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The Role of Moose in Landscape Processes: Effects of Biogeography, Population Dynamics, and Predation

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10.1 Introduction

Moose (*Alces alces*) are a dominant feature of Holarctic landscapes. Their massive size (Schladweiler and Stevens 1973, Peterson 1974, Franzmann et al. 1978, Saether 1985, Schwartz et al. 1987), herbivorous diet (Peek 1974), and wide distribution (Peterson 1955, Franzmann 1981) make them a pivotal organism in understanding the dynamics of boreal ecosystems in which they live. An increasing body of evidence suggests these large herbivores play a crucial role in determining the structure and function of the ecosystem they inhabit. Moreover, we contend that the role that moose and other large herbivores play in ecosystem processes has been neglected by many ecologists and that future advances in ecosystem science will require integrating the behavior and population ecology of large mammals into the existing paradigms of landscape ecology.

Our understanding of how moose interact with their environment, however, is inchoate. Even though there has been substantial effort expended to determine how moose and other herbivores affect their food supply and how plants are adapted to herbivory (Bryant et al. 1991), how the life-history strategies and population dynamics of moose interact in this system

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have yet to be adequately studied. The purpose of this paper is to review how moose interact with landscapes in which they live and to suggest avenues for future investigations to better address and understand these interactions.

10.2 Evolutionary Constraints and Biogeography

How moose interact with their environment is the result of a complex interplay of phylogenetic constraints, biogeography, and adaptations to living in a boreal forest ecosystem. Thus, the role of moose in the dynamics of these landscapes cannot be appreciated fully without an understanding of their evolutionary history, especially in the New World.

Moose are relatively recent colonists of North America. Modern moose (*Alces alces*) arrived in Beringia probably no earlier than about 12,000 years ago via the Bering land bridge (Guthrie 1990a, 1990b). Progenitors of modern moose once were thought to have colonized the New World much earlier, and *Alces* was believed to have evolved from *Cervacles*, which roamed both Beringia and areas south of the ice sheet during the last full glacial in North America (Peterson 1955, Kelsall and Telfer 1974). Recent morphological data, however, do not support that view (Azzaroli 1985, Churcher and Pinsof 1987, Guthrie 1990a), and it is likely that *Cervacles* was long extinct by the time *Alces alces* arrived in the New World (Guthrie 1990a, Bowyer et al. 1991).

Four subspecies of moose currently are recognized in North America: *A. a. gigas*, *A. a. andersoni*, *A. a. shirshi*, and *A. a. americana* (Peterson 1955, Franzmann 1981, Coady 1982). Although Alaskan moose (*A. a. gigas*) were hypothesized to have been separated from the other subspecies during the Wisconsin Glaciation, dates for *Alces alces* in Alaska of generally <12,000 years ago (Guthrie 1990a) make this idea unlikely. Indeed, a more probable scenario for the colonization of the New World by this large cervid involves the presence of an ice-free corridor (Burns 1990, Catto and Mandryk 1990) in western North America towards the end of the Wisconsin Glaciation (Figure 10.1). Thus, progenitors of modern moose, which were somewhat larger than present-day *A. a. gigas* (Guthrie 1984), crossed the land bridge and rapidly dispersed across North America.

Moose are well adapted to living in boreal and subarctic environments (Kelsall 1969, Kelsall and Telfer 1974, Coady 1982, Van Ballenberghe 1993). Their long legs help them cope with deep snow, and their massive size buffers them against low temperatures that characterize these landscapes. The lower extreme of the thermal-neutral zone (the temperature below which moose must expend energy beyond that necessary for basal metabolism to maintain body heat) has never been measured in moose, but lies somewhere below -30°C (Renecker and Hudson 1986). Moose are

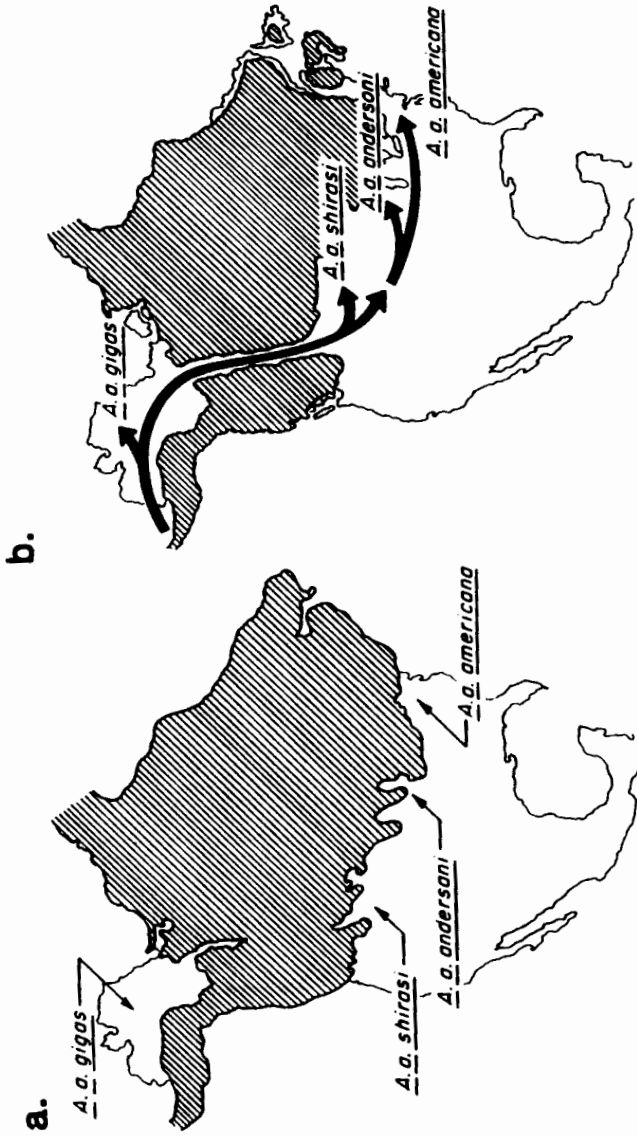


FIGURE 10.1. (a) Traditional view (Peterson 1955) of moose subspeciation in North America caused by the Wisconsin ice-sheet (shaded) isolating moose in Beringia (*A. a. gigas*) from those to the south. (b) The ice-free corridor hypothesis for subspeciation of moose in North America (from Bowyer et al. 1991).

susceptible to heat stress (Renecker and Hudson 1990), however, and this may have helped limit the southern distribution of this ungulate.

Moose are well equipped with dentition to utilize woody vegetation (browse) as the mainstay of their diet (Peterson 1955). Snow tends to cover most plants except tall shrubs and trees in boreal environments for at least one-half of each year (up to nine months in Alaska). Moose can flourish even where only browse is available year-round (Miquelle and Van Ballenberghe 1989, Van Ballenberghe et al. 1989). Nonetheless, moose also are adapted to foraging on aquatic plants during summer, ostensibly to obtain sodium (Belovsky and Jordan 1981).

Despite filling a similar ecological niche, the subspecies of moose in North America are quite different in a number of characteristics. Alaskan moose are distinct in their larger body size (Franzmann 1981), more massive antlers with a "butterfly" configuration (Gasaway et al. 1987), and in their conspicuously marked pledge (Bowyer et al. 1991) than are other subspecies. One of the smaller and most darkly colored subspecies in North America is *A. a. americana*, which has the most easterly distribution. The other subspecies are intermediate in external features—these observations, along with other differences in cranial morphometrics among the subspecies (Peterson 1955), support the pattern of subspeciation depicted in Figure 10.1. Moreover, Alaskan moose differ from other North American *Alces* in one other fundamental way—they exhibit a different mating system.

Alaskan moose often occur in more open habitats than other subspecies (Molvar and Bowyer 1994), tend to occur in larger groups (Peek et al. 1974), and exhibit a harem mating system (Molvar and Bowyer 1994) similar to that of North American elk (*Cervus elaphus*; Bowyer 1981). Other subspecies of moose in North America possess a tending-bond system of mating more typical of North American deer (*Odocoileus*; Hirth 1977, Bowyer 1986). This collection of distributional, historic, morphological, and behavioral data suggests that moose have undergone extremely rapid evolution since their arrival in the New World not much more than 10,000 years ago. These data further indicate that the subspecies have, to some extent, adapted to regional areas of the boreal environments they inhabit. Similarly, woody plants would be expected to have coevolved deterrents to browsers (Bryant et al. 1989), given strong selection, sufficient time, and the necessary genetic variability.

Consequently, plant-animal interactions must be viewed in both an evolutionary and biogeographic framework. For instance, much of the area where the boreal forest is distributed today was covered by ice when moose colonized the New World. The exception was the glacial refugium in Beringia (Kurtén and Anderson 1980). Thus, moose in eastern North America have interacted with the trees and shrubs on which they feed for a comparatively short period of time, whereas large herbivores, including some browsers, have coevolved with plants in Beringia for millennia

(Guthrie 1990b). Presumed differences in the defense systems of plants against herbivores, especially secondary compounds, between Alaska and eastern North America, then, should be evident. Bryant, Tahvaninen et al. (1989), and Bryant, Swihart et al. (1994) have documented this pattern for snowshoe hares (*Lepus americana*) and birch (*Betula*), and we hypothesize an analogous situation for moose and their forage.

Moose in eastern North America consume large amounts of conifers in winter. For instance, Ludewig and Bowyer (1985) reported that winter diets of moose in Maine were composed of 73% conifers and dominated by balsam fir (*Abies balsamea*), but also included white spruce (*Picea glauca*). Diets of moose in Alaska, however, contain little white spruce or other conifers in any season (Peek 1974, Oldemeyer 1983, Risenhoover 1989, Van Ballenberghe et al. 1989). Moose inhabiting the midcontinent do consume conifers in winter (mostly *Abies balsamea*), but select hardwoods where the appropriate species are available (Peek 1974). Thus, white spruce, which dominates better drained sites in the northwestern boreal forest, is little affected by foraging moose, whereas this same species (and other conifers as well) are likely influenced by herbivory by moose and white-tailed deer (*Odocoileus virginianus*; Ludewig and Bowyer 1985) in the east. We hypothesize that such dietary differences relate to the defense of these plants via secondary compounds, as Bryant, Tahvaninen et al. (1989), and Bryant, Swihart et al. (1994) documented for hares and birch. Such biogeographic effects have been largely overlooked in studies of plant-animal interactions and mostly ignored in studies of ecosystem structure and function. This is an area clearly in need of additional research to help improve our understanding of variation in the life-history parameters of moose and why they vary across landscapes.

Moose have the ability, under certain conditions, to modify strongly the environments in which they live. Several important studies (Pastor, Naiman et al. 1988, Pastor and Naiman 1992, Pastor, Dewey et al. 1993) demonstrated that herbivory by moose altered patterns of plant succession in the midwestern United States. In that system, foraging by moose presumably caused a shift in species composition from hardwoods to conifers (Risenhoover and Maass 1987). Exclosures that prevented feeding by moose were dominated by hardwoods that were preferred as forage, whereas areas where moose were abundant had mostly conifers (Pastor et al. 1993). This change in species composition was accompanied by lower rates of nutrient cycling in conifer-dominated habitats (Pastor et al. 1993) and likely affected an array of other invertebrates and vertebrates that rely on hardwoods, conifers, or edge for their principal habitats. But, contrary to studies of "herbivore optimization" elsewhere (McNaughton 1984, 1985, 1988, Ruess and McNaughton 1987, Frank and McNaughton 1993), moose in Pastor's system appeared to affect rates of nutrient cycling negatively (Pastor et al. 1993). This outcome needs to be viewed in a broad context. Moose in Pastor's system eat conifers, and the availability of palatable

evergreen forage may help keep population densities of moose high enough to alter plant succession. Shifts in succession from hardwoods to conifers may have played a more important role in affecting nutrient cycling than fecal and urine inputs from moose. Thus, plant-animal interactions are not independent of the dynamics of either plant or animal populations. This is a theme to which we will return later. For now, it is sufficient to note that outcomes from studies of the role of large mammals on ecosystem process represent a single point in the dynamics of both plants and animals nested within a geographic setting in which both have evolved. Moreover, primary productivity is strongly correlated with biodiversity in grassland ecosystems (Tilman et al. 1996), and we suspect a similar relationship exists in the boreal forest.

Studies of moose in Alaska in plant communities that are not undergoing rapid succession (treeline stands of white spruce with willow [*Salix*] understories) strongly suggest that moose have a positive effect on rates of nutrient cycling, presumably in part because of the deposition of urine and fecal material (Molvar et al. 1993). Rates of nitrogen mineralization were higher in an area of relatively high density ($5.60 \mu\text{g} \frac{\text{N}}{\text{g soil}} \times \frac{-1}{\text{day}}$) of moose compared with a low-density ($0.48 \mu\text{g} \frac{\text{N}}{\text{g soil}} \times \frac{-1}{\text{day}}$) area (Molvar et al. 1993). We caution, however, that even in the high-density area, moose were regulated by predators (Gasaway et al. 1992, Van Ballenberghe and Ballard 1994) and that a negative effect likely would have been obtained at very high densities of moose. The point we wish to emphasize is that future research needs to disentangle the effects of plant succession from herbivore optimization (Hilbert et al. 1981, Hik and Jefferies 1990) if we are to gain a more complete understanding of the role of large mammals in ecosystem processes.

Finally, we believe it is essential to begin thinking about large herbivores as more than merely consumers of plants and conveyors of urine and feces. Their interactions with their environment are complex and go far beyond these outcomes. Obvious effects, such as trampling of vegetation (Packer 1953, Pegau 1970) or compaction of soil (Packer 1963) by large mammals have received too little attention. Less well-known behaviors such as the digging of rutting pits by moose (Miquelle 1991) or their scent marking of trees (Bowyer et al. 1994, Figure 10.2) may have considerable effects on the landscapes moose inhabit, but have yet to be considered in studies of ecosystem dynamics. Indeed, selecting specific trees for scent marking (Figure 10.3) may have effects on stand structure via differential mortality of young trees (Bowyer et al. 1994).

We reiterate that studies of ecosystem processes need to be viewed with respect to both the evolutionary history and biogeography of plants and animals. The scale for understanding such processes is continental (or larger), and future insights into such landscape dynamics will likely hinge on our ability to incorporate these notions into our research.



FIGURE 10.2. Female (left) and male Alaskan moose scent marking (rubbing) poll-sized white spruce (from Bowyer et al. 1994).

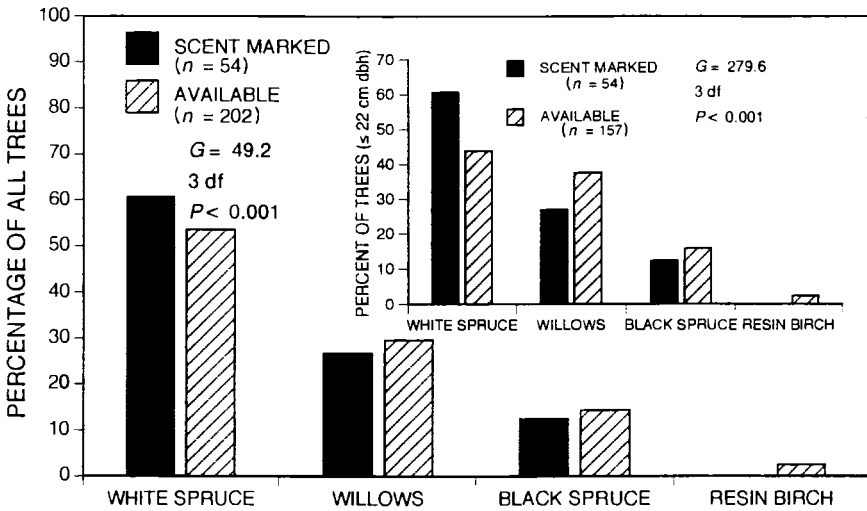


FIGURE 10.3. Selection of trees by Alaskan moose for scent marking (from Bowyer et al. 1994).

10.3 Population Dynamics and Sexual Segregation

Fertilization of plants via inputs of herbivore feces and urine can enhance the quality of browse (McKendrick et al. 1980, Day and Detling 1990). Large mammalian herbivores tend to defecate at feeding sites (Etchberger et al. 1988), and nitrogen in their feces increases with forage quality (Leslie and Starkey 1985, Hodgman and Bowyer 1986), at least temporarily resulting in a positive feedback. Heavy browsing, however, can have negative effects on quality of plants to herbivores including shorter, stout stems and inducing defense systems that lower the palatability of forage (Bryant 1981, Bryant, Chapin et al. 1983, Bryant and Chapin 1986, Bryant, Reichardt et al. 1992). The literature on this topic is large, complex, and far beyond the scope of this paper. Nonetheless, the density of ungulates and how they are distributed across the landscape will play a critical role in plant-animal interactions. Our goal is to discuss the role of ungulate population dynamics in these interactions and to suggest ways in which incorporating population dynamics can provide a more complete understanding of this process. Furthermore, we hope to evaluate how this process might vary across landscapes.

Populations of ungulates typically are regulated by density-dependent mechanisms (McCullough 1979). This concept does not exclude the roles of predation or severe weather in limiting populations of large herbivores. Rather, as McCullough (1979) noted, if predators or winter conditions fail to limit such populations, then intraspecific competition for food will do so. Thus, density-dependent effects are mostly mediated by nutrition (Simkin 1974, Saether and Haagenrud 1983, Schwartz and Hundertmark 1993). At the level of the population, such effects typically involve declines in physical condition, ovulation rates, litter size, and survivorship of young or even adults with increasing population size (McCullough 1979). Likewise, increases in age at first reproduction, birth intervals, and hence, mean generation time typically accompany increasing populations as they approach K .

Species of large herbivores differ in their responses to density, but there is little question that density dependence plays an important role in their dynamics; this observation holds for moose (Edwards and Ritchey 1958, Pimlott, 1959, 1961, Coady 1982). Because the physical condition of moose is a function of their food supply, and food supply is related to the number of animals competing for this forage, the population dynamics of this herbivore must play a key role in plant-animal interactions, and by extension, to landscape processes. Such a spatially explicit approach has been used to understand the dynamics of animal populations (Pimm and Gilpin 1989) but has yet to be incorporated into models of plant-animal interactions. The herbivore-optimization model (Hik and Jefferies 1990) clearly notes the importance of animal abundance, but does not yet incorporate the dynamics of herbivore populations. Clearly, both spatial and temporal models are required to fully understand how large mammals affect ecosystem processes.

The plant communities inhabited by moose are inherently patchy (Miquelle et al. 1992). Thus, the density of moose is not distributed evenly across the landscape because moose select those patches of habitat in which they are most likely to meet their nutritional or other needs. For instance, some populations of moose are migratory (Le Resche 1974, Van Ballenberghe 1977, Sweanor and Sandegren 1988, Histøl and Hjeljord 1993), creating patchy distributions of these large mammals across the landscape on a seasonal basis. Obviously, severe weather can have adverse effects on populations of moose and other large mammals (Coady 1974, Peterson and Allen 1974, Mech et al. 1987). Moreover, deep snow impedes movements, can cause moose to exhaust energy reserves in winter, and has the potential to limit populations. Snow also can alter the distribution of moose across the landscape and thereby influence plant-animal interactions and, hence, the effects of herbivore optimization. In addition, snow may protect low-growing shrubs from herbivory during winter, even when the density of moose is high. Moose in such a population would likely be distributed in areas with shallower snow, where heavy browsing might initiate strong negative feedbacks between moose and their forage at those sites where moose concentrated. A low-density population of moose, however, might interact far differently with their forage under identical conditions of snow cover. For example, levels of browsing in an area with lower snow depths might result in positive nutritional feedbacks on the population of moose. Similarly, variability in snow cover across the landscape in the same year would result in different levels of browsing and thereby spatial variation in plant-animal interactions, even in homogenous vegetation types. Effects of slope steepness, aspect, ruggedness, and a host of other factors would have consequences even with other variables held constant. It is a daunting prospect to consider just the effects of snowfall in the dynamics of moose and the plants on which they feed. Year-to-year variation in snow depth and structure are likely to have profound effects on moose populations and the manner in which moose use patches of habitat across the landscape. Both snow and population density of moose have consequences on the ecosystem dynamics of such areas.

We see an opportunity to wed modern global positioning (GPS; Moen et al. 1996) and geographic information systems (GIS; Nicholson and Mather 1996) with remote sensing to understand better how moose distribute themselves across the landscape under a variety of environmental conditions. A better understanding of the dynamics of landscapes also will require the integration of models of herbivore optimization with the dynamics of moose and plant populations. We believe this is an essential first step for future research in this area.

Perhaps no other life-history characteristic affects the distribution of moose upon the landscape more than the segregation of the sexes outside of rut. Sexual segregation is a phenomenon common to most ungulates (Bowyer 1984, Bowyer et al. 1996, Main et al. 1996, Bleich et al. 1997), even

if the causes of segregation remain uncertain in some species. What is certain is that sexual segregation creates a patchy distribution of moose for much of the year (Miquelle et al. 1992; Figure 10.4), and that this variation in local density has important implications for understanding plant-herbivore interactions. For instance, note the concentration of female groups in the East End and male groups around Jenney Creek in Denali National Park, ALASKA, during winter and at calving; moreover, note that

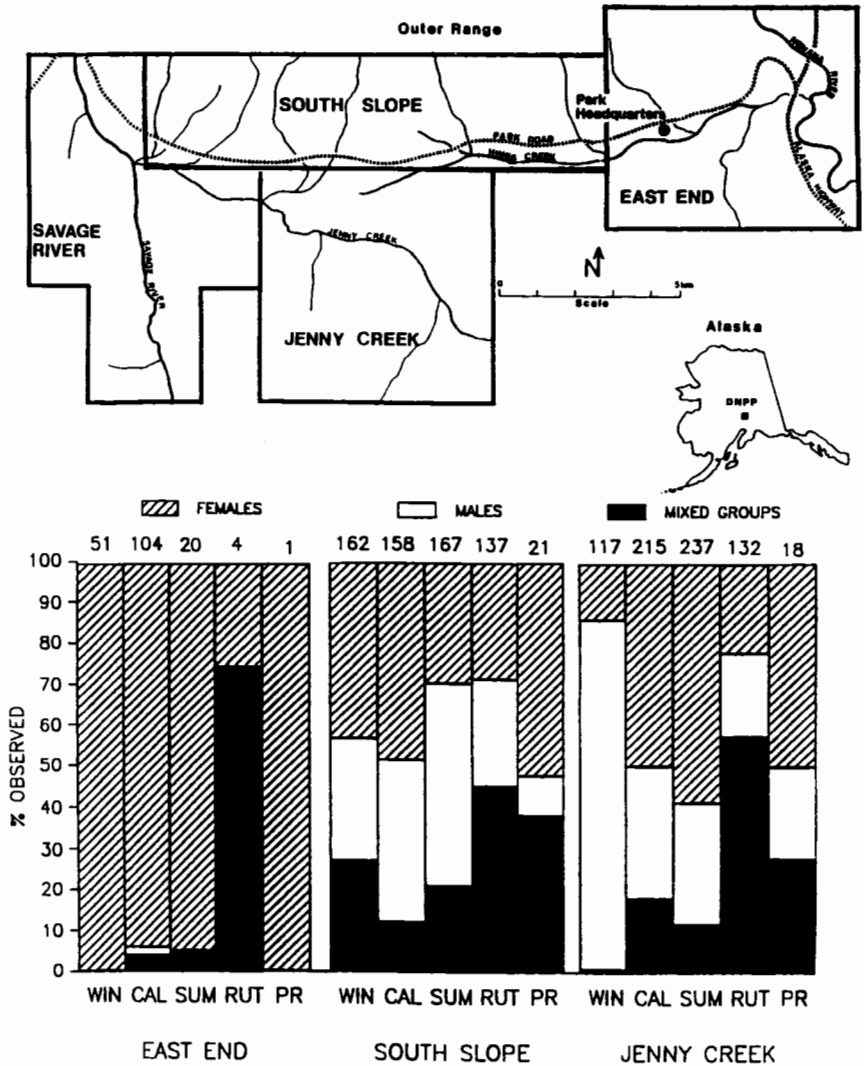


FIGURE 10.4. Spatial segregation of male, female, and mixed-sexed groups of moose through the seasons (winter, calving, summer, rut, and post-rut) at Denali National Park and Preserve, Alaska (from Miquelle et al. 1992).

these areas are generally >5 km apart (Figure 10.4). Males and females may select habitats or forage differentially while the sexes are segregated (Miquelle et al. 1992). Thus, a model of foraging dynamics that fails to consider the needs of both sexes is likely to fall short of predicting reality. Additionally, the scale at which sexual segregation is evaluated is likely to have a profound effect upon our interpretation of this process (Bowyer et al. 1996). Because adult sex ratios often favor females in ungulates (Peterson 1955) and males often have larger home ranges than do females (Hundertmark, in press), males typically occur at low densities when segregated compared with females. These life-history patterns of moose and other ungulates, when considered in relation to the patchy distributions of habitat and forage, determine levels of foraging in particular areas and the response of plants to these levels of herbivory. We suggest that the extreme sexual dimorphism exhibited by ungulates (Ralls 1977) and the differing life-history strategies of the sexes (Main et al. 1996) have profound effects on ecosystem processes and on interpreting hypotheses concerning herbivore optimization. Further advances in these and related plant-herbivore studies will require a more nearly complete understanding of how and why the sexes of ungulates segregate.

The scale over which moose segregate sexually is moderate (Figure 10.4) compared with other ungulates (Bowyer et al. 1996). Nonetheless, selecting the scale at which to measure segregation may be problematical (Bowyer et al. 1996). For instance, by varying the size of the sampling unit or the time interval over which data are collected, it is possible to obtain almost any degree of sexual segregation (Figure 10.5). The effects of scale in understanding this and other phenomena has received too little attention in the literature. Moreover, spatial separation of the sexes causes localized differences in the population, with males typically occurring at lower density (Bowyer 1984), with implications for plant-herbivore interactions. Similar problems exist in understanding how moose "decide" to use a particular patch of habitat, plants within that patch, or stems of an individual plant. A vast body of literature concerns models that address questions related to the use of patches and their varying quality (Stephens and Krebs 1986). Far less attention, however, has been directed toward identifying the scale at which moose (or other large mammals) make decisions. The question of what scale is relevant to a moose is likely to change with the nature of the question being asked. For example, a relatively small patch might be sufficient to meet the short-term needs of a female and her neonate, but be far too small to support her nutritional requirements for lactation later in summer. Nevertheless, answering such conundrums may be necessary to interpret fully the role of moose in ecosystem processes. Failure to select the correct scale can lead to the misinterpretation of data (Morris 1987, Wiens 1989, Powell 1994, Bowyer et al. 1996).

Although our knowledge of the seasonal dynamics of moose home ranges will be improved by recent advances in methodology (Worton 1989, 1995,

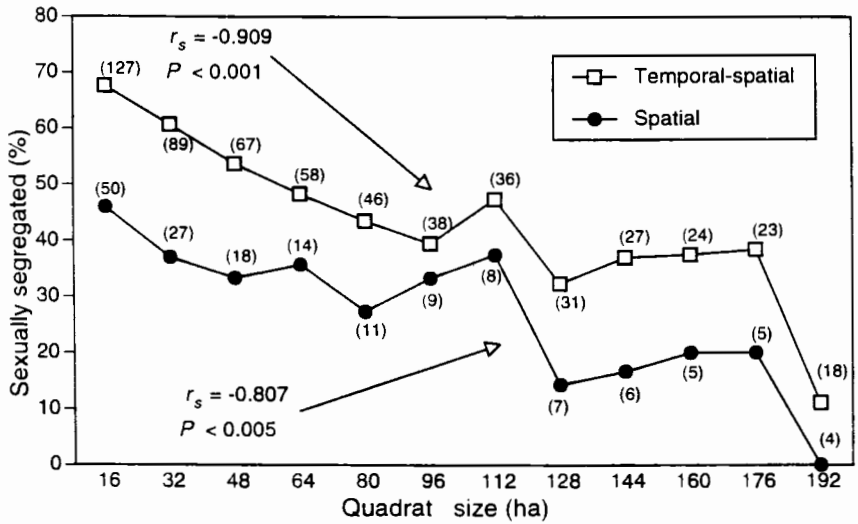


FIGURE 10.5. Reduction in degree of sexual segregation in black-tailed deer with increasing quadrat size (from Bowyer et al. 1996). The spatial scale is for five weeks combined, whereas the temporal-spatial scale is analyzed by week. Similar problems of scale likely cloud interpretation of spatial separation of the sexes for most ungulates.

Kie et al. 1996), we suspect it will be sometime before those studying foraging dynamics, behavioral ecology, and ecosystem processes can integrate their views to produce a more cohesive theory; much exciting work remains to be accomplished (see Ritchie, this volume).

10.4 Use of Patches Across the Landscape

Despite the aforementioned problems associated with patch size, scale, and their importance in understanding how moose are distributed upon the landscape, some generalizations are possible. First, it is obvious that a patch must be sufficiently large to support the needs of moose for forage for there to be more than transitory use of that patch. Moreover, a moose must have a sufficient number of such patches within its home range to meet its dietary needs for survival and successful reproduction (McNab 1963, Ford 1983, Swihart et al. 1988), if a moose population is to persist. The sex and age class of moose also affect the size of home ranges (Cederlund and Sand 1994). Even this simplistic representation of the importance of patches to moose, however, offers challenges to our understanding of landscape ecology. For instance, would the value of such patches to moose be similar at high and low population density? Clearly, per capita availability of forage to moose within a patch would decline with increasing population size, but the rela-

tive contributions of abundance and quality of forage in relation to this process remain uncertain. Would the correct outcome be predicted by optimization models (i.e., give-up times on foraging within a depleted patch), would moose switch to smaller patches, or move to patches of suboptimal habitat (*sensu* Fretwell 1972)? There is a vast body of theory, but little empirical evidence.

How might interactions between the biomass of forage available to moose and its quality effect population dynamics of herbivores (White 1983)? Large herbivores likely alter the forage they consume in several important ways. First, browsing reduces the number of growing points so that regrowth of remaining stems is greater than for plants that were unbrowsed. Likewise, browsing releases stems from apical dominance and, in consequence, lateral stems grow longer (Bergstrom and Danell 1987, Molvar et al. 1993). Indeed, moose may obtain larger stems by repeatedly browsing them in subsequent years, thereby reducing the effort necessary to meet their nutritional needs (Vivas et al. 1991). For instance, dry biomass of willow stems that had not been browsed for two years was about 0.6 g per leader of current annual growth; stems browsed in the previous winter, but not the current one, had 0.8 g of available growth. Current annual growth of stems browsed in both winters, however, was nearly 4.0 g (Bowyer and Bowyer, 1997). Browsing also may alter the carbon-nutrient balance of the plant, thereby reducing secondary defense compounds, at least at moderate levels of herbivory (Bryant et al. 1991). Litter from browsed plants decomposes more rapidly than litter from unbrowsed plants (Flanagan and Van Cleve 1983), thereby increasing nutrient availability to the browsed plant. Finally, large herbivores may stimulate plant growth through inputs of urine and feces that fertilize the plant (McKendrick et al. 1980). The net effect is plants with longer stems and larger leaves that are more palatable to moose (Molvar et al. 1993). So, at the same time increasing populations of moose reduce per capita availability of stems on which to feed, they improve the quality of forage over a wide range of population densities.

Within a patch, then, there is likely variation in the availability and quality of plants for moose. How such variation relates to the use of that patch by moose or in relation to other patches is largely unknown. Moreover, how trade-offs between biomass and quality are likely to alter the importance of a patch to moose requires more study.

We have already discussed the complicating effects of snow cover on the distribution of moose upon the landscape and will not reiterate it here. Imagine, however, how a patchy distribution of snow superimposed over an environment with variation in biomass and quality of forage might affect the selection of a patch (or the plants within it) by moose.

There are many other site-specific variables that likely affect the quality of forage for moose (e.g., slope, aspect, litter depth, soil moisture) that we acknowledge but will not expand upon here. One additional complication we will address, however, is shading. Willows growing in sunny areas had

higher cell-wall contents than those growing in the shade (Molvar et al. 1993). Indeed, both nitrogen content and digestibility were lower for plants growing in the sun compared with their counterparts in the shade (Molvar et al. 1993). These outcomes suggest that plants growing in direct sunlight may be of less value to moose than shaded ones; Hjeljord et al. (1990) reached similar conclusions. Bryant and Chapin (1986) suggested that such differences occurred because growth of plants in sunny areas outstripped the availability of nutrients in the soil, as a result of higher rates of photosynthesis and subsequent carbon fixation. This process also affects carbon-nutrient balance within the plant and may result in more carbon-based secondary compounds. What is less obvious, however, is that population density of moose has a strong interaction with the effects of shading. For instance, Molvar et al. (1993) reported that when level of browsing was treated as a covariate, leaves and stems were larger in the sun than in the shade where moose density was high, but smaller where moose density was low. A likely explanation is that increased levels of nutrients from urine and feces of moose resulted in greater growth for plants in the sun on the high-density area. Presumably, differences in forage quantity and quality from these interactions would effect the distribution of moose within and among patches. In this instance, moose density (via inputs of urine and feces) may have offset the detrimental effects of sunlight on the palatability of forage (Molvar et al. 1993).

10.5 Predation

It is naive to believe that only forage quantity and quality will influence the distribution and density of moose. There is clear evidence that large mammalian predators (e.g., wolves, *Canis lupus*, and bears, *Ursus*) are capable of holding moose populations at low levels (Gasaway, Stephenson et al. 1983, Gasaway, Boertje et al. 1992, Van Ballenberghe 1987, Messier 1994, Van Ballenberghe and Ballard 1994). Where populations of moose are held at relatively low density (Van Ballenberghe and Ballard 1994), negative feedbacks from the overbrowsing of range are unlikely. In many areas of Alaska, then, a natural and abundant fauna of predators plays a major role in the functioning of ecosystem processes. Additionally, McLaren and Peterson (1994) suggested the "top-down" regulation of the Isle Royale ecosystem, whereby wolves limit the number of moose, which in turn affects rates of growth for balsam fir. There is debate over the best model to explain population regulation of moose by their predators, but there is little question that moose are held at low densities by predators for long periods of time (Gasaway et al. 1992, Van Ballenberghe 1987, Van Ballenberghe and Ballard 1994). We suggest that the extirpation of wolves and brown bears from much of their previous range holds the potential to bias our understanding of ecosystem dynamics in many environments and that mul-

tiple ungulate prey and plants with well-developed secondary compounds for defense against large herbivores might alter our interpretation of landscape processes in these systems.

Predators do more than help to determine the number of prey. Moose respond in several important ways to the risk of predation. Ungulates typically respond to predation by increasing group size (Hirth 1977). In general, large groups are less vulnerable to attack because of more ears, noses, and eyes with which to detect a predator or the alarm signal of a conspecific (Bowyer et al. 1991). Moreover, the more animals in a group, the lower the probability of an individual being selected as prey (*sensu* Hamilton's [1971] selfish herd). Thus, risk of predation holds the potential to alter group size. Indeed, there are numerous studies of large herbivores, including moose (Molvar and Bowyer 1994) that document an increase in group size with increasing distance from cover (a measure of predation risk). Thus, ungulates foraging in more risky habitats would be expected to form larger groups. Such groups would concentrate foraging activities in specific areas as well as the deposition of urine and feces. These concentrated effects of herbivory are no doubt much different from those of the same number of moose spread more evenly through a patch or across the landscape. Group size, however, is not a component of any foraging model with which we are familiar. Moreover, this information will be difficult to obtain via telemetry and remote sensing unless all animals are telemetered.

Group size and distance from cover also affect the amount of time an animal spends foraging and the selectivity with which it feeds (Edwards 1983; Figure 10.6). Molvar and Bowyer (1994) documented that as moose ventured farther from escape cover and encountered smaller stems, the bites they took were larger and more variable, as evidenced from the willows on which they fed (Figure 10.7). Likewise, moose in the open lowered their feeding efficiency (i.e., spent less of their active time feeding; Figure 10.6). There may be some areas that individuals do not exploit that are of high quality because risk of predation is too great. For instance, females with young use habitats differently and spend more time surveying for predators than do females without young (Miquelle et al. 1992, Molvar and Bowyer 1994). Variables such as group size are seldom considered in studies of ecosystem dynamics, yet have the potential to be major determinants in the patchy distribution of large herbivores across the landscape.

10.6 Conclusions

We foresee major breakthroughs in our understand of landscape ecology via studies of plant-animal interactions. We suggest that the time is at hand to meld new technology with a more integrated approach to understanding

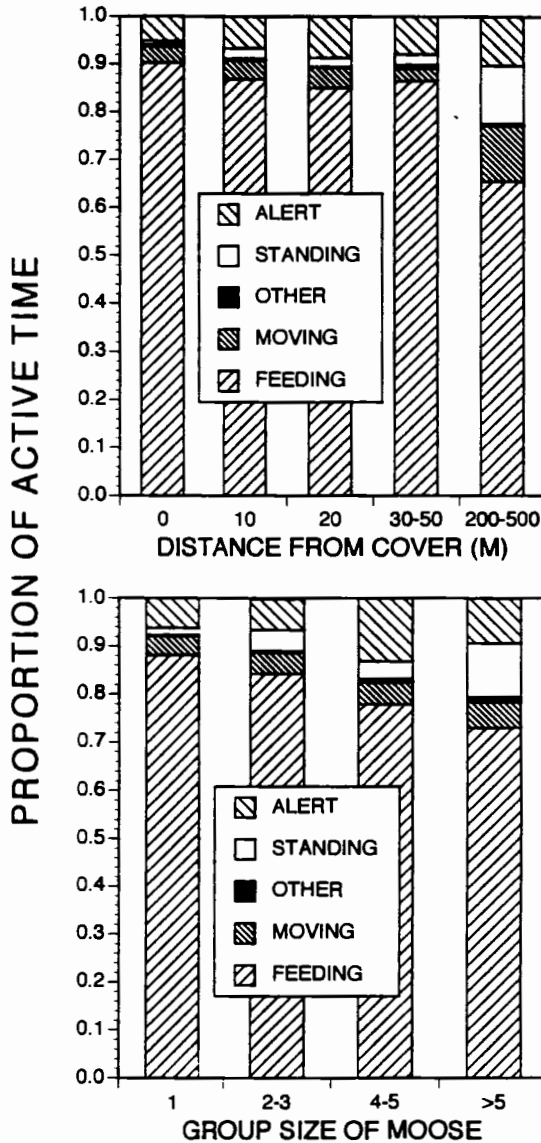


FIGURE 10.6. Proportion of active time spent in various behaviors by Alaskan moose relative to distance from escape cover (above) and group size (below) (from Molvar and Bowyer 1994).

theories related to herbivore optimization, population dynamics of herbivores, the effects of predation, and even their biogeography and evolution. We recognize, however, that this is a tall order and will not be accomplished easily.

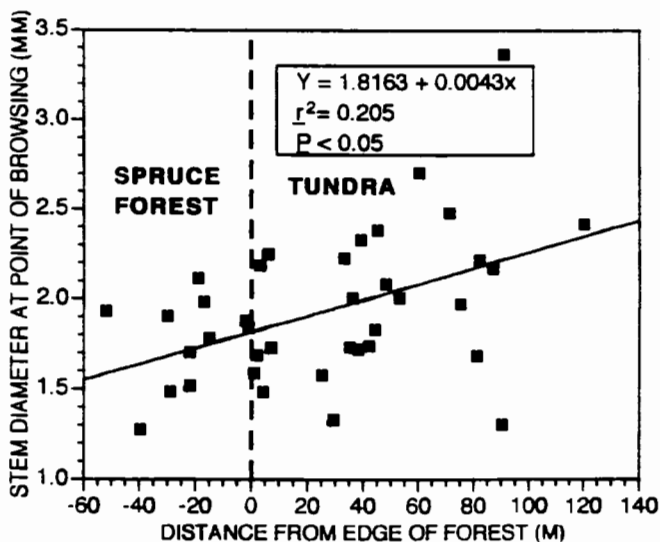


FIGURE 10.7. Relationship between twig diameter at point of browsing by moose on stems of diamondleaf willow and distance from the edge of the forest. Negative values indicate moose were foraging within the forest (from Molvar and Bowyer 1994).

We applaud ongoing attempts to model the interaction of large herbivores with the landscapes in which they live. We caution only that realistic constraints such as differences in sex and age play a role in such efforts and that the population dynamics of the animals be given the same level of attention as the cycling of their nutrients.

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