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COSTS AND BENEFITS OF GROUP LIVING IN A RECENTLY SOCIAL UNGULATE: THE ALASKAN MOOSE

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Risk of predation is considered a major influence on foraging behavior and the evolution of social groups. We measured foraging efficiency (percentage of active time spent foraging) for Alaskan moose (*Alces alces gigas*) in various categories of predation risk in Denali National Park, Alaska, in 1991. For a particular group size, foraging efficiency declined significantly with distance from cover. Foraging selectivity by moose for diamondleaf willow (*Salix planifolia pulchra*) also decreased as distance from cover increased. Adult females accompanied by young foraged less efficiently than either females without young or adult males. Group size was positively correlated with distance from cover, which suggests that social grouping in moose is an adaptation to increased predation risk. Surprisingly, group size was inversely related to foraging efficiency because of the overriding negative effects of aggressive behavior. This finding contrasts with behavioral trends in more social ungulates, which display increased foraging efficiency with increasing group size. We suggest that the lowered foraging efficiency in Alaskan moose is a result of the recent evolution of gregarious behavior in this subspecies and that increased foraging efficiency within groups of social ungulates may be a subsequent adaptation rather than an a priori selective advantage that led to the evolution of social behavior.

Key words: Alaskan moose, *Alces alces gigas*, foraging efficiency, social behavior, group living, Denali National Park, Alaska

The evolution of sociality in ungulates is thought to have occurred largely in response to the constraint of minimizing risk of predation while obtaining food or other limited resources (Gosling, 1986; Hirth, 1977; Jarman, 1974). One common outcome of empirical studies of group living in ungulates is a strong positive relationship between group size and foraging efficiency (Alados, 1985; Berger, 1978; Hirth, 1977; Lipetz and Bekoff, 1982; and others). This result is believed to occur because ungulates in larger groups have a lower probability of being selected as prey (Hamilton, 1971), more individuals to detect predators, and a greater likelihood of confusing the predator once a pursuit begins than would solitary animals (Bertram, 1978; Harvey and Greenwood, 1978). Nonetheless, there may be limits to group living that include increased competition as well as phyloge-

netic and social constraints on the size of groups (Lott, 1991).

How then would ungulates that are comparatively intolerant of one another respond to proximal, ecological needs to live in groups? What costs might be incurred by such individuals while being social? Can sociality evolve without the benefits of the enhanced foraging efficiency exhibited by many open-land ungulates? Alaskan moose (*Alces alces gigas*) offer a unique opportunity to gain insights into these questions.

Progenitors of modern moose evolved in the boreal forests of Eurasia sometime during the early Pleistocene (Peterson, 1955). Many authors (Geist, 1987b; Guthrie, 1990a) now believe that *Cervalces* became extinct in North America prior to the arrival of the ancestor of modern *A. alces* (Guthrie, 1984), which colonized the New World as recently as 9,000 years ago (Guthrie,

1990a). These moose likely spread southward via an ice-free corridor thought to be present during the late Pleistocene (Bowyer et al., 1991). Mitochondrial DNA of subspecies of moose in North America shows no variability (Cronin, 1991), further corroborating the comparatively recent arrival of this cervid in the New World.

Alaskan moose tend to occur in extremely open areas in comparison with the boreal-forest habitats occupied by other North American subspecies (Van Ballenberghe, 1992). Alaskan moose also exhibit a variety of characteristics that ostensibly are adaptations to living in open environments, including distinctively marked pelage (Bowyer et al., 1991), large body size (Peterson, 1955), large, complex antlers (Gasaway et al., 1987; Geist, 1987a), formation of large social groups (Miquelle et al., 1992; Peek et al., 1974), and the occurrence of a harem mating system (Lott, 1991). By contrast, subspecies inhabiting the boreal forests elsewhere in North America ordinarily show strong social intolerance for conspecifics (Altmann, 1959; Geist, 1963).

To investigate factors that influence sociality in moose and to examine the influence of predation risk on foraging strategies, we tested the following predictions related to group living: 1) foraging efficiency should increase and vigilance should decrease with increasing group size; 2) group size should increase with increasing distance from cover; 3) with effects of group size held constant, foraging efficiency should decrease with increasing distance from cover; 4) female moose with young should spend more time in vigilance and less time foraging than other moose because of greater vulnerability of nursing females and young to predators.

METHODS

Study area.—We conducted research in Denali National Park in central Alaska (63°45'N, 150°W). The study area was bounded on the east by Park Headquarters and on the west by the Savage River, encompassing ca. 150 km².

Moose typically occurred at elevations of 750–1,200 m in a broad valley bounded to the north and south by steep foothills. The vegetation was typified by open, brushy tundra dominated by dwarf birch (*Betula glandulosa*), interspersed with open stands of white spruce (*Picea glauca*) with a willow (*Salix* sp.) understory.

Moose in this study area primarily were browsers; aquatic vegetation was not a significant component of their diet (Van Ballenberghe et al., 1989). Moose in the park were not hunted and accommodated readily to the presence of humans (Peek et al., 1986). Consequently, moose could be approached closely without eliciting an alert-alarm response or other apparent changes in behavior.

Denali National Park was host to a full complement of the natural predators of moose. Densities of grizzly bears (*Ursus arctos*) were unusually high in the park (Albert and Bowyer, 1991), and gray wolves (*Canis lupus*) were likewise abundant (T. Meier, pers. comm.). This unique combination of an observable population of moose inhabiting a predator-rich ecosystem provided an ideal setting for studying the behavioral responses of moose.

Definitions and sampling.—We defined a social group as at least two adult animals that appeared to be aware of one another, moved together, and showed evidence of other synchronized activities such as feeding and bedding. The maximum distance between animals and their nearest conspecific in the group was set at 50 m. In practice, it was relatively easy to categorize moose into groups because of their clumped distribution in the study area. Mixed groups contained both adult males and adult females; female groups excluded adult males, but could contain yearlings of either sex and young-of-the-year. Likewise, male groups did not have adult females present, but could include yearlings of either sex (Bowyer, 1984; Hirth, 1977), although we never observed groups with only adult males and yearling females. Pairs of adult females and young were scored as a single animal because of their propensity to move together (Altmann, 1958; Gillingham and Klein, 1992). Single animals were treated as groups of one for statistical purposes. Foraging efficiency was defined as the proportion of time spent feeding and searching for food (moving) divided by total time spent active (Berger, 1978, 1991).

We observed moose during daylight hours be-

tween mid-May and mid-September 1991. Behavioral observations after 25 August were excluded from analyses because moose began engaging in rutting behaviors. Miquelle (1990) observed that adult male moose decreased time spent feeding during rut, which would bias our measurements of foraging efficiency.

We located moose visually or by using radio-telemetry; 11 radiocollared individuals inhabited the study area. Once a group was located, a complete circuit usually was walked around these animals to verify group size and composition. For each group observed, we measured a number of variables. Cover was defined as vegetation tall enough to hide a moose from view. We visually estimated distance from cover to the nearest 10 m. Cover was further classified into two categories: open forest dominated by spruce; dense brush that was tall enough to conceal a moose. If moose were foraging in vegetation that provided 100% concealment at a distance of ca. 100 m, they were classified as foraging within cover. These two measurements (distance to cover and whether the moose was in cover) allowed us to evaluate whether occurring in cover or occupying an area adjacent to cover was more important. Animals that foraged in ravines or depressions that similarly concealed them from view were scored as foraging within topographical cover. For each observational period, the weather was recorded as sunny or cloudy. Moose might be more obvious to predators on sunny as opposed to cloudy days, because Alaskan moose possess shiny black pelage across their rumps that is obvious at a distance (Bowyer et al., 1991).

We then selected a focal animal (Altmann, 1974) at random from the group. The sex of the focal animal and whether it was accompanied by young-of-the-year or yearling also was recorded. We observed this focal animal at a distance of 20–500 m and recorded its behavior on a second-by-second basis for the duration of that observation bout. Observation bouts of <20-min duration were excluded from statistical analyses to minimize the potential of a biased measure of foraging efficiency. The mean (± 1 SD) time spent observing each focal animal was 31 ± 15 min. We terminated behavioral observations if moose appeared to be disturbed by our presence.

The population of moose inhabiting the study area was ca. 150 animals (V. Van Ballenberghe, pers. comm.); 208 sightings of groups were

made between mid-May and 25 August, of which 123 observation bouts were used in analyses of foraging behavior by moose. We never recorded data from an individual (or group) more than once during a day, but individual animals likely were observed more than once during this study. We assumed that observations of the same animal on different days under different environmental and behavioral conditions were not strongly autocorrelated (Hjeljord et al., 1990) and, thus, did not strongly bias our statistical analyses.

We classed behaviors exhibited by the focal animal into the following mutually exclusive categories. Feeding was defined as the biting or chewing of food; moving consisted of walking in a slow and continuous manner by an undisturbed animal. Alert-alarm behavior included both the alert posture with ears erect and body held still and trotting or running in response to a disturbance. Social interactions between animals (Geist, 1963) were further divided into either aggressive or maternal behavior. The latter category was observed only between mother and offspring. Standing was defined as remaining motionless with ears not held erect, while not apparently engaged in the processing of food. Grooming encompassed behavior in which a moose licked or scratched any part of its body. Bedding was defined as all behaviors engaged in while lying down, including ruminating, sleeping, alert postures, and grooming. Activity patterns that lasted <4 s were not differentiated from the previous behavior.

Foraging selectivity of moose at varying distances from cover was indexed by the twig diameter of stems of diamondleaf willow (*Salix planifolia pulchra*) at the point of browsing (Vivas and Saether, 1987). Diamondleaf willow comprised the largest single component of summer diets of moose in the park (Van Ballenberghe et al., 1989). Moose foraging more selectively took smaller bites from twigs of similar quality, because plant nutrients become more concentrated closer to the terminal bud (Hjeljord et al., 1982). Animals foraging less selectively would be expected to ingest less-digestible forage—in this case, leave behind willow stems with a larger diameter at the point where they were browsed. These data were collected in late September 1991, shortly after the moose switched from leaf-stripping to browsing, so that results would reflect accumulated foraging effort

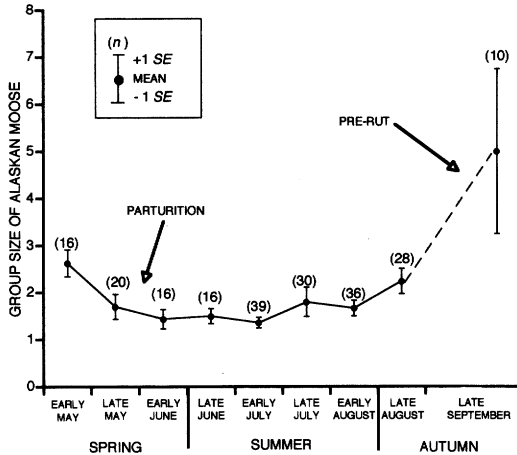


FIG. 1.—Group size of Alaskan moose from early May through late September in Denali National Park, Alaska, 1991.

through spring and summer, yet not be influenced by changes in food abundance and body condition of moose associated with the progression of winter (*sensu* Schwartz et al., 1988). Randomly located transects, sampled from 50 m inside the forest edge to 150 m into the open tundra, were used to locate willows; all browsing by moose was measured from stem diameter at point of browsing along the entire length of each transect at sites ≥ 3 m apart. We considered each discrete clump of willows as an individual; our spacing between samples reduced the possibility that clumps were clones of the same plant. Measures of diameter at point of browsing for willows were obtained by averaging at least three stems for each plant.

Statistical analyses.—Percentage data were arcsine-square root transformed for purposes of statistical analysis to meet assumptions of normality and homoskedasticity (Neter et al., 1990). We used stepwise regression to select variables that affected foraging efficiency. Mallow's C_p statistic and R^2_a (an adjusted coefficient of multiple determination) were used as criteria to select the most unbiased model (Neter et al., 1990). A multivariate analysis of variance (MANOVA) was performed on foraging efficiency and alert-alarm behavior, using independent variables selected by the stepwise procedure. We used univariate analysis of covariance to model the role of variables in accounting for the variance in foraging efficiency and alert-alarm behavior. Multiple regression equations

also were developed to model the response of foraging efficiency and alert-alarm behavior to significant independent variables. We tested effects of distance from cover on group size and selectivity using analysis of variance (ANOVA) and developed simple regression equations to model the responses of the dependent variables.

RESULTS

The size of social groups of moose varied across spring and summer; mean size of groups was higher in early May, declined during and immediately following the period of parturition in early June, and increased in late August (Fig. 1). This increase continued into late September with the approach of rut. Of 76 groups (at least two adults) of moose, 34.2% were mixed, 43.4% were female, and 22.4% were male. An additional 112 solitary moose were observed. Female groups with young composed 5.8% of the overall sample. The mean (± 1 SD) size of mixed groups (3.41 ± 1.62) was highest, followed by female groups (2.42 ± 0.66) and male groups (2.24 ± 0.44) during spring and summer.

Group size was positively related to distance from cover ($r^2 = 0.07$, $d.f. = 186$, $P < 0.004$; $\hat{Y} = 1.608 + 0.004x$). This relationship exhibited substantial variation and was driven by the propensity of moose in groups of one or two to remain quite close to cover. Indeed, 95.6% of 188 groups were ≤ 50 m from cover (Fig. 2). Larger groups (at least four moose) were seen both near to and far from cover with about equal frequency ($n = 13$) and did not tend to disband upon moving closer to cover. All observations of moose at distances > 50 m from cover were made during the latter part of May, when open, south-facing slopes were clear of snow and forested areas remained buried beneath ≤ 1.5 m of snow.

Both foraging efficiency and alert-alarm behavior (dependent variables) were affected significantly (MANOVA; $d.f. = 1,118$) by distance from cover ($F = 7.68$, $P < 0.001$), group size ($F = 6.22$, $P < 0.003$), the presence of young ($F = 5.04$, $P <$

0.008), and the sex of the focal animal ($F = 4.56, P < 0.02$). Weather, topographical cover, type of vegetative cover (spruce or brush), and presence of a yearling were not related significantly ($P > 0.10$) to these dependent variables. Likewise, multiple linear regression with foraging efficiency as the dependent variable produced a similar model ($\hat{Y} = 1.336 \pm 0.076$ group size $- 0.031$ sex of animal $- 0.208$ presence of young $- 0.001$ distance from cover; $R^2_a = 0.263, F = 10.44, d.f. = 118; P < 0.001$).

Both statistical tests indicated that sex of animal had a strong effect on foraging efficiency, with males foraging significantly more efficiently than females. Pooling group size and distance from cover, adult males showed the highest foraging efficiency ($\bar{X} \pm 1 SD = 93.5 \pm 9.9\%$), followed by adult females without young ($88.6 \pm 9.5\%$) and adult females with young ($77.3 \pm 14.3\%$).

With group size held constant, distance from cover was negatively correlated with foraging efficiency (partial $r^2 = 0.03, P < 0.03$); with distance held constant, group size also was negatively related to foraging efficiency (partial $r^2 = 0.08, P < 0.002$). Because an inverse relationship between foraging efficiency and group size was completely unexpected, we further explored this outcome with a posteriori modeling.

To test whether aggressive behavior in larger groups was responsible for the decline in foraging efficiency with increasing group size, we offered a dummy variable (aggressiveness), coded one if a focal animal engaged in aggressive behavior during an observation bout and zero if it did not, to our stepwise regression model. Aggressiveness ($F = 46.56, P < 0.001$) replaced group size ($F = 0.66, P > 0.10$) in this model that again included sex, presence of young, and distance from cover. Within groups of two or more moose, percentage of time spent in aggressive activities was positively correlated with group size ($\hat{Y} = -0.002 + 0.003x, r^2 = 0.162, P < 0.01$).

Percentage of time spent by moose in

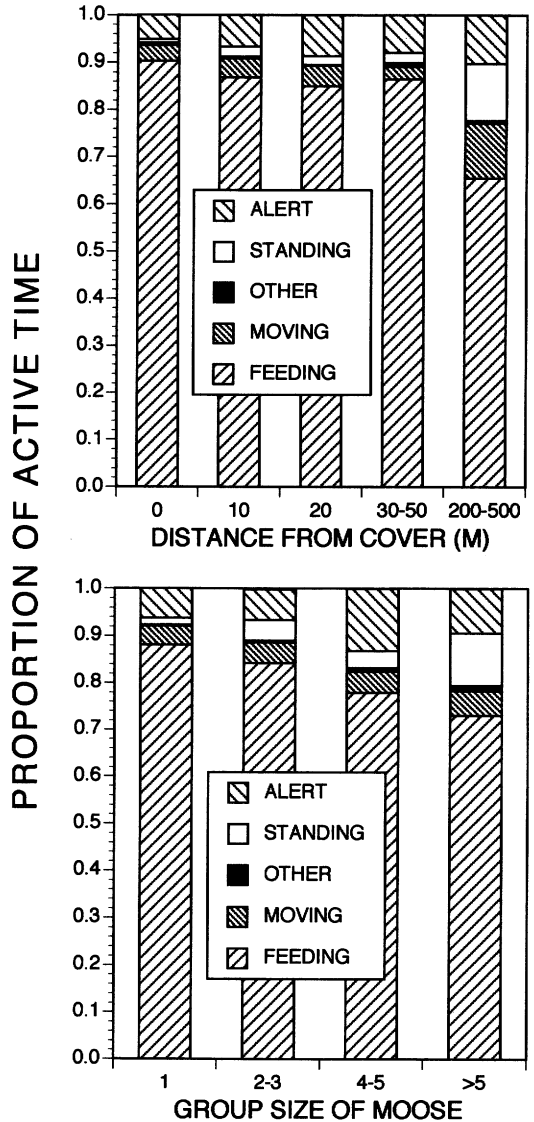


FIG. 2.—Proportion of active time spent in various behaviors by Alaskan moose in relation to distance from cover (above) and group size (below) during early May through late August in Denali National Park, Alaska, 1991.

alert-alarm behavior was affected by a similar suite of variables as was foraging efficiency (ANOVA; $d.f. = 1,118$): sex of focal animal ($F = 13.76, P < 0.001$), presence of young ($F = 9.49, P < 0.002$), whether the animal was in cover ($F = 7.21, P < 0.02$), and group size ($F = 5.13, P < 0.03$). Weather, topographical cover, type of veg-

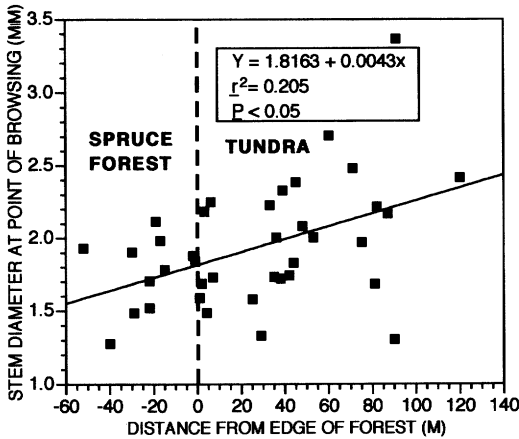


FIG. 3.—Relationship between twig diameter at point of browsing by moose on stems of diamondleaf willow and distance from the edge of the forest, Denali National Park, Alaska, September 1991. The negative values for distance indicate that moose were foraging within the spruce forest.

etative cover, presence of a yearling, and distance from cover were not significantly ($P > 0.10$) related to alert-alarm behavior.

Adult males spent less time in alert-alarm behaviors ($\bar{X} \pm 1 SD = 4.5 \pm 6.4\%$) than did females without young ($7.9 \pm 6.9\%$). Adult females with young spent more time in alert-alarm postures ($17.4 \pm 13.3\%$) than did adult females without young. Time spent in alert-alarm behavior of all moose increased significantly with group size. Indeed, the overall model for alert-alarm behavior explained substantial variation in this dependent variable ($\hat{Y} = 0.217 + 0.002$ sex of focal animal + 0.194 presence of young - 0.055 hiding cover + 0.02 group size; $R^2_a = 0.65$, $df. = 118$, $P < 0.001$). When aggressiveness was offered as a dummy independent variable, it again replaced group size in this stepwise model.

Diameter of stem at point of browsing on diamondleaf willow increased significantly with distance from the forest edge (Fig. 3). Moose took much smaller bites (< 2.3 mm) inside treeline than in the open, where they obtained generally larger bites with much greater variability (Fig. 3).

DISCUSSION

Trade-offs between foraging efficiency and predation risk have been demonstrated in aquatic insects (Sih, 1980), fishes (Milinski and Heller, 1978; Werner et al., 1983), birds (Caraco et al., 1980; Grubb and Greenwald, 1982; Martindale, 1982), and rodents (Anderson, 1986; Lima et al., 1985). In ungulates, animals vulnerable to predation are constrained to forage in relatively safe areas near cover even when forage is superior in quantity and quality elsewhere (Berger, 1991; Edwards, 1983; Festa-Bianchet, 1988). A reduction in foraging efficiency by females with young beyond that observed for females without young or for adult males strongly suggests that predation risk plays an important role in the feeding behavior of moose—young are known to experience especially high rates of predation in interior Alaska (Gasaway et al., 1992; Miquelle et al., 1992).

Females with young foraged at the greatest risk; increases in alert-alarm behavior corresponded with decreases in foraging efficiency compared to other moose. Moose that foraged far from cover did so at the cost of reduced foraging efficiency. Foraging at great distance from cover constrained moose to forage in social groups, which decreased foraging efficiency because of increased social aggression. Indeed, within a particular group size, foraging efficiency decreased the further away from cover the group foraged, as we initially hypothesized.

Moose foraged less selectively as distance from cover increased, as evidenced by their foraging on larger and more variable sizes of stems of willow further from cover (Fig. 3). This occurred even though willow stems were larger in the spruce forest than in the adjacent tundra in the area where we sampled (Molvar et al., 1993). Thus, moose likely were forced to make trade-offs between time spent foraging and predation risk.

Our findings suggest that moose engaged in two distinct patterns to reduce predation

risk: forming social groups; remaining solitary to avoid detection. Single animals and groups of two foraged almost exclusively in and near cover. In contrast, larger groups were able to exploit areas far from cover, where all moose were likely obvious to predators, regardless of group size. Because available cover for moose is greatest during summer and most scarce when deciduous brush loses its leaves, moose would not be expected to employ a hiding strategy frequently during winter. Mean group size was lowest near the time of parturition (Fig. 1), and Miquelle et al. (1992) recorded its nonrut peak in winter; Alaskan moose may form exceptionally large groups (>36) during the mating season.

We reject the hypothesis that foraging efficiency in moose is enhanced as group size increases. On the contrary, group size was negatively correlated with foraging efficiency, indicating that Alaskan moose that joined a group did so at the cost of reducing active time spent feeding. In addition, browsers that reduce the amount of available forage as they feed probably incur a cost associated with localized competition between members of a group (Jarman, 1974). Thus, moose that joined larger groups did so at a potential cost in fitness related to reduced foraging efficiency. If moose in large groups acquire greater quantities or quality of food far from cover that are not available to moose in smaller groups, then moose in large groups might be at a selective advantage. Nonetheless, the resources that are available to large groups far from cover during summer are likely inferior in quality to those inside the forest edge due to the decreased stem growth and greater fiber content of forage in areas exposed to direct sunlight (Hjeljord et al., 1990; Molvar et al., 1993). Furthermore, willows and other palatable forage appeared to be most abundant in areas typified by abundant cover. Only in early spring, when open south-facing slopes lose their snow cover before shaded areas do, is the availability and quality of food re-

sources greater far from cover than within cover. Indeed, the only time during this study when we observed moose at distances >50 m from cover was early spring. Therefore, moose foraging in large groups may have greater access to patches of abundant forage during late winter and early spring.

Nevertheless, some moose formed groups throughout the summer and into autumn, so there must be other advantages to social moose to counterbalance the cost of reduced feeding. Indeed, social groups of ungulates are thought to benefit from both their enhanced ability to detect predators and a dilution in their probability of being selected as potential prey (Dehn, 1990). The probability that an individual animal is attacked in an encounter with a predator decreases as group size increases (Hamilton, 1971). Groups of moose spend more time in surveillance for predators as group size increases because alert-alarm behavior per capita increases as group size increases. Predators frequently abandon the attack if their presence is discovered (Bowyer, 1987; Kruuk, 1972). In addition, moose that are not surprised by predators stand a much greater chance of surviving an encounter than moose that are caught unaware (Mech, 1970; Peterson, 1977). Therefore, the argument that a greater group size leads to a greater ability to detect predators and hence to greater individual survival per encounter likely holds for moose. Additionally, the possible confusion associated with a number of fleeing ungulates might decrease the success rate of a predator (Kruuk, 1972).

The most vulnerable moose in a group would be less likely to reap the benefits of group living associated with gregarious behavior (Hirth and McCullough, 1977) because the probability of being attacked by a selective predator would be high each time a predator encountered that group. For this reason, moose that are obviously more vulnerable to predation should avoid groups and instead engage in a hiding strategy. Females with young that we observed always occurred by themselves. This finding agrees

with the assessments of Peek et al. (1974) and Miquelle et al. (1992), who noted that females accompanied by young were typically solitary. On the Kenai Peninsula, Alaska, females with young that did associate with groups immediately left the group when it was disturbed, while other moose remained together (Sigman, 1977). The avoidance of social groups by vulnerable individuals provides a likely explanation for the observed decrease in group size for moose during the parturition and postparturition period (Fig. 1), given the high availability of cover during midsummer.

We demonstrated that group size was correlated with distance from cover, indicating that predation risk might increase further from cover. Predation risk from coursing predators like wolves would be expected to be greatest far from cover. Conversely, stalking predators (Armitage, 1982), such as grizzly bears, might be more effective in areas with cover; we have observed these predators using cover to conceal their approach. Thus, predation risk for moose in forested areas, while presumably lower from wolves, may be equal or greater from grizzly bears, resulting in only a small reduction in overall predation risk in and near cover. Variation in hunting styles of the major predators of moose on the study area would account for the relatively small effect that distance from cover had on foraging efficiency and alert-alarm behavior in comparison with other significant variables.

We hypothesize that the formation of social groups is a recently evolved adaptation in Alaskan moose in response to high densities of predators and relatively open terrain. Moose probably arrived in Alaska via the Bering land bridge only ca. 9,000 years ago (Guthrie, 1990a); all moose on the North American continent likely originated from a common stock (Bowyer et al., 1991; Cronin, 1991). Old World moose, which evolved in a forested environment, are typically solitary (Baskin, 1987). Other subspecies of New World moose, which also inhabit boreal forests, are similarly solitary

unless constrained by deep snows where they engage in yarding (Peterson, 1955). Even under these circumstances, moose seldom move together, synchronize activities, or engage in other behaviors that would cause them to be classified as social groups. Likewise, harem mating has been described only for Alaskan moose (Lott, 1991).

Moose arriving in Alaska encountered much more open habitat than occurred elsewhere in the range of the species. The landscape at the time of their arrival is characterized as mammoth steppe, with vast, open expanses with little cover and a rich and abundant predator fauna (Guthrie, 1990b). As succession has transformed this habitat into open boreal forest and brushy tundra, moose in interior Alaska continue to occupy open areas around treeline, with associated open tundra. In addition, the predator fauna in Alaska remains one of the richest and most abundant in the boreal north (Van Ballenberghe, 1987). These factors appear to have created a selective force for the evolution of gregariousness in Alaskan moose. Because European and New World subspecies of moose outside Alaska tend to be solitary, we suggest that adaptations of Alaskan moose are recently evolved, probably in response to high pressure of predation and open terrain.

Groups of Alaskan moose do not engage in some highly evolved behaviors exhibited by extremely gregarious species. These moose formed social groups that were loosely organized with much interchange of individuals between groups. Large groups of Alaskan moose spent more time in alert-alarm postures and foraged less efficiently because of increased aggressive interactions. Other than alert postures and taking flight, moose neither actively signaled with visual or vocal warnings when aggregated into social groups nor engaged in cooperative defense. Additionally, we never observed moose mutually grooming. We believe the lack of these and other social behaviors indicates a less-developed state

of sociality in moose than in many open-land species.

Our findings suggest that social groups can form despite lowered foraging efficiency for group members. Social groups of Alaskan moose may represent an evolutionary intermediate between a solitary existence and a highly gregarious one. If moose are typical of other social ungulates, then behaviors allowing increased foraging efficiency in these gregarious species must have evolved to cope with increased social aggression inherent to larger groups. Consequently, enhanced foraging efficiency is not a prerequisite for the evolution of sociality in ungulates.

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