdistance predators. Nonetheless wolves have been reported to prey on Dall's sheep, and diets of this canid contained 2% to 25% of Dall's sheep (112, 66, 113, 7, 114). Predation by wolves and coyotes may increase during periods of deep snow (108). Other predators of Dall's sheep include grizzly bears, black bears, wolverines, lynx, and golden eagles (7, 115, 89, 66, 116). Dall's sheep also may perish from accidental falls and be killed by avalanches (66, 108).

We concur with Nichols that predation does not exert an important influence on populations of Dall's sheep under most circumstances (2). For instance, Nichols noted that rates of increase in interior Alaska averaged 11% even though wolves were abundant (2, 117). Likewise, Rachlow and Bowyer noted that losses of young to predators in this same area were slight from May through July (78). Nichols reported that wolves may kill Dall's sheep more frequently when population size exceeds K , and sheep are weakened or forced by competition and food scarcity to forage far from escape terrain (2). These outcomes, however, likely involve substantial amounts of compensatory mortality, and it is questionable if predators typically regulate populations of Dall's sheep. This outcome is in stark contrast to the effects of predators on other northern ungulates that cannot seek protection in steep, rugged terrain (118, 119, 120, 79).

Dall's sheep also are infected or infested with numerous disease organisms and parasites, some of which may be capable of limiting or regulating their populations. Lungworm has been reported from Dall's sheep, but there have not been massive die-offs of Dall's sheep from this parasite and its associated pneumonias or hemorrhagic septicemia as reported for bighorn sheep (121, 122, 35). As with other sources of mor-

tality, this disease complex may be more prevalent in populations on a low nutritional plain (69). Other nematodes have been reported in Dall's sheep but caused no obvious pathology (69, 123). Perhaps low temperatures in winter or a short summer growing season at high latitudes helps limit direct transmission of parasite larvae or does not provide suitable conditions for intermediate hosts of pathogenic parasites that debilitate populations of bighorn sheep. Additionally, domestic sheep and cattle are uncommon throughout the range of Dall's sheep. Parasitic coccidia, however, have been isolated from feces of Dall's sheep (124). Further, positive titers in blood sera have been reported for several arboviruses, contagious ecthyma, parainfluenza III, epizootic hemorrhagic disease, and Q fever (125, 126, 127, 128, 97, 129, 130). Serology also indicated that Dall's sheep were exposed to the bacteria *Brucella* spp., and *Campylobacter feti* (97, 127). *Mycoplasma ovipneumoniae* has killed captive Dall's sheep, but was not reported for free-ranging sheep (131, 132).

Necrosis of horn cores and the mandible are prevalent in Dall's sheep; *Corynebacterium pyogenes*, *Fusobacterium necropitorum*, *Proteus* spp., *Micrococci* spp., and *Escherichia* spp. have been associated with infections of lumpy jaw (133, 7, 134, 135, 66, 136, 137). Causes of horn aberrations in Dall's sheep are uncertain but may involve *Actinomyces* spp. (137). Skull asymmetry was caused by osteoporosis in bighorn sheep (138). Dall's sheep may be predisposed to mandibular infections from excessive tooth wear because of wind-blown silt deposited on forage (139). At present, there is no evidence that diseases play a major role in regulating or limiting populations of Dall's sheep.

Competition between Dall's sheep and other large herbivores with sympatric distributions has not been documented (1). Caribou, moose, and mountain goats use different habitats or select diets differently than Dall's sheep (140, 141, 142).

POPULATION MANAGEMENT

Currently, there is no reason to attempt to manage populations of Dall's sheep using predator control or by intervening in disease processes; predators or diseases do not regulate populations of this mountain ungulate often enough to be of consequence. Effective management, then, is restricted largely to regulating sport and subsistence harvest or providing viewing opportunities for aesthetic and other nonconsumptive uses (1).

Dall's sheep are managed by different state, federal, and provincial government agencies within their distribution. In general, Dall's sheep are managed to furnish trophies for hunters; subsistence take is thought to be small (2, 143). Although some harvesting of females was permitted in the past, harvests now are restricted mostly to three-fourths or full-curl males (143, 144, 145, 146). The total harvest relative to the total size of populations is typically less than 2% (1). Most large males are harvested by nonresident hunters, who are required to follow a set of regulations that includes hiring guides or outfitters, payment of special fees, and hunting only in specified areas (1).

Nichols concluded that the harvest of large males did not influence reproduction in populations of Dall's sheep, and this practice was not sufficient to reduce herd numbers (2). This is not surprising because large males only use the same ranges as females during rut, and one consequence of sexual segregation is a reduction in competition of large males with females and young for much of the year. Thus, only the harvest of females can affect populations in a density-dependent manner, and their density interacting with climatic conditions is the primary factor regulating productivity of populations of Dall's sheep.

This interaction between density and climate also plays an important role in determining horn size in males and, hence, the quality of trophies available to harvest. For instance, Bunnell reported a strong positive relationship between precipitation (an index to primary productivity) and horn growth for male Dall's sheep (92). Moreover, years

with depressed recruitment were years in which growth of horns also was diminished (92). The quality (i.e., growth) of horns of young males is mediated through the physical condition of the females, and this effect can be observed for up to 5 years of age (92). Annual growth of horns is much greater in males than females, and there is marked interannual variation in growth. Annual growth of horns and body mass were not correlated significantly for males (92). This analysis, however, was complicated by the horns composing 8% to 12% of body mass in large males and that some broming (i.e., wear) of horn tips occurred (11). Bunnell interpreted this lack of significance to mean that a male could recover from a period of nutritional deprivation and regain its body mass, but that this period of hardship was recorded in its horns (92). That the cause of differences in horn size was related to nutrition was demonstrated by greater growth of horns in a male held on a game farm than for individuals in a free-ranging population from which the captive male was obtained (92). Finally, Bunnell calculated an index to horn quality that varied markedly among years (92). Clearly, there are not populations of high and low quality, but variable environmental conditions that cause changes in quality within a population that may vary through time and are dependent on nutrition.

One manner in which the harvest of large males might affect population demography was proposed by Geist (11). He argued that young males (i.e., less than a three-quarter curl) would experience high rates of mortality if large males were harvested heavily because younger individuals would begin participating in rutting activities that lead to high rates of mortality in larger males. Heimer and others offered some support for Geist's hypothesis (127, 11). Murphy and others, however, provided the only critical test of this hypothesis (147). They reported no relationship between the ratios of old or younger males to females across a number of populations throughout Alaska, and concluded that a reduction in older males via hunting did not affect survivorship of younger males.

One final way in which the harvest of large males might affect the demographics of a population is via the role of large males in initiation of estrus in females. The presence of a rutting male can hasten onset of estrus in bovids and cervids (148). Whether young but sexually mature males can fulfill this role in Dall's sheep is unknown. Even if estrus is delayed in populations without a sufficient number of large males, whether this would markedly affect timing or synchrony of parturition is uncertain because of the apparent ability of females to adjust the length of gestation (78, 83). Moreover, whether there might be a cost (e.g., low weight of a neonate) from adopting such a strategy requires more study. Indeed, this is one of the least known aspects of the biology of Dall's sheep.

HABITAT REQUIREMENTS

Dall's sheep generally inhabit windswept, dry, steep, and rugged mountains characterized by subalpine-grass and low-shrub communities typical of high elevations and high latitudes (7, 11, 48, 149, 71). Most populations of Dall's sheep are migratory and occupy different ranges in summer and winter, although a few populations are relatively sedentary (6, 7, 11, 66). Typical of other polygynous and sexually dimorphic ruminants, the sexes of adult Dall's sheep spatially segregate around the time of parturition (150, 101, 58, 71). Movements of Dall's sheep between seasonal ranges have been related to plant phenology, temperature, and depth of snow (66). Seasonal movements from 8 to 48 kilometers have been reported (66). Because summers are short at northern latitudes, Dall's sheep spend most of the year on winter range (males 271 to 303 days, females 240 to 263 days; 11). Windswept areas with sufficient forage and suitable escape terrain to elude predators are likely the key elements of winter habitat for Dall's sheep. For instance, Dall's sheep in Kluane National Park, Yukon, spent 70% of their time foraging in areas with little or no snow (less than 5 centimeters



Figure 24–10 Lambing habitat for Dall's sheep in interior Alaska was characterized by steep, rugged terrain intermixed with forage including grasses and dryas. (Photograph by J. L. Rachlow.)

deep), and less than 10% of their time in areas with snow depths greater than 15 centimeters (66). Primary productivity of plants on winter range (29–120 grams per square meter) is an important component of overwinter survival and for production of young (149, 139).

Adult males may occupy a variety of ranges throughout the year including areas inhabited during pre-rut, rut, early to midwinter, late winter, spring, and summer; these sheep also may move to areas with salt licks (11). Geist reported that such ranges were smallest in midwinter (about 0.8 kilometers in diameter) and largest in spring and summer (6 kilometers) (11). Adult females were reported to inhabit seasonal ranges in spring, for lambing, during summer, and in winter (11). Estimates of home-range size from modern, quantitative methods, however, are unavailable (151, 152). Additional information on habitat use outside the lambing period is provided by Hoefs and Cowan and Burles and Hoefs (66, 108).

Because of the severity of winters in the Arctic and sub-Arctic, growth and development of young Dall's sheep and replenishment of female body reserves must occur during the short summer (85, 78, 73). Moreover, maternal females are likely constrained in their selection of habitat because of the vulnerability of young to predators and to exposure and hypothermia from severe climatic conditions (153, 71, 75). Consequently, suitable lambing habitat may be a crucial component affecting the productivity of sheep populations.

Lambing habitat for Dall's sheep in interior Alaska was characterized by steep, rugged terrain intermixed with forage including grasses and dryas (Figure 24–10) (71). Lambing sites typically occurred at high elevation (above 1,180 meters) and were free of snow. Rachlow and Bowyer noted that a suite of variables was useful in discriminating lambing sites from random ones including distance to escape terrain, cover of grasses, cover of dryas, slope aspect, slope brokenness, slope steepness, and presence of snow (Figure 24–11) (71). Moreover, maternal females altered selection of habitat with the chronology of lambing, with additional variables entering at peak lambing that related to climate (windchill and cover from wind provided by browse). Additionally, females selected terrain features more strongly in a year with adequate food, but selected forages in a year with reduced availability of food (71).

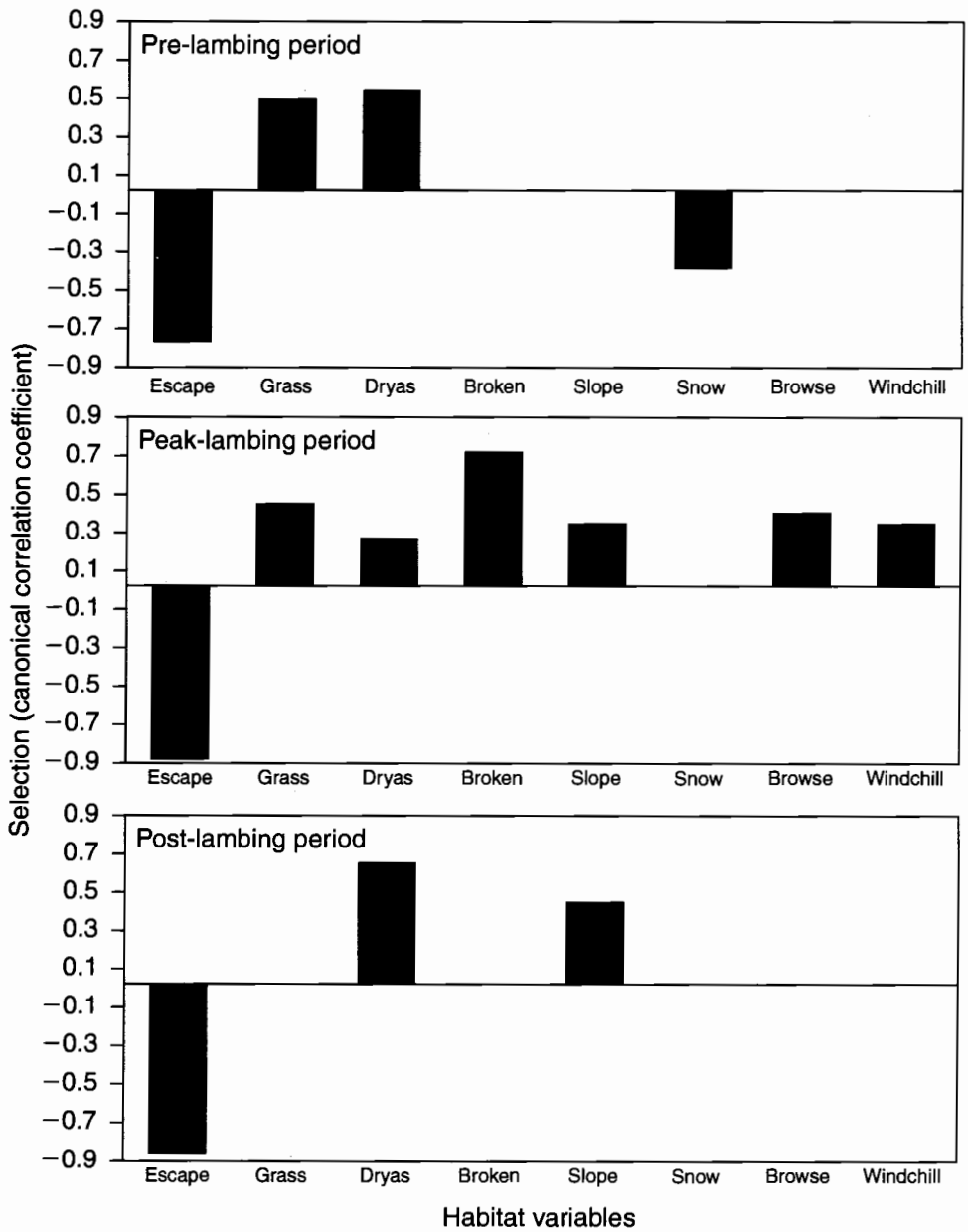


Figure 24-11 Selection of habitat by female Dall's sheep during pre, peak, and post lambing periods in interior Alaska, USA, 1988-1989. (Escape = distance to escape terrain, grass = percent cover of grasses, dryas = percent cover of dryas, broken = brokenness of terrain, slope = percent slope, snow = presence of absence of snow, browse = percent cover of browse, and windchill). Canonical correlations indicate the strength and direction of selection. For instance, the negative correlation for distance to escape terrain indicates females used sites closer to such terrain than randomly located sites. The positive correlation for grass indicates there was more of this forage at sites used by females than at random sites. (From Ref. 71.)

Young Dall's sheep apparently acquire home ranges from adults. Females typically have ranges that are similar to their mother (or maternal group), whereas males gradually disassociate from their mothers and begin associating with groups of mature males; as with many large mammals, males are the initial dispersers (11).

Nonetheless, Dall's sheep exhibit a high degree of fidelity to seasonal ranges (males, 88%; females, 90%) (11).

HABITAT MANAGEMENT

Because of the remote and rugged terrain occupied by Dall's sheep, manipulation of habitat is rare. Subalpine ranges in British Columbia, Canada, were burned in spring to improve habitat (144, 69). Elliott noted that such burning was capable of slowing population declines and enhancing horn size in males (144). Nutrient quality of burned areas was not superior to that of unburned ranges in spring and summer, but burned areas had a greater quantity of forage than unburned areas in winter (69).

Mineral exploration and extraction, road construction, harassment by low-flying aircraft, and other human disturbances of Dall's sheep, especially on lambing grounds, have the potential to affect populations of sheep (12, 145, 146). Nonetheless, most of the range of Dall's sheep remains remote, pristine, and relatively unaffected by human developments or other activities.

Compared with other large mammals in North America, our understanding of the biology of Dall's sheep is incomplete. Much remains to be learned about these unique ungulates that inhabit mountainous areas of the far north.

SUMMARY

Dall's sheep occur in windswept, precipitous mountain ranges in Alaska and western Canada and are the northernmost species of mountain sheep in the New World. Three subspecies of Dall's sheep are recognized; Stone's sheep possess dark pelage and a rump patch, whereas the other subspecies are white or off-white and lack rump patches. Dall's sheep are stocky ungulates that are well suited to the steep, rocky terrain they inhabit. Males are larger in body mass than females and also possess much larger horns.

Dall's sheep feed mostly on graminoids but consume a wide variety of plant species. Forage is only of high quality during the brief summer growing season when sheep must accumulate sufficient body reserves to survive the long and often severe winter.

Dall's sheep are polygynous with a tending-bond mating system and are highly gregarious, especially during rut, which occurs from November to December. No evidence of territoriality has been observed. A single young typically is born in May after a gestation period of about 171 days. Births are highly synchronized, but marked interannual variation in both timing and synchrony of parturition has been reported. The sexes of Dall's sheep tend to be spatially separated outside the mating season.

The population dynamics of Dall's sheep are affected by a combination of density-independent and density-dependent processes. Young to female ratios are negatively correlated with snowfall in the winter prior to the birth of young, and intraspecific competition between females likely exacerbates the influence of such climatic extremes. Females also alter maternal investment in young in relation to environmental conditions in spring and summer. The growth of horns for males is dependent on their nutrition early in life when most horn growth occurs and influences the number of trophy males available for harvest.

Dall's sheep are preyed on by a variety of predators, but the rugged terrain inhabited by these mountain ungulates reduces the effects of predation. Predation, disease, or hunting of large males currently has few negative effects on populations of Dall's sheep.

Management of habitat for Dall's sheep is uncommon; burning of subalpine areas to improve range quality has occurred in British Columbia. Human disturbance holds the potential to affect populations of Dall's sheep, but most areas inhabited by these northern ungulates remain pristine and undisturbed.

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