BEHAVIORAL ADAPTATIONS OF MOOSE TO TREELINE HABITATS IN SUBARCTIC ALASKA

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ABSTRACT: Moose (*Alces alces*) in mountainous, treeline habitats of subarctic Alaska use several behavioral adaptations to cope with high predation risks, short growing seasons, deep snows, patchy habitats, and low ecosystem productivity. Adaptations include extensive daily and seasonal movements, modified foraging behavior and activity patterns, increased sociality, sexual segregation, and predator avoidance. These adaptations are reviewed and discussed in relation to risks and constraints, and comparisons are drawn with moose living in lowland habitats where environmental conditions, habitat features, and predation risks are different.

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Moose in Alaska use a variety of habitats ranging from highly productive coastal wetlands to alluvial shrub habitats north of the arctic circle (LeResche *et al.* 1974). Diverse terrestrial and aquatic habitats throughout the state are exploited by moose for food and cover. These habitats follow both a north-south gradient and elevational gradients from sea level to about 1300 meters. In the major mountain ranges of subarctic Alaska, including the Chugach, Wrangell, and Alaska ranges, moose occupy habitats near treeline both seasonally and throughout the year. Treeline habitats differ floristically from lowland habitats used by moose, and weather patterns in mountainous areas affect plant productivity and increase energy expenditures of moose forced to cope with deep snow. In addition, moose may face increased risks of predation in mountainous areas where brown bear (*Ursus arctos*) and wolf (*Canis lupus*) densities are high.

Moose in certain areas of subarctic Alaska use several behavioral adaptations to cope with the constraints and risks associated with living in mountainous areas. These include extensive daily and seasonal movements, modified foraging behavior and activity patterns, increased sociality, sexual segregation, and predator avoidance. This paper reviews recent literature describing the characteristics of treeline habitats of moose in Alaska, describes the behavioral adaptations that moose have evolved to live there, and compares features of mountainous and lowland habitats in relation to their ability to support moose. Several of the studies and much of the data reviewed here resulted from research on moose and moose-habitat interactions at Denali National Park, Alaska. The park study area is located in central Alaska (63°40'N, 149°20'W) on the north side of the Alaska Range, a crescent shaped mountain range in central Alaska.

CHARACTERISTICS OF TREELINE HABITATS

Mountains in Alaska that contain treeline habitats are generally colder, wetter, and windier during summer than are adjacent lowlands. In winter, wind velocity, wind duration, snow depths, and drifting snow are greater in mountains, but temperature inversions may produce warmer conditions at higher elevations. Elevation gradients as small as 200-300 m may result in temperature inversions of 10-15°C during the coldest winter days. Temperature and precipitation data along a north-south gradient in central Alaska indicate that mean summer temperatures at low elevations both north and south of Denali National Park Headquarters (elevation 690 m) are warmer, but mean winter temperatures to the north (Nenana) are colder than both Denali and to the south (Talkeetna, Table 1). Oceanic effects originating 160 km south of Talkeetna result in warmer winter temperatures at that site along with deep snow (259 cm total snowfall, Table 1) compared to Nenana (122 cm) located in the precipitation shadow of the mountains surrounding Denali National Park.

Delayed springs and early frosts in mountains compared to adjacent lowlands result in shorter growing seasons for shrubs and forbs consumed by moose. At Denali, bud-break for shrubs is commonly two weeks later in spring than at elevations 500 m lower, and first frosts in fall are commonly 10-14 days earlier.

Research on factors responsible for the limits of tree distribution in Alaska extends back to the early work of Griggs (1934). Viereck *et al.* (1986) discussed the effects of slope, aspect, elevation, soil parent material, and succession after wildfire as the most important determinants of vegetation development in taiga, and identified treeline in central Alaska (latitude 64°N) as occuring at about 750 m. In the intermontane plateau between the Brooks and Alaska mountain ranges, Van Cleve et al. (1983) indicated that 17% of the land area was above treeline (900 m) and covered with subalpine shrub stands, tundra sedge meadows, heaths, and fell fields. Black spruce (*Picea mariana*) forests covering 44% of the area were indentified as the dominant vegetation type below treeline.

Viereck (1979) discussed characteristics of treeline plant communities in Alaska. He identified white spruce (*Picea glauca*)/resin birch (*Betula glandulosa*) and black spruce/white spruce/resin birch as dominant vegetation types below treeline in the Alaska Range. Continuous shrub communities, 1 to 2 m in height of resin birch, alder (*Alnus crispa*) and willows (*Salix* spp.) were identified as surrounding the scattered spruce stands. Tree-height shrubs including feltleaf willow (*Salix alaxensis*), Richardson willow (*S. lanata*), and alder had distributions well beyond treeline. Shrub types such as alder thickets, resin birch (most common in interior Alaska), and willow/alder occupied the nonforested areas near treeline on moist sites. Viereck (1979) identified climate and post-glacial history as the most important factors controlling the location of treeline in Alaska, and discussed the effects of wind, fire, insects, mammals, net solar radiation, and temperature effects on tree distribution and regeneration.

Slope, aspect, and microclimate differences due mainly to variations in soil temperature and moisture result in a mosaic of habitats for moose in mountainous areas. Distribution of favorable habitats (as defined by high forage biomass of palatable shrubs) is

Table 1. Weather data along a north/south gradient through Denali National Park, Alaska. The north end of the gradient (Nenana) is in interior Alaska where the climate is strongly continental. The south end (Talkeetna) is in southcentral Alaska where the climate is moderated by maritime effects. Denali is near treeline. Nenana and Talkeetna are in low-elevation taiga sites.

			Temperature (°C)		Annual Precipitation (cm)	
		Distance/Direction	Mean High/Low			
Location	Elev.(m)	from Denali (km)	Winter	Summer	Total Snowfall	Total Precipitation
Nenana	119	110-N	-11/-27	21/6	121	30
Denali Headquarters	690	0	- 8/-19	18/5	193	38
Talkeetna	115	219-S	5/-18	20/7	259	74

often discontinuous within much larger areas that are either unsuitable for moose or of low quality. In short, high-quality moose habitat at treeline is patchy. In addition, certain high-quality habitats common at lowland sites may be rare or absent at treeline, including lakes and ponds of suitable depth and chemistry to support aquatic plants palatable to moose. MacCracken and Van Ballenberghe (unpublished data) estimated that certain aquatic habitats in a low elevation, coastal wetland of Alaska contained about 2,500 kg/ha (dry weight) of moose forage, about one order of magnitude higher than shrub biomass in adjacent terrestrial sites. In contrast, Van Ballenberghe *et al.* (1989) reported that ponds and lakes were rare in eastern Denali National Park and moose consumed virtually no aquatic plants.

Wildfire frequencies in treeline environments appear to be low compared to adjacent lowlands. Shrub tundra does not accumulate large quantities of fuel and consequently does not carry fire well except during the driest conditions. Cloudy spring and summer weather in the mountains, cool temperatures, and high humidity seldom result in the extreme dryness that adjacent lowlands experience. In addition, lightning may miss mountains because cloudy conditions and high elevations prevent heat build-up and thunderhead formation. The net result is that treeline habitats typically experience infrequent fires compared to lowlands; habitats exploited by moose at treeline are therefore less dynamic but consistently productive, lacking the wide swings in forage quantity and quality characteristic of lowland sites where wildfire is common (Viereck and Shandelmeir 1980). At Denali National Park where wildfire at treeline is rare, Sheldon's (1930) descriptions of moose habitat during 1906-08 are remarkably similar to present-day conditions.

Because moose habitat is patchy at treeline and tree density is low, moose are often readily visible to predators including wolves and brown bears. In addition, predator densities in mountains may be higher than in adjacent lowlands. This is especially true for brown bears that find optimal habitat near treeline (Mealey *et. al* 1977, Murie 1981, Pearson 1975). Dean (1987) reported a brown bear density of 32/1000 km^2 in Denali National Park, a relatively high density. Gasaway *et al.* (1983) indicated a density of 15/1000 km^2 for a hunted bear population in the northern foothills of the Alaska Range east of Denali. In contrast, biologists observed only 1 brown bear in 10 years of surveys in adjacent lowlands (Gasaway *et al.* 1983). That brown bears can be a major mortality factor for neonate moose and can severely depress rate of increase of moose has been documented by several studies in Alaska and northwestern Canada (Ballard and Larsen 1987, Van Ballenberghe 1987).

Vegetation characteristics

Miquelle (1990:57-59) classified important treeline habitats of moose in Denali National Park, Alaska, as follows:

> "Eight habitats were defined on the basis of a vegetation classification scheme devised by Viereck and Dyrness (1980), habitats identified by Risenhoover (1987), and dominant species found on sites. **Alluvial willow** stands lay along river bottoms and were dominated by tall (>1.5 m) feltleaf willow with some balsam poplar (*Populus balsamifera*), Richardson, and littletree willow (*S. arbusculoides*) intermixed. Upland willow stands were classified into two types: **tall upland willow** was typically dominated by grayleaf (*S. glauca*) and Richardson willows, while in **low upland willow** stands both diamondleaf (*S. planifolia pulchra*), and Richardson willow predominated. **Alluvial spruce-willow** stands had an outwash gravel and soil substrate with a mature white spruce canopy, and grayleaf willow dominating

the understory. **Birch-willow** stands were primarily composed of resin birch and diamondleaf willow, with a mixture of other willows, such as Barclay (*S. barclayi*), intermixed. **Alder-willow** stands were dominated by American green alder with a lower shrub community composed primarily of diamondleaf willow. At lower elevations (below 900 m) **lowland spruce-willow** communities were comprised of white or black spruce with an understory of resin birch, diamondleaf and grayleaf willow. **Aspen-spruce** forests contained white spruce and aspen (*Populus tremuloides*) in the overstory, with bebb willow (*S. bebbiana*) and alder the most common understory shrubs (Miquelle and Van Ballenberghe 1989)."

Risenhoover (1987) identified additional habitats dominated by spruce, including spruce-riparian, open spruce-willow, and spruce. Some habitats, notably aspen-spruce, technically lie below treeline, but moose inhabiting mountains must move only short distances to exploit them.

Shrub-dominated habitats, including those where willow, resin birch, or alder are dominant, compose 65% of the eastern Denali National Park study area. To the south, the crest of the Alaska Range rises to 1300 m, and shrub communities give way to alpine tundra, or permanent snow. To the north and east, elevations drop below 750 m and large, continuous blocks of spruce forest occur. To the west, elevations between 1000 and 3000 m are common and productive moose habitat is discontinuous and mainly confined to major drainages.

Forage biomass

Telfer (1984) compared gross primary productivity of 5 major moose habitats and found tundra and alpine habitats far less productive than flood plains, mixed forests, boreal forest, or stream valley shrubs. Telfer (1984) estimated that tundra and alpine sites had gross primary productivity about one order of magnitude less than other habitats. Nonetheless, much of the productivity of the former may be usable by moose, as opposed to the latter where a large fraction is out of reach or unpalatable.

Available biomass of forage species for moose recently has been estimated in several habitats throughout North America. Wickstrom *et al.* (1984) noted that rates at which deer (*Odocoileus* spp.) harvested food dropped sharply when forage biomass was less than 25 kg/ha. Crete (1987), however, estimated that annual production of 14 kg/ha of deciduous twigs in eastern Canada provided enough food for 19 moose/10 km^2 for a winter period of 240 days. Leaf production in the same stands during summer was 81 kg/ha, and annual production of balsam fir (*Abies balsamifera*) exceeded 200 kg/ha.

MacCracken and Viereck (1990) estimated a total stem biomass of 1,667 kg/ha of quaking aspen 1-3 years post-fire at a low-elevation site in central Alaska. LeResche and Davis (1973) quoted Bishop (1969) as estimating paper birch annual production at 249-496 kg/ha at low-elevation sites on the Kenai peninsula, Alaska, 24 years post-fire. Oldemeyer (1983:490) reviewed browse production in several areas of North America's moose range at low-elevation and reported that values of 100-200 kg/ha of deciduous browse species were typical. Klein (1986) reported that annual production of willow could exceed 250 kg/ha for low elevation sites at 76° north latitude for certain locations in northwestern Canada, and one site at 70° north latitude in Alaska produced 1,075 kg/ha. It is important, however, to recognize that highly productive stands at high latitudes may be severely limited in size and distribution and are therefore unlikely to support high densities of moose over large areas.

Values of forage biomass for moose in habitats at treeline may be comparable to those typical of lower elevations. In Denali National Park, Wolff and Cowling (1981) reported 39-111 kg/ha of available biomass during winter in willow-dominated stands on alluvial soils. Risenhoover (1987) estimated species biomass for winter diets at Denali of 23 and 222 kg/ha in spruce and willow riparian-lowland types, respectively. Other types generally contained 54 to 169 kg/ha. Similarly, Miquelle (1990) reported 44 to 202 kg/ha of forage biomass at Denali National Park for winter habitats used by moose. Again, patchy distribution of highly productive habitats at treeline may reduce the potential for dense moose populations compared to less patchy, highly productive sites at lower elevations.

BEHAVIOR OF MOOSE AT TREELINE

In the following discussion I do not mean to suggest that moose living at treeline are genotypically different than lowland moose. I do recognize that moose in the subarctic have evolved behavioral plasticity that apparently allows them to respond to different environments in different ways through a broad array of behavioral adaptations. These include differences in seasonal movement patterns, foraging behavior, sociality, sexual segregation, and predator avoidance.

Movements

From the previous descriptions of treeline habitats in subarctic Alaska, it is obvious that moose living in such areas must obtain energy and nutrients in a patchy environment. They must exploit annual and seasonal changes in forage quantity and quality. Moose at treeline also must respond to changes in weather conditions, notably snow depth, that influence their ability to exploit the environment, and, they must avoid predators while doing so. A fundamental response that moose have evolved to cope with their environment is to alter daily and seasonal movement patterns to better match environmental constraints.

Hanley (1982) suggested that deer in western Washington traveled from plant to plant within a small home range, whereas elk (*Cervus elaphus*) moved from habitat patch to habitat patch within a relatively large home range. My observations of moose at Denali suggest that moose, like elk, respond to patchy habitat by occupying larger home ranges than elsewhere. Risenhoover (1987) reported that winter home ranges at Denali averaged about 13 km^2. Although LeResche (1974) characterized moose in Alaska as having seasonal home ranges similar to those of moose elsewhere in North America, Van Ballenberghe and Peek (1971) reported winter home ranges averaging only 2.0 km^2 in northeastern Minnesota. Garton et al. (1985) noted core (about 50% of total use) home ranges of bull moose at Denali in winter to be 4.4-5.6 km^2.

Summer home ranges of moose at Denali National Park also are relatively large. One female with calves occupied an area about 21 km long (Van Ballenberghe, unpublished data). Moose also were observed during summer moving distances up to 8 km from the center of their home range to a well-used mineral lick, apparently the only one available in this area.

Risenhoover (1987) estimated daily distance traveled by moose at Denali National Park during late-January through late-April. During January-March, moose moved about 1.0 km/day. Miquelle (1990) worked in the same area and reported distance traveled per foraging bout (about 90-280 minutes) during winter varied from 42 to 223 m depending upon snow depth, habitat, and size/sex of animals. Risenhoover (1987) noted that distance traveled per day by moose at Isle Royale National Park, Michigan, was up to twice that for moose at Denali National Park and related this to lower forage biomass at Isle Royale. Perhaps moose in black spruce stands below treeline in Alaska also have extensive daily movements in response to low forage biomass.

In contrast to Isle Royale, moose at Denali increased daily travel during late April nearly 2.5 times compared to early April (Risenhoover 1987). This pattern of extensive daily movements persists through late June (VanBallenberghe, unpublished data), especially for bulls and cows without calves. This is apparently a response both to local variations in plant phenology and forage quality, and to the need to utilize mineral licks. A similar peak in daily movements at Denali occurs in November as moose use forage supplies at high elevations during the post-rutting period (Van Ballenberghe, unpublished data).

Migration between seasonal ranges has long been recognized as an adaptive "strategy" used by moose in both treeline and lowland habitats (LeResche 1974). At treeline, snow depth during the period November through April may force moose to migrate during most years. Van Ballenberghe (1977:108) emphasized the flexible timing and extent of moose migrations from treeline in southcentral Alaska as follows:

> "Moose demonstrated considerable flexibility in their capacity to use a wide variety of habitats under varying environmental conditions. By adjusting the timing, extent and duration of their migratory movements to the relative habitability of a given area, moose could optimally exploit a patchy environment of low overall carrying capacity. Moose demonstrated their ability to vary their rate of movement during autumn migration, thus increasing their efficiency of exploitation of habitats along migratory routes that sometimes exceeded 100 km in length. Such habitats were used as long as they were usable; forage supplies in wintering areas were thereby conserved or, during the mildest winters, were not utilized at all."

Van Ballenberghe (1977) documented that mean extent of individual migratory movements ranged from 21 to 52 km (straight-line-distance) during a 3-year period for moose in treeline habitats on the south side of the Alaska Range. Snow depth was highly variable during this period; moose appeared to occupy summer-autumn habitats until snow depths of about 40 cm triggered migration. Certain individuals, however, migrated independently of snow conditions.

Gasaway *et al.* (1983) reported that migratory movements commonly exceeded 40 km for a population of moose near Fairbanks, Alaska. Patterns of movements in this population, wherein cows moved to lowland sites in February-April and moved again to adjacent hills and mountains in August-October, contrasted with movements at Denali and migrations described by VanBallenberghe (1977). Moose there displayed the classic autumn-spring pattern of movements to and from winter and summer ranges.

Finally, Van Ballenberghe (1977) stressed patterns of traditional use of seasonal ranges and migration corridors. Gasaway *et al.* (1989) also noted traditional movement patterns that prevented moose from discovering high-quality habitat in burns located short distances from migration routes. If moose at treeline occupy stable, productive habitats rarely influenced by fire, long-distance dispersals or pioneering of new areas may not be adaptive.

Foraging behavior and activity budgets

Clearly, moose adapt to local differences in plant distribution and density by exploiting a wide diversity of species for food and cover. Moose have catholic food habits (Peek 1974) and adapt well to the vegetation of many diverse habitats in boreal and subarctic regions (Telfer 1984). Treeline habitats with their unique combination of habitats and forage species provide opportunities for moose to obtain energy and nutrients seasonally, but may differ substantially from habitats in adjacent lowlands. Therefore, moose are required to modify their foraging behavior and activity to efficiently exploit treeline areas.

Van Ballenberghe *et al.* (1989) reported that moose in eastern Denali National Park consumed virtually no aquatic plants and ate only 2 species of forbs that composed only 2% of summer diets. The lack of nonbrowse species in the diet was attributed to the fact that ponds and lakes were rare in the mountainous area of eastern Denali, and forbs were rare in shrub-dominated habitats at treeline. Moose in Denali fed on woody plants almost exclusively during summer in contrast to moose in many other areas below treeline. Furthermore, summer diets at Denali had remarkably low diversity with 7 willow species composing 80-85% of diets in June, July, and August.

Winter diets of moose in Denali were also primarily willow. Risenhoover (1987) reported 94% of the winter diet was willow; 2 willow species composed 63% of the diet. Moose in other areas of Alaska, including the Kenai peninsula, rely much more on paper birch and aspen (Regelin *et al.* 1987), species that are relatively rare at treeline. That moose can thrive without them is demonstrated at Denali where densities of about 1 moose/km^2 exist in local areas (Van Ballenberghe, unpublished data).

Miquelle and Van Ballenberghe (1989) examined the extent of bark stripping of aspen and willow by moose at Denali in habitats adjacent to treeline. They noted less than 4% of the diet consisted of bark and moose ate bark when availability of browse was low. Despite the low fraction of bark in the diet, over 75% of aspen and willow canopy trees showed evidence of debarking and moose were affecting rates of forest succession.

Risenhoover (1986) studied winter activity budgets of moose at Denali and noted they were active a mean of 6.5 hours/day. Mean feeding time/day was 4.9 hours. Van Ballenberghe and Miquelle (1990) reported 10.1 and 7.5 hours/day respectively, for the same activities during summer. Peak activity (12.8 hours/day) occurred in early June and was associated with leaf-out. Annual minimum daily active time (5.8 hours in late March) reported by Risenhoover (1986) correlated well with seasonal patterns of food intake (Schwartz *et al.* 1984) and metabolic rates (Regelin *et al.* 1985) of captive moose.

Risenhoover (1987) reported that moose at Isle Royale, Michigan, were active on average 37% more (2-3 hours/day longer) during winter than moose at Denali National Park and attributed this to low forage biomass at Isle Royale. A general pattern of uniformly low daily activity from January through March, with much higher activity by late April, was evident in both areas. Perhaps moose in Alaska wintering in low-elevation black spruce forests with low forage availability also would display elevated daily activity compared to moose at treeline. MacCracken and Van Ballenberghe (unpublished data) studied winter activity of moose in an Alaska coastal wetland with shallow snow and noted activity patterns much different than in Denali. Moose were much more active in March, apparently in response to availability of highly digestible forage at the margins of aquatic habitats. Similarly, Renecker and Hudson (1989) reported seasonal activity patterns for moose in boreal aspen forests much different than those evident at Denali. Daily feeding time averaged 10 hours/day throughout the year in Renecker and Hudson's (1989) study.

Sociality

Moose often have been considered the least gregarious of the North American cervids (Peterson 1955, Altmann 1956) but aggregations in certain populations during some seasons are known to be large (Peek et al. 1974). Numerous factors influence aggregation size including intrinsic effects such as sex of animal, breeding activities, aggressive behavior, family care, group life, and population sex ratio. Extrinsic effects include predators, patterns of food availability, snow depth and hardness, vegetative cover, and topography (Peek *et al.* 1974). That moose are adaptable to a variety of habitat conditions is reflected by differences in aggregation patterns in moose populations in Alaska, Minnesota, and Montana (Peek *et al.* 1974). Alpine tundra contained relatively stable, long-lived plant communities in contrast to transitory seral communities in the boreal forest. Differences in habitat stability were considered a major influence upon the social system and aggregation patterns of different moose populations occupying these areas.

In the Kenai, Alaska moose population studied by Peek *et al.* (1974), relatively large and variable group sizes were related to high population density. Group size was largest (up to 24) in autumn through early winter and smallest in summer. Cows were quite gregarious, in contrast to Minnesota and Montana; this was related to a sex ratio strongly favoring females. Females with calves were largely solitary, as they are throughout North America, apparently as a strategy to avoid predators.

Moose aggregations above and below treeline at Kenai were different for all types of groups, combined, during August, March, and June-July (Peek *et al.* 1974). Mean group sizes were higher above treeline than below during the 3 seasonal periods, and the upper range of group sizes was about twice as large above treeline (12-15 versus 6-7).

Miquelle (1990) presented data on group composition of moose in Denali National Park. Mixed male-female groups were most common during the rutting period (74.5% of groups) and least common in winter (19%). Mixed groups occurred even during the calving period (30.2%) and during summer (28.6%). Except during the rut and post-rut, females with calves were solitary (98.8%) but only 23% of females without calves were alone. From June through August, males were consistently gregarious.

Aggregation data from another Alaska moose population at treeline in the Nelchina Basin of southcentral Alaska are presented in Table 2. These data were obtained from radiocollared animals over a 3-year period and should be relatively unbiased compared to other observation techniques that underestimate the occurence of small, less visible groups. Females with calves rarely were aggregated with other moose, even during the rut. Females without calves and males seldom were solitary during rut. Males and females without calves were aggregated with other moose about half the time during autumn-winter.

My observations at Denali suggest that moose have a highly polygynous mating system, whereas moose in many other parts of the world are considered to be serially monogomous (Markgren 1973, Bubenik 1985). Most of the observed mating at Denali has involved rutting groups as large as 40 individuals, rather than tending bonds of one male and one female. Fighting is common among males that compete in a dominance hierarchy (Peek *et al.* 1986).

Several ecological factors contribute to the mating system evolved by moose at timberline. Open habitat enables animals to observe conspecifics from afar. Periodic harsh winters and differential predation on males both contribute to a skewed adult sex ratio; in recent years the Denali population has been 70% female despite prohibition of hunting for 60 years. Mortality of calves, primarily caused by predation (VanBallenberghe 1987), typically results in 80-90% of the females being without calves during rut. This facilitates formation of rutting groups as females with calves are notoriously anti-social. Together, these factors encourage aggregations during rut and discourage pair bonds. Several of the characteristics of treeline habitats discussed above contribute to the underlying factors influencing the breeding system, in specific, and sociality, in general, of moose inhabiting these areas.

Table 2. Aggregation data for radiocollared moose in the Nelchina Basin, southcentral Alaska, 1974-1977. Moose occupied treeline habitats during April-January, and migrated to adjacent habitats during other months. Numbers in the body of the table are percent of groups where moose were solitary.

Time period	Females		Females with Calves		Males	
	%	n	%	n	%	n
20 May - 19 June	85.6	118	99.1	117	73.6	53
20 June - 19 July	70.7	82	100	41	94.1	34
20 July - 19 Aug	64.6	96	94.4	18	65.5	29
20 Aug - 19 Sept	52.0	75	100	21	57.5	40
20 Sept - 19 Oct	17.1	152	90.0	40	10.2	49
20 Oct - 19 Nov	46.8	79	95.5	22	42.3	26
20 Nov - 19 Dec	46.4	181	100	33	46.7	45
20 Dec - 19 Jan	58.9	90	100	13	45.5	22
20 Jan - 19 Feb	51.5	101	100	22	42.1	19
20 Feb - 19 Mar	67.5	123	100	30	48.0	25
20 Mar - 19 Apr	53.2	173	98.5	65	69.0	42
20 Apr - 19 May	53.5	142	90.8	120	76.4	55

Sexual segregation

Segregation of the sexes on seasonal ranges has been documented for numerous species of boreal, north temperate, and tropical ungulates. Main and Coblentz (1990) recently reviewed 5 hypotheses proposed to explain sexual segregation including: 1) departure of males from high-quality ranges to minimize competition with females, their young, and potential offspring; 2) predator avoidance by males after rut; 3) minimization of aggression among males during the nonbreeding season; 4) use of open habitats by males to facilitate dominance hierachies and minimize damage to growing antlers; and, 5) optimization of forage resources by males and selection of habitats suitable for raising young by females. Main and Coblentz (1990) dismissed the first 4 hypotheses and provided several lines of evidence supporting the fifth. They concluded that males and females selected habitats according to different criteria as a consequence of different reproductive strategies. Although a wide variety of ungulate species in different environments display sexual segregation, all females are required to select areas for raising young, and most males must optimize body condition to compete with other males during the breeding season.

Miquelle (1990) observed that sexual segregation had not been well documented in moose. He provided strong evidence that such segregation occurred during both summer (females with calves) and winter (mature males) at Denali National Park and tested 8 hypotheses explaining this behavior, most notably that segregation results from different nutritional-energetic requirements associated with differences in body size. Miquelle (1990) concluded that females with calves segregated from other moose in summer and preferred forested habitats. This was thought to provide increased survival of calves through predator avoidance. Solitary behavior of females broke down through summer as many females lost calves.

Segregation during winter was variable

depending upon snow depth; in shallow-snow winters females and smaller males jointly used a portion of the study area that females abandoned during deep-snow winters. Mature males used isolated drainages that females avoided during both types of winters. Such drainages contained dense stands of willows with high forage biomass compared to areas used by females, either near treeline or in aspen-spruce forests at lower elevations.

Miquelle (1990) concluded that no single hypothesis fully explained winter habitat segregation. No evidence existed that males selected habitats that provided thermal cover. Association with females did not impose costs to males as rates of social interactions of males did not increase in mixed groups. Availability of forage was relatively high; segregation due to resource competition therefore appeared unlikely. Males may have segregated to lower the risk of predation, but other factors including differences in activity budgets and foraging ecology suggested that ecological and body size dimorphism and their relationship to energetics, were more important. Miquelle (1990) constructed an energy budget simulation model suggesting that large-bodied males incurred greater energy costs than small males or females. Large males were at greater risk of depleting fat reserves due to a greater energy deficit and a greater reduction of fat reserves during rut. During deep-snow winters, large males reduced energy expenditure by reducing activity, decreasing travel, increasing bite size, and selecting habitats with high forage biomass.

Moose habitat near treeline in Denali is very patchy. Mature males that lose about 15-20% of their body weight during rut must select winter habitats that provide high-energy food resources that can be efficiently harvested during deep-snow conditions. Moose were most able to forage efficiently on feltleaf willow with a distribution in dense stands limited to alluvial sites. These are confined to about 7% of the landscape in eastern Denali. In adjacent lowlands where moose exploit burned areas during winter as well as valley bottoms, it is likely that sexual segregation is not as pronounced. Large, continuous areas of regrowth that provide forage biomass exceeding 200 kg/ha likely allow all sex-age classes of moose to satisfy energy demands without the need to segregate.

Predator avoidance

Predation by wolves and brown bears has caused powerful selection pressures during the entire evolutionary history of moose. Most life-history tactics of moose, including habitat selection, have been shaped by this pressure. Moose at treeline, where bear and wolf densities are high, must adapt to increased risks of predation and increased probability of detection due to open terrain. There is evidence that moose have achieved this; in the naturally regulated moose and predator populations in Denali National Park moose suffer low calf survival but population density in local areas of favorable habitat exceeds 1 moose/km^2 (Van Ballenberghe 1987).

Because wolves at treeline often have access to alternate prey including caribou (*Rangifer tarandus*) and Dall's sheep (*Ovis dalli*), their population density and potential impact on moose may remain high even if moose density is low. Murie (1944) described a multi-prey system at Denali where wolves depended largely on caribou year-round. Dall's sheep populations in this area fluctuated widely over time, reaching very high levels and furnishing considerable food for wolves during certain periods. Moose were much less abundant than when studied 30 years later in the same area by Haber (1977) after alternate prey had declined. Brown bears were known to be major predators on moose calves in this area by the late 1970's, and were thought to be responsible for persistently low recruitment (VanBallenberghe 1987). Nevertheless, bear density (unlike wolf density) did not appear closely tied to moose numbers.

Miquelle (1990) found that female moose with calves at Denali were solitary 98.8% of the time except during the breeding season, while only 23% of the females without calves were alone. He found that females with calves were also spatially segregated from other moose in spring and summer, prefering forested habitats. As calves were lost, sociality of females increased. These findings were all consistent with the hypothesis that females segregated to reduce predation on calves.

During winter, large, mature male moose at Denali selected alluvial habitats with high forage biomass. These areas often were in remote valleys seldom visited by females or smaller males. Although large males were predictably distributed, wolves were at a disadvantage in the deep, soft snow occurring in the valley bottoms. Wind and sun conditions in the sheltered valleys may not result in drifting and crusting and wolves would have difficulty traveling in deep, unpacked snow. In shallow snow years, neither moose nor wolves would be handicapped by snow conditions.

Finally, Van Ballenberghe (1987) emphasized the importance of spatial relationships in a wide variety of predator-prey relationships including moose-wolf-bear systems in the subarctic. That naturally regulated moose populations preyed upon by wolves and brown bears tend to remain at low density is in part related to wide spacing of individuals and groups and resultant lengthening of predator search time. I have observed wide spacing of females at Denali during calving, including use of uniform, large areas of shrub-tundra where forage biomass is very low, as well as aspen-spruce forests where females extensively eat bark (Miquelle and VanBallenberghe 1989). Wide spacing of individuals occurs both within and between habitat types and seems clearly related to predator avoidance.

SUMMARY

I have suggested that treeline habitats used by moose in subarctic Alaska present several unique constraints and risks to moose compared to forested habitats at lower elevations. Moose at treeline must obtain energy and nutrients during short growing seasons in habitats of inherently low productivity. Favorable habitats at treeline are patchy and widely spaced; large areas with a high biomass of less preferred shrubs are common. Lakes and ponds may be rare near treeline; as a result moose must forego highly digestible aquatic plants rich in protein and sodium. Forbs also may be scarce in shrub-dominated stands. During winter, deep snow and heavy drifting may cover food plants and increase energy expenditures for moose that remain near treeline. Wolves and brown bears may reach high densities near treeline and may be efficient at detecting moose in relatively open terrain.

Obviously, moose have adapted to such risks and constraints; they successfully occupy treeline habitats across a broad expanse of subarctic Alaska. Behavioral adaptations include extensive daily and seasonal movements whereby moose exploit patchy environments of low overall carrying capacity. Daily movements between favorable habitat patches and to unique environmental features (such as mineral licks) are quite extensive. Seasonal home ranges are large. Seasonal migrations to and from treeline enable moose to avoid deep snow while foraging during summer in productive, high elevation sites where shrubs are dominant. Moose also have modified their foraging behavior and activity budgets to treeline habitats.

Moose near treeline generally form larger groups than in adjacent lowlands and may modify their sociality in response to habitat variables such as more open terrain. Several factors, including low calf survival (largely a function of intense predation) and female-skewed adult sex ratios, result in a polygynous mating system with large rutting aggregations. Sexual segregation is apparent as well, with females segregating to bear and rear calves in summer and large males selecting alluvial sites with dense willow stands during winter. The latter strategy apparently relates to body size dimorphism, energetics, and the need to maintain high rates of forage intake during winter to avoid starvation.

Finally, moose at treeline must avoid predation from dense populations of wolves and brown bears. Females with calves space themselves widely and remain solitary in forested habitats throughout the year. Large males select isolated, deep valleys in winter where wolves are inefficient due to deep, soft snow during most years. Although recruitment in naturally regulated moose-wolf-brown bear systems is low, moose can reach densities exceeding l/km^2 in areas of favorable treeline habitat, thereby demonstrating their ability to cope with predation losses and other environmental constraints.

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