ECOLOGY OF MOOSE IN DENALI NATIONAL PARK AND PRESERVE, ALASKA: A RESEARCH SUMMARY , 1980-1996

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Moose occupy a broad area of Alaska from the southeastern panhandle to the North Slope adjacent to the Arctic ocean. Moose are important consumers of vegetation in the taiga and they in turn serve as a food source for humans and several species of subarctic carnivores and scavengers. Moose play important ecological roles in the communities they occupy; understanding the structure and function of such roles is important to the management and protection of habitats in many areas of Alaska. Ecological research including studies of population dynamics, behavioral ecology, and foraging ecology, through long-term field studies can contribute to better understanding of the ecological importance of moose and provide guidelines to assist managers.

In Alaska, moose use a variety of habitats ranging from highly productive coastal wetlands to alluvial shrub communities north of the Arctic circle. In the major mountain ranges of subarctic Alaska, including the Chugach, Wrangell, and Alaska ranges, moose occupy treeline habitats both seasonally and throughout the year. These differ floristically from lowland habitats and are subject to different weather patterns that affect plant productivity and increase energy

expenditures of moose forced to cope with deep snow during certain years.

Denali National Park and Preserve in the central Alaska Range contains treeline habitats typical of those found across a broad area of interior Alaska. Moose in the eastern quarter of the park inhabit these habitats at densities approaching 1/km^2. Access to these areas is possible from the park road by vehicle during summer and skis, snowshoes, and dog team during winter. Moose are tolerant of humans as hunting has been prohibited for 70 years; close-range observations are feasible. The moose population is naturally regulated, one of only a few such populations in North America. A full complement of native predators and scavengers is present including brown and black bears, wolves, red foxes, coyotes, wolverines, lynx, ravens, and eagles. These characteristics combine to provide an ideal study location for long-term research on moose ecology. In addition, the status of Denali as an International Biosphere Reserve provides additional impetus to monitor the moose population there due to the central role that moose play in functioning of the ecosystems they occupy.

In April 1980, we began research on moose ecology at Denali by collaring 11 adults with radio- transmitters. The study had several components including foraging ecology, population dynamics, and behavioral ecology focusing on rutting behavior. Over the next 17 years, 1980-1996, we conducted field studies each year and gathered data during a variety of seasons yearlong. Collared animals have been monitored and additional animals were collared as others died or more animals were needed. Various cooperators from 3 different universities assisted with the studies; these included 2 doctoral students whose dissertations were largely or wholly based on work at Denali, one professor on sabbatical, and 1 master's student. The following summary reviews each of the major segments of this research.

FORAGING ECOLOGY

The foraging ecology studies initially were designed to gather basic data on habitat selection, seasonal movements, and food habits. By radiotracking moose it was possible to determine which habitats were preferred and which were avoided. The floristic composition of these habitats was determined by vegetation sampling; stem density and biomass production of important forage species were also estimated. Seasonal home ranges were estimated by plotting daily locations of collared moose, connecting the outermost locations, and measuring the area of the enclosed polygons. Migratory movements were estimated by comparing locations of areas used during summer with winter locations. Food habits were determined from direct observations of individual moose during foraging bouts. Observers identified plant species consumed, counted bites of forage by species, and estimated bite size by cropping simulated bites from nearby forage plants and determining weight per bite. Daily activity budgets were determined by observing moose continuously for 24-hour periods and instantaneously sampling behavior at 2-minute intervals. Activity was also monitored with Russtrack recorders that monitored radio signal strength and fluctuation.

Miquelle (1990a: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, Richardson, and littletree willow intermixed. Upland willow stands were classified into two types: **tall upland willow** was typically dominated by grayleaf and Richardson willows, while in **low upland willow** stands both diamondleaf, and Richardson willow predominated. **Alluvial spruce-willow** stands had an outwash gravel and soil substrate with 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, 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 in the overstory, with bebb willow 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. Shrub-dominated habitats, including those where willow, resin birch, or alder are dominant, compose 65% of the eastern Denali National study area.

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 has been estimated in several habitats throughout North America. Wickstrom *et al.* 1984 noted that rates at which deer 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 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 s

(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.

In Denali, 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.

Hanley (1982) suggested that deer in western Washington traveled from plant to plant within a small home range, whereas elk moved from habitat patch to habitat patch within a relatively large home range. 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 (Van Ballenberghe, 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).

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 Van Ballenberghe (1977). Moose there displayed the classic autumn-spring pattern of movements to and from winter and summer ranges.

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.

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 areas 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's (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.

Following the first phase of the foraging ecology studies at Denali, a second phase was initiated in 1990 in order to investigate herbivory by moose in relation to browse quality and nutrient cycling. Herbivore browsing in subarctic ecosystems can change the composition of plant communities as palatable plants are reduced in frequency. Growth forms of plants may be altered. Browsing may also alter carbon-nutrient balance; moderate browsing may increase

growth and leaf nutrient content. Extreme herbivory may cause shrubs to revert to an unpalatable juvenile form high in secondary defense compounds (Bryant 1981).

Herbivores may facilitate nutrient transfers in soil. Urinary and fecal nitrogen enriches soil and stimulates plant growth. Soil nitrogen mineralization may increase thus benefiting plants. Positive feedback loops may result with herbivores reusing previously browsed sites with increasing rates of nutrient cycling. Consequently, we examined effects of browsing to test effects of moose on morphological characteristics of willows, their quality as forage, and rates of nitrogen mineralization.

Molvar et al. (1993) tested the hypotheses that: 1) Overall plant growth, the C:N ratio, and C- based plant defenses should be lower in the shade than in full sunlight. 2) Willow productivity per growing point should be higher in an area of high moose density due to fertilization by moose urine and feces. 3) Individual browsed stems should show greater regrowth than unbrowsed stems. 4) Differences in chemistry of plant litter affected by moose density should lead to increased rates of decomposition as the intensity of browsing increases.

Molvar et al. (1993) found that moose browsing on diamondleaf willow caused significant increases in subsequent growth of stems and leaves in treeline plant communities. Willows growing in shade were significantly more palatable for moose than those growing in sun. Moose density had strong effects on rates of nutrient cycling, ostensibly through effects of browsing and inputs from fecal and urinary nitrogen. Moose are a keystone herbivore that likely mediate rates of nutrient cycling in northern ecosystems.

In 1992 as an extention of the foraging studies we initiated a birth site study to investigate several aspects of site choice by females. Hypotheses include:

1) Sites used for parturition and the postpartum care of neonates will differ significantly from random locations.
2) Selection of habitat will either minimize the predation: forage ratio or "balance" predation and forage.

3) The physical condition of the mother will determine the relative importance of predation and forage in selection of habitat.

4) Birthing sites as well as those selected for postpartum care will differ between moose and deer because of disparate strategies for protecting young from predators.

5) Moose (subarctic species) will exhibit significantly stronger selection for habitat characteristics related to predation and forage than deer (temperate species).

6) Variables indentified in models of habitat selection will be significantly related to survivorship of neonates.

POPULATION DYNAMICS

In our initial discussions with NPS personnel at Denali we emphasized our interest in conducting a long-term population dynamics study of moose in an area with naturally regulated populations of moose and their predators. Such opportunities are rare in North America because most moose populations are hunted, exist without naturally regulated predators, or occur in habitats heavily influenced by humans. Because moose are long-lived (up to 21 years for certain individuals) and the dynamics of their populations are slow to respond, long-term studies are required. Meaningful conclusions based on short-term studies are suspect, in part because ecological conditions (including snow depths, important in vulnerability to predation) vary with time. This has been amply demonstrated at Isle Royale where studies of moose and wolves underway since 1958 have demonstrated the pitfalls of short-term research.

Although the moose population at the east end of Denali is not completely naturally regulated it is as close to that condition as possible. Some moose are killed by a variety of "non-natural" agents including motor vehicles, trains, poaching, and other human-related sources. Similarly, wolves are subject to some human mortality, and a human-caused fire in 1924 influenced moose habitat in a portion of the park near headquarters. However, most of the

ecological processes operating on ecosystem dynamics in this area are not influenced by people and the moose population has largely been free of human influence since protected from hunting about 70 years ago.

Objectives of the population dynamics segment of the study included estimating calf production and survival rates, adult survival, and rate of increase of the population. Long-term population trends would be monitored. Mortality causes would be determined, and the roles of nutrition and predation in the dynamics of the population would be assessed.

Procedures included radiocollaring a sample of adults and following their fates over a 10-20 year period. Additional moose would be collared as others were lost. This would result in survival rates for adults and identification of mortality agents. Birth rates of collared females would result in unbiased samples for estimates of calf production. Random sightings of uncollared females during late May and early June would add to these data. Survival of calves born to collared females would be monitored to obtain calf survival rate estimates and would be combined with aerial surveys in autumn to determine composition of the population (bulls, cows, and calves) and estimate recruitment. Aerial surveys would also result in population estimates (and density estimates) when done with high search intensity under good conditions of snow cover, wind, and sunlight. Visibility correction factors for animals missed during aerial surveys would be determined from the observed fractions of collared moose known to be in the survey area. This series of population estimates would provide data points for monitoring population trends and computing rates of increase. Survival and fecundity estimates would be combined to estimate rate of increase to compare with observed changes in population size.

During the interval 1980-1996 we conducted these procedures annually, except for the aerial surveys that were not possible each year due to unfavorable weather or a shortage of funds. Data were obtained on birth rates, calf survival, adult survival, mortality causes, and population size. During this interval, the moose population at the eastern end of Denali declined sharply. Density declined from about 2.5/mi^2 to about 1.0/mi^2. Birth rates have been high, about 120/100

adult females, but survival was poor. Only 10-20 calves of each 100 born survived to autumn. The main cause of calf deaths was bear predation. Adult female survival has been high, even for older (12-18) animals. Survival of males was lower than females with few males living to more than 12 years. Rutting injuries, energetic demands of rutting, and higher rates of predation result in lower average life spans for males. In general, poor recruitment has resulted in a declining population despite high survival rates of adults, and density is now much lower than at the start of the study. We have not published most of these data in anticipation of several more years of data collection and perhaps the opportunity to observe reversal of the trends of the past 17 years.

BEHAVIORAL ECOLOGY

Because moose at Denali are protected from hunting and therefore tolerate human presence at distances as close as 50 yards, it is possible to conduct research on moose behavior that can be seen in few other places in North America. Furthermore, the treeline habitat that moose occupy at Denali is relatively open thereby facilitating observations. Also, protection from hunting has allowed adult males to survive to older ages at Denali; the resulting age distribution and social structure provide opportunities to observe long-term relationships among individuals, document age-related changes in behavior, and determine attributes like life-time breeding success that are not possible to study in other areas. Accordingly, we were interested in initiating behavioral research in 1980 with an emphasis on rutting behavior and its implications for several aspects of behavioral ecology.

Objectives of the behavioral research included documenting rutting behavior of male and female moose in order to produce an ethogram of moose during the mating season, determining frequencies and rates of sparring and fighting and relating these to individual mating success, determining frequency and causes of antler breakage, determining traditional use of rutting areas and describing the characteristics of such areas, testing several hypotheses (listed below) on scent

marking by moose, and testing several hypotheses (below) on sexual segregation of moose and the behavioral and ecological factors responsible for it.

Hypotheses related to scent marking included:

1) Significant differences exist in rates of scent-marking among sex and age classes of moose.
2) Rates and types of scent-marking vary significantly throughout rut.
3) Scent-marking is associated significantly more often with agonistic or sexual behaviors.
4) A significant relationship exists between when a scent-mark is made and the time-interval for other sex and age-classes of moose to respond.
5) The ingredient in rutting pits that attracts other moose is urine, and there is a difference in the attractiveness of urine from dominant and subordinate bulls.
6) The order in which captive female moose visit scent-marks is related to onset of estrus.
7) Scent-marking behavior is related to local or yearly changes in population size or composition.
8) The spatial distribution of scent-marks is not random and is related to other rutting activities of moose.
9) Moose select tree species to mark in proportion to the availability of these woody species, and show preferences for particular characteristics of trees.
10) Significant differences in the aforementioned attributes of moose behavior (nos. 1-9) will occur among years.

Hypotheses related to sexual segregation included:

1) In spring and summer, segregation occurs because females with calves act to reduce risk of predation on neonates, whereas males act to maximize nutrient intake.
2) During the postrut, large males segregate to avoid females because, being exhausted from the rut and easily recognized by the presence of antlers, they are more vulnerable to selective culling if in a mixed group.
3) In winter, males that shed antlers should employ a female mimicry strategy to reduce the

risk of predation and, therefore, should not segregate, unless male agonistic behavior inhibits sociality.

4) Males segregate from females in winter independent of antler status because, due to declining body condition, they are more vulnerable to predation and, therefore, more likely to be selected by predators when in mixed groups.
5) Due to poor body condition in winter, large males segregate because they require thermally favorable habitats more than do females and small males.
6) Large males segregate from females to avoid unnecessary energy expenditure associated with intrasexual competition.
7) Males are segregated from females in summer because they select habitats that are favorable for social interactions, that reduce risk of antler damage, and that provide cover from predators.
8) Males are outcompeted by females when forage availability is limited due to differences in the ratio of metabolic weight and bite size and, therefore, must select alternate habitats.
9) Segregation in winter results from dimorphisms in body size and seasonal patterns of energy expenditure.

Procedures used in the behavioral research included radiocollaring males and females in order to have identifiable individuals recognizable from day-to-day and year-to-year. An average of 18 collared animals per year was maintained. In addition, certain individual uncollared males were recognizable from year-to-year by antler, bell, facial scar, and ear characteristics. Collared animals were located daily; they and their associates provided focal animals and groups for observations. Data on rates of social behavior were collected. Rates and interactions between individuals were recorded as behavioral acts per active hour using focal group sampling and an all occurrences log (Altman 1974).

Several technical articles summarizing the behavioral ecology research at Denali were published including studies on mating, dominance relationships, the functions of the moose's

"bell", scent marking, and appetite suppression of males during the rut. In addition, a monograph summarizing certain aspects of foraging behavior, seasonal energetics, rutting behavior, and predator avoidance was published under the general heading of sexual segregation. The following discussion briefly highlights the major conclusions of these papers.

Miquelle and Van Ballenberghe (1985) studied the function of the moose's bell in order to determine if it served as a visual or olfactory communicator. Two current hypotheses that explain the evolutionary significance of the moose bell are: 1) during the rut the male bell disseminates and transfers by contact, the urine of the bull close to or directly onto the cow, and; 2) the bell acts a visual cue that relates to sex and age, which in turn may be associated with rank. We tested the first hypothesis by describing wallowing behavior, and determining whether females initiated contact with bulls' bells more than expected by chance. The second hypothesis was tested by comparing bell morphology in two populations of moose, and by relating the outcome of agonistic interactions to bell shape. Observations on wallowing behavior supported the hypothesis that the bell acts as a carrier of olfactory cues. However, females make physical contact with male bells less than expected by chance. Populations in Alaska and Ontario had similar age- and sex-related variations in bell shape. No relationship was found between bell morphology and dominance among females or among males during the antlerless period. We hypothesized that bell shape is a secondary sexual characteristic most important during the rut, and that moose may use bell morphology to assess social status of conspecifics.

Peek et al. (1986) studied dominance relationships during the rut among bulls. Interactions included sparring, displays, escorts, rushes, and fights. Interactions between large bulls were more intensive than between large bulls and small bulls or between small bulls. Fighting occurred primarily among large bulls. Interactions were more intensive among bulls of equal size. The data indicated that a dominance hierarchy existed among bulls with the largest acquiring top rank.

Miquelle (1990b) studied appetite suppression of bulls during the rut. Reduced forage

intake by males is generally believed to coincide with the peak of rutting activities in many ungulates. Activity budgets of bull moose in Denali National Park and Preserve (DNPP) and Isle Royale National Park (IRNP) were analyzed to assess: (1) if time spent foraging decreased during the rut; (2) the timing of reduced forage intake; (3) whether there was variation in feeding time among bulls of varying size; and (4) the proximate mechanism and adaptive value of reduced forage intake. Time spent feeding by bull moose began to decrease around 1 September: large bulls completely ceased feeding for approximately 2 weeks, with median dates of feeding cessation at 18 and 20 September for IRNP and DNPP, respectively. Small bulls fed at reduced rates, but did not cease feeding. Although large bulls in both study sites spent large amounts of time engaged in social behavior during the period of appetite suppression, much of their active time was also spent standing inattentive, i.e., engaged in no activity (45.5% in IRNP, 29.8% in DNPP), suggesting that a constraint in time budgets did not limit opportunities to feed. Forage intake reduction is more likely mediated through a physiological mechanism. Feeding cessation did not coincide with the peak of the rut: at DNPP the median date of feeding cessation was significantly earlier than the median date of breeding behavior and fighting. The timing of feeding cessation coincided with that of scent-urination at both study sites, raising the possibility that appetite suppression may be a byproduct of physiological processes associated with chemical communication.

Miquelle (1991) studied scent urination during the rut. Scent urination likely serves a variety of functions, depending on the species and environment in which it is expressed. Evidence derived from observations in Denali suggests that scent urination induces ovulation in cows. Testing of this hypothesis should be possible in captive populations. Males also appear to use urine as a means of attracting females. Female competition for a male resource is rare in mammalian mating systems, yet cow moose in aggressively compete for access to bull urine, suggesting that male urinary components may increase the probability of successful reproduction. While priming pheromones may be required by cows to ensure birthing when calf survival will

be highest, whether or not bulls produce such pheromones may be dependent on the relative benefits accrued to them. Mature bulls that scent urinate may increase reproductive success by inducing ovulation before their body condition declines and attracting cows by their scent so that courtship is possible. Subadult bull moose do not scent urinate yet attempt to acquire some of its benefits by obtaining attractive odors from mature bulls. The evolution of scent urination as an important component of moose breeding behavior may be related to the evolution of moose in the circumpolar boreal forests. Females in low-density populations may increase reproductive success by being assured of the presence of a breeding bull before ovulation. Use of scent urination as a mechanism to time breeding appears to be one facet of an ecological opportunist strategy employed by moose to exploit environments that are either low quality (mature boreal forests) or temporary and unpredictably distributed (seral shrub communities).

Miquelle et al. (1992) studied sexual segregation in moose. Data on group composition, spatial distribution, habitat selection, social behavior, activity patterns, foraging ecology, and forage quality and quantity were collected to assess 9 hypotheses that have been proposed to explain sexual segregation in ungulates. Predictions for each hypothesis were compared to empirical observations of 4 sex-age classes (small males, large males, adult females without calves, adult females with calves). A factorial energy budget model was developed as an aid to assessing the importance of size dimorphism and variation in allocation of energy for reproduction.

There were clear differences in spatial distribution of females with calves versus other sex-age classes in summer. Segregation in early summer appeared to be due to dimorphic predator avoidance strategies: female moose with calves remained solitary and preferred forested habitats whereas males selected habitats with high forage biomass. Solitary behavior of females and sexual segregation diminished through the summer as females lost calves. Aggregations of males in summer did not appear to be associated with assessment of dominance.

Segregation was greatest in winter, but varied between the 2 winters of observation.

Spatial segregation in the 1985 winter resulted from changes in spatial distribution of both sexes, but in 1986 it was due primarily to movement by males out of areas used by females. Male moose did not employ a female mimicry strategy in the postrut or winter seasons. There was no evidence that habitat selection by large males was dependent on availability of thermal cover. Rates of social interaction of males were low when in mixed groups in winter, suggesting that sociality and association with females imposed little cost to males. Segregation due to competition for resources appeared unlikely: the hypothesized differential competitive ability based on allometric relationships between body size and bite size was not supported for the data for moose, and availability of forage was relatively high, suggesting that competition for a limited resource was not occurring. Males may have segregated to lower the risk of predation, but patterns in spatial distribution, activity budgets, and foraging ecology appeared to be primarily the result of ecological and body size dimorphism. Results of the energy budget simulation model suggested that large males incurred greater energy costs than small males or females, due primarily to their greater size and lower fat reserves. Due to a greater energy deficit, large males faced a greater risk of starvation before the end of winter. During the severe winter in 1985, large males appeared to reduce energy expenditure by reducing activity levels, decreasing travel distances, increasing bite size, and selecting areas of high forage biomass.

The seasonal pattern of energy expenditure associated with the life history strategy of mature male moose likely put them at greater risk of winter mortality than other sex-age classes, which may partially explain the disparate sex ratio in DNPP.

Van Ballenberghe and Miquelle (1993) studied mating in moose. The median date of observed copulations for all years was 2 October, with small shifts among years. Of 191 mounting sequences observed, all occurred between 24 September and 8 October. Only 2% of copulations (n = 86) involved the mating of a female and two males. Large males performed 82% of all mountings and 88% of all copulations. One male copulated with at least 12 females during one mating season. Male and female behavioral patterns associated with mating were

similar to those observed in other cervids and included tongue flicking, courtship croaking, genital smelling, chinning by males, and tree rubbing by females. Both sexes displayed little obvious postcopulation behavior.

LITERATURE CITED

ALTMANN, J. 1974. Observational study of behavior:sampling methods. Behavior 49:227-268.

BISHOP, R. H. 1969. Moose Report. Annu. Proj.Segment Rep. Vol.X.Alaska W-15-R-3. Work Plan K. 152pp.

BRYANT, J. P. 1981. Photochemical deterrence of snowshoe hare browsing by adventitous shoots of four Alaskan trees. Science 213:889-890.

CRETE, M. 1987. Approximation of *K* carrying capacity for moose in eastern Quebec. Can. J. Zool. 67:373-380.

GARTON, E. O., M. D. SAMUEL, and J. M. PEEK. 1985. Analysis of moose home ranges. Alces 21:77-89.

GASAWAY, W. C., R. O. STEPHENSON, J. L. DAVIS, P. E. K. SHEPHERD, and O. E. BURRIS. 1983. Interrelationships of wolves, prey, and man in interior Alaska. Wildl. Monogr. 84, 50pp.

GASAWAY, W. C., S. D. DUBOIS, R. D. BOERTJE, D. J. REED, and D. T. SIMPSON. 1989. Response of radio-collared moose to a large burn in central Alaska. Can.J.Zool. 67:325-329.

HANLEY, T. A. 1982. Cervid activity patterns in relation to foraging constraints: western Washington. Northwest Sci. 56:208-217.

KLEIN, D. R. 1986. Latitudinal variation in foraging strategies. Pages 237-246 *in:* O. Gudmundson (ed.) Grazing research at northern latitudes. Plenum Pub. Corp.

LERESCHE, R. E. 1974. Moose migrations in North America. Naturaliste can. 101:393-415.

LERESCHE, R. E., and J. L. DAVIS. 1973. Importance of nonbrowse foods to moose on the Kenai Peninsula, Alaska. J. Wildl. Mange. 37:279-287.

MACCRACKEN, J. G. and L. A. VIERECK. 1990. Browse regrowth and use by moose after fire in interior Alaska. Northwest Sci. (64):11-18.

MIQUELLE, D. G. 1990a. Behavioral ecology of moose in Denali National Park and Preserve, Alaska. Ph.D. Thesis, Univ. Idaho, Moscow. 152pp.

MIQUELLE, D. G. 1990b. Why don't bull moose eat during the rut? Behav. Ecol. Sociobiol. 27:145-151.

MIQUELLE, D. G. 1991. Are moose mice? The function of scent-urination in the breeding behavior of moose. Am. Nat. 138:460-477.

MIQUELLE, D. G., and V. VAN BALLENBERGHE. 1985. The moose bell: a visual or olfactory communicator? Alces 21:191-213.

MIQUELLE, D. G. and V. VAN BALLENBERGHE. 1989. Impact of bark stripping on aspen-spruce communities. J. Wildl. Manage. 53:577-586.

MIQUELLE, D. G., J. M. PEEK, and V. VAN BALLENBERGHE. 1992. Sexual segregation in Alaskan moose. Wildlife Monogr. 122.

MOLVAR, E., R. T. BOWYER, and V. VAN BALLENBERGHE. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia 94:472-479.

OLDEMEYER, J. L. 1993. Browse production and its use by moose and snowshoe hares at the Kenai Moose Research Center, Alaska. J. Wildl. Manage. 47:486-496.

PEEK, J. M., V. VAN BALLENBERGHE, and D. G. MIQUELLE. 1986. Intensity of interactions between rutting bull moose in central Alaska. J. Mammal. 67:423-426.

REGELIN, W. L., C. C. SCHWARTZ, and A. W. FRANZMANN. 1985. Seasonal energy metabolism of adult moose. J.Wildl.Manage. 49:388-393.

REGELIN, W. L., M. E. HUBBERT, C. C. SCHWARTZ, and D. J. REED. 1987. Field test of a carrying capacity model. Alces 23:243-284.

RENECKER, L. A. and R. J. HUDSON. 1989. Seasonal activity budgets of moose in aspen-dominated boreal forests. J.Wildl.Manage. 53:296-302.

RISENHOOVER, K. R. 1986. Winter activity patterns of moose in interior Alaska. J.Wildl.Manage. 50:727-734.

RISENHOOVER, K. R. 1987. Winter foraging strategies of moose in subarctic and boreal forest habitats, Ph.D. Dissertation. Mich. Tech. Univ., Houghton. 108pp.

SCHWARTZ, C. C., W. L. REGELIN, and A. W. FRANZMANN. 1984. Seasonal dynamics of food intake in moose. Alces 20:223-244.

TELFER, E. S. 1984. Circumpolar distribution and habitat requirements of moose (*Alces alces*). Pages 145-182 *in*:R. Olsen, R. Hastings, and F. Geddes (eds.) Northern ecology and resource management. Univ. Alberta Press, Edmonton.

VAN BALLENBERGHE, V. 1977. Migratory behavior of moose in southcentral Alaska. Int. Congr. Game Biol. 13:103-109.

VAN BALLENBERGHE, V., and J. M. PEEK. 1971. Radio-telemetry studies of moose in northeastern Minnesota. J.Wildl.Manage. 35:63-70.

VAN BALLENBERGHE V., D. G. MIQUELLE, and J. G. MACCRACKEN. 1989. Heavy utilization of woody plants by moose during summer at Denali National Park, Alaska. Alces 25:31-35.

VAN BALLENBERGHE V. and D. G. MIQUELLE. 1990. Activity of moose during spring and summer in interior Alaska. J.Widl.Manage. 54:391-396.

VAN BALLENBERGHE V. and D. G. MIQUELLE. 1993. Mating in moose:timing, behavior, and male access patterns. Can. J. Zool. 71-(8):1676-1690.

VIERECK, L. AND C. T. DYRNESS. 1980. A preliminary classification system for vegetation of Alaska. USDA For. Serv. Gen Tech. Rep. PNW-106.

WICKSTROM, M. L., C. T. ROBBINS, T. A. HANLEY, D. E. SPALINGER, and S. M. PARISH. 1984. Food intake and foraging energetics of elk and mule deer. J.Wildl.Manage. 48:1285-1301.

WOLFF, J. O. and J. COWLING. 1981. Moose browse utilization in Mount McKinley National Park, Alaska, Can. Field Nat. 95:85-88.

V / C

24 years 1980

USFS 20 years

UAF - Adjunct

Tok, Nikka and East —

Foraging

Pop Dynamics - Survival -

Behavior Ecology - RS individuals

10-20% survival / break of Blogs

w Life Ford =

★ Key Issue =

2-3 wks spring

6 wks August / 20 - October

3 -

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