

FIFTY YEARS OF FOOD AND FORAGING IN MOOSE: LESSONS IN ECOLOGY FROM A MODEL HERBIVORE

Lisa A. Shipley

Department of Natural Resource Sciences, Washington State University, Pullman, Washington 99164-6410, USA

ABSTRACT: For more than half a century, biologists have intensively studied food habits and foraging behavior of moose (*Alces alces*) across their circumpolar range. This focus stems, in part, from the economic, recreational, and ecosystem values of moose, and because they are relatively easy to observe. As a result of this research effort and the relatively simple and intact ecosystems in which they often reside, moose have emerged as a model herbivore through which many key ecological questions have been examined. First, dietary specialization has traditionally been defined solely based on a narrow, realized diet (e.g., obtaining >60% of its diet from 1 plant genus). This definition has not been particularly useful in understanding herbivore adaptations because >99% of mammalian herbivores are thus classified as generalists. Although moose consume a variety of browses across their range, many populations consume 50-99% of their diets from 1 genus (e.g., *Salix*). Like obligatory herbivores, moose have demonstrated adaptations to the chemistry and morphology of their nearly monospecific diets, which precludes them from eating large amounts of grass and many forbs. New classifications for dietary niche suggest that moose fit on the continuum between facultative specialists and facultative generalists. Second, moose have been the subject of early and influential models predicting foraging behavior based on the tradeoffs between quality and quantity in plants. Subsequent models have predicted the size of stems selected by moose based on the tradeoffs between fast harvesting (large twigs) and quick digestion (small twigs). Because of their size, moose require many hours to harvest food, often selecting large bites as browse density declines. Finally, long-term monitoring of moose populations has provided evidence of how populations and communities are regulated. Low reproductive rates and long-term population trends shaped by moose density and forage availability on Isle Royale suggest a strong bottom-up effect on moose populations. Empirical data and simulation models suggest that moose may shape their own forage supply, influencing their community and their own populations, especially when large predators are scarce. Likewise, predation is the primary factor affecting calf survival and thus moose populations in Alaska, demonstrating the important role of top-down factors. Moose will continue to provide a model for examining ecological questions such as tolerances for plant chemistry, what governs animal movements over landscapes, and reciprocal interactions between predation and reproduction.

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For more than half a century, biologists have intensively studied food habits, foraging behavior, and nutrition of moose (*Alces alces*) (Table 1, Fig. 1-3, reviews by Gasaway and Coady 1974 and Schwartz 1992). This large body of research has arisen both because moose are of global interest occupying a circumpolar range spanning northern parts of North

America, Europe, and Asia, and their large size, magnificent antlers, and fascinating behavior make them valuable for consumptive and non-consumptive recreation and subsistence (Storaas et al. 2001, Timmerman and Rodgers 2005.) For example, a recent economic analysis estimated the annual harvest value of moose in Alaska alone at nearly \$364 million

Table 1. Time spent foraging and ruminating by moose.

Location	Season	Feeding (hr)	Ruminating (hr)	Reference
Central Alberta	Winter	9.8	11	Renecker and Hudson 1989
Centra Alberta	Summer	10.3	6.5	Renecker and Hudson 1989
Denali National Park, Alaska	Winter	4.8	9.6	Risenhoover 1986
Denali National Park, Alaska	Summer	7.2	7.2	Van Ballenberghe and Miquelle 1990
Rocky Mountain National Park, Colorado	Summer	8.9	9.1	Dungan et al. 2010

and viewing value at \$62 million (Northern Economics, Inc. 2006). Besides research aimed directly at better management of wild and captive populations of moose, moose have emerged in the ecological literature as a model herbivore through which many key broad ecological processes have been examined. Here, I will review examples from the past 50 years of how and why moose have been used to test and demonstrate ecological theory related to food and foraging. Specifically I will highlight how research with moose has contributed to 3 dichotomies in herbivore ecology: 1) how to define niche breadth relative to specialist and generalist herbivores, 2) how herbivores trade off food quality and quantity when selecting diets, and 3) the roles of top-down and bottom-up processes in regulating populations.

DIETARY NICHE:

SPECIALIST OR GENERALIST?

The question of what governs the dietary niche has been the focus of community ecology for decades (e.g., Hutchinson 1957, Levins 1962, Futuyma and Moreno 1988, Kawachi 1994, Julliard et al. 2006). Many articles have examined the question of why some herbivores consume a diverse diet consisting of many plant species, whereas others consume a very narrow diet (e.g., Freeland and Janzen 1974, Westoby 1978, Sorensen and Dearing 2003). Because dietary specialization is so common in herbivorous insects, specialists have been traditionally defined as an animal consuming only 1 plant species (i.e., monophagous, Crawley 1983). However, dietary specialization is rare in vertebrate

herbivores, thus Dearing et al. (2000) relaxed the definition of a specialist for herbivores to include animals consuming at least 60% of their diet from 1 plant genus. Regardless, <1% of mammalian herbivores can be classified as a specialist using this definition (Dearing et al. 2000, Shipley et al. 2009), which limits its usefulness for understanding dietary strategies in most herbivores.

Moose provide a good example of the difficulties in assigning herbivores to a specialist-generalist category. In the literature they have been referred to as both a “generalist herbivore” (Belovsky 1978) and a “specialist browser” (Hagerman and Robbins 1993). Across much of the moose’s range in western North America, summer and winter diets consist of 75-91% willow (*Salix* spp., Fig. 1a-e). Likewise, diets in parts of eastern North America and Sweden consist of primarily of 1 species/genus specific to location (Fig. 2a-d). In contrast, in other areas moose consume a more diverse diet in which no single genus comprises >60% of their diet (Fig. 3a-c). Therefore, how moose are classified according to the traditional definition of specialization depends on the location and scale that their diet is measured.

Because assigning herbivores like moose to a specialization category based on their realized diet alone can be problematic, many have suggested characteristics of food plants and the forager that are consistent with dietary specialization. Specialist herbivores are expected to compete well in habitats where large, predictable, mono-specific patches of chemically or physically defended foods occur that

are avoided by other animals (Freeland and Janzen 1974, Westoby 1978, Crawley 1983, Lawler et al. 1998, Dearing et al. 2000, Moore et al. 2004). Because this food is normally less nutritious, these animals tend to be small with lower absolute energy requirements, or have relatively low mass-specific metabolic rates. The food often offers conspicuous stimuli for easy detection, which requires lower neural sophistication when selecting a diet, thus less energy invested towards brain tissue (Smith 1979, Bernays and Funk 1999, Martin and Handasyde 1999). Specialists are expected to have specialized anatomical, physiological, or behavioral adaptations for consuming their primary food, especially advanced and less expensive detoxification systems for a narrow range of plant chemicals (Freeland and Janzen 1974, Crawley 1983, Dearing et

al. 2000, Sorensen et al. 2005a). However, these adaptations reduce the range of plants, especially novel plants, that they can consume (Futuyma and Moreno 1988, Berenbaum and Zangerl 1994, Sorensen et al. 2005b). As a result, specialists are difficult to feed in captivity (Pahl and Hume 1991), respond poorly to a changing environment, and are most likely to become vulnerable to extinction (Fisher et al. 2003, Smith 2008.)

Moose generally conform with many, but not all of these criteria. In particular, moose are adapted to foods that form the bulk of their diet. Willow and certain other hardwood browse species contain linear condensed tannins that reduce protein digestibility (Hager-

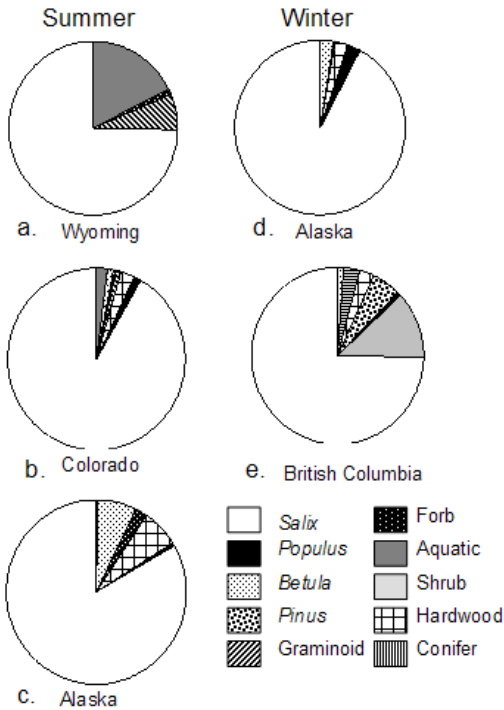


Fig. 1. Examples of moose consuming a “specialist” diet of > 60% willow (*Salix* spp.) in the summer in a) Wyoming (McMillan 1953), b) Colorado (Dungan and Wright 2005), c) Alaska (Van Ballenberghe et al. 1989), and during winter in Alaska (Risenhoover 1987) and British Columbia (Poole and Stuart Smith 2005).

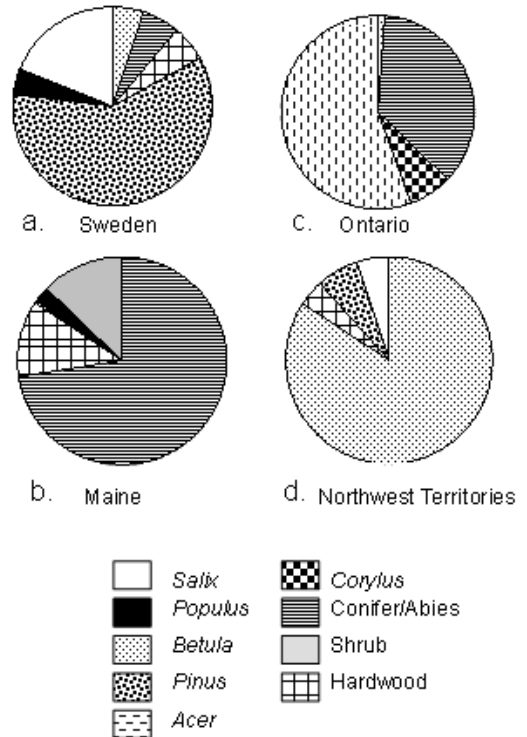


Fig. 2. Examples of moose consuming a “specialist” diet of > 60% of a plant genus on a variety of browse species in winter across its range, including a) Scots pine (*Pinus sylvestris*, Shipley et al. 1998), b) balsam fir (*Abies balsamea*, Ludewig and Bowyer 1985), c) 3 species of maple (*Acer* spp., Routledge and Roese 2004), and d) birch (*Betula* spp., especially *B. papyrifera*, Thomas 1990).

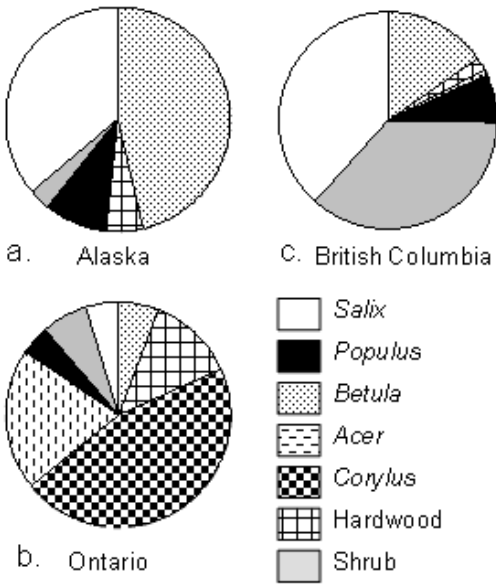


Fig. 3. Examples of moose consuming a “generalist” diet where no plant genus constitutes > 60% of the winter diet in Alaska (Wixelman et al. 1998), b) Ontario (Cummings 1987), and British Columbia (Poole and Stuart Smith 2005).

man and Robbins 1993). Moose produce specific salivary binding proteins particularly efficient at binding linear condensed tannins, whereas herbivores like mule deer (*Odocoileus hemionus*) that consume a more diverse diet produce salivary binding proteins aimed at both branched and linear tannins (Hagerman and Robbins 1993). Willows also produce salicylates, a bitter phenolic glycoside, that deters feeding by some herbivores, for example brushtail possums (*Trichosurus vulpecula*) (Markham 1971, Edwards 1978, DeGabriel et al. 2010). Likewise, conifers consumed in large amounts contain monoterpenes and other plant secondary metabolites that deter feeding by herbivores such as snowshoe hares (*Lepus americanus*; Rodgers et al. 1993) and rodents (Murphy and Linhart 1999) Although little is known about how moose deal with large amounts of these plant chemicals, other animals that specialize on terpenes such as woodrats (*Neotoma* spp.) and arboreal marsupials have adapted efficient and less expensive detoxification enzymes in the liver (Boyle et

al. 1999, Sorensen et al. 2005a). Moose have a relatively large liver for their size (Hofmann and Nygren 1992), thus an increased capacity to detoxify conifer browse with cytochrome P-450 enzymes (MacArthur et al. 1991). The moose has adapted an unusually large amount of room between the nasals and premaxillae which has allowed the development of a long, muscular, prehensile nose with widely spaced nostrils (Bubenik 2007). Presumably this anatomy aids stripping of willow leaves to increase bite size and harvest rate. However, this long nose is a liability when consuming small bites of forbs. Shipley et al. (1994) found that moose have the longest cropping time (min/bite) of 13 herbivores ranging from 0.01-500 kg. The anatomy of their nose allows moose to swallow underwater, enabling efficient consumption of aquatic plants that are avoided by most North American cervids (Geist 1999).

Moose also resemble specialist herbivores because they are difficult to feed in captivity. The typical herbivore diet consisting of grain-based pellets supplemented with alfalfa or grass hay causes diarrhea, enteritis, and wasting in moose (Schwartz et al. 1985, Shochat et al. 1997). Although general diets of herbivores are much higher in starch than a typical moose diet dominated by browse, moose do not lack enzymes (e.g., pancreatic alpha amylase and intestinal maltase) for digesting starch (Schwartz et al. 1996, Shochat et al. 1997). However, moose only thrive in captivity when fed large amounts of supplemental browse and aspen-based herbivore pellets (Schwartz et al. 1985, Shochat et al. 1997). Therefore, other components of browse diets such as lignin, tannins, and salicin may contribute to the digestive health of moose.

Because many other herbivores fall in the gray area between a specialist and generalist, Shipley et al. (2009) developed a specialization key designed to more accurately place a herbivore along the specialist-generalist continuum, thus accounting for a variety of

dietary strategies and forming a framework for comparative studies. The key assigns the modifiers “obligatory” and “facultative” to the terms “specialist” and “generalist” based on 1) relative breadth of the animal’s realized niche and diet (what it eats), 2) relative breadth of the fundamental niche and available diet (what it could eat), 3) the extent of chemical or physical characteristics, termed “difficulty”, that make food items either low in value or unpalatable to most herbivores, and 4) relevant temporal and spatial scales at which diets and niche breadth are measured.

Obligatory specialists always consume a narrow diet of a difficult plant. They have unique adaptations that allow them to consume this plant that is generally abundant in their habitat, but these adaptations also tend to prevent them from expanding their diet as environmental conditions change. Like the obligatory specialist, facultative specialists always have a consistently narrow, realized niche for difficult foods during at least 1 spatial or temporal scale such as winter, but because their fundamental niche is broader, they can expand their diet to include less difficult foods when environmental conditions allow, such as summer. Like facultative specialists, the realized niche of the facultative generalist can change depending on the local conditions. However, they differ from facultative specialists in that their diet is more commonly broad, they focus on different plant species in different seasons or locations, and when their diet becomes narrow, they tend to focus on less difficult plants that are also consumed readily by other herbivores. Finally, obligatory generalists always consume a mixed diet because they have a low tolerance for difficult foods that precludes them from eating much of any difficult plant. Therefore, based on these criteria, moose would fall on the continuum between the facultative specialist and the facultative generalist, because their diets consist of only 1 species and genus of moderately difficult plants in many areas, but their diet can expand

or change across their range.

DIET SELECTION: QUALITY OR QUANTITY?

The fibrous cell walls of plants are difficult for herbivores to digest, thus the nutritional quality and biomass of plants are usually inversely related (Van Soest 1984). Therefore, herbivores must make tradeoffs when selecting diets, a process which forms the backbone of most models predicting diet selection for herbivores. Many innovations in optimal foraging models have been designed for and tested with moose. One of the first and best-known optimal foraging models for mammalian herbivores was Belovsky’s linear programming model (Belovsky 1978). This model was based on the simple tradeoffs moose in northeastern USA make when choosing whether to consume deciduous leaves or aquatic plants. Deciduous leaves are less fibrous and easier to harvest and digest than aquatic plants, but because many boreal forests are depauperate in sodium (Belovsky and Jordan 1981), forest plants typically have less sodium than aquatic plants. To effectively meet their daily sodium requirement, moose need to consume a minimal amount of aquatic plants. Based on simple intake and digestion models, Belovsky (1978) suggested that moose needed to consume either a large amount of aquatic plants or a moderate amount of deciduous plants to meet their energy requirements, but because of digestion limitations, could only consume a moderate amount of aquatic plants or a large amount of deciduous plants. His model, therefore, predicted that moose must consume a mixture of aquatic and terrestrial plants within a narrow range of possibilities. He suggested that the exact mixture a moose should consume depends on its goal – whether to maximize energy by consuming the minimal amount of aquatic plants possible with the maximum amount of deciduous plants subject to digestion limitations, or to minimize time spent feeding by consuming the minimum of

both types of plants to provide more time for other life requisites. His data on diet composition of moose from Isle Royale National Park in Michigan fit most closely with the energy maximizing strategy.

Two decades later, moose were also the subject of several models designed to examine diet selection on a finer scale – what twig diameter a moose should select when foraging on deciduous browse in winter (Vivås et al. 1991, Kielland and Osborne 1998, Shipley et al. 1999). These models incorporated more mechanistic intake and digestion models to examine tradeoffs between consuming bites of a larger or smaller stem diameter. Cropping stems at larger diameters allows moose to take larger bites (Vivås et al. 1991, Shipley et al. 1998, 1999), and in turn, taking larger bites allows moose to harvest food faster (Risenhoover 1987, Shipley and Spalinger 1992, Gross et al. 1993). However, smaller stem diameters have less fiber making them easier to crop, chew, and digest (Shipley and Spalinger 1992, Kielland and Osborne 1998, Shipley et al. 1998). Keilland and Osborne (1998) and Shipley et al. (1999) predicted the twig size that herbivores should select to maximize digestible energy/d based on mass-specific constraints on consumption and digestion based on specific architecture and chemistry of browse species. In Sweden, moose selected twig diameters very consistent with the predictions of the optimal bite size model when fed 5 deciduous browse species varying in structure and chemistry in concentrated patches (Shipley et al. 1999). Likewise, the twig diameters that moose selected from feltleaf willow (*Salix alaxensis*) in Alaska (Keilland and Osborne 1998) and pubescent birch (*Betula pubescens*) in Norway (Vivås et al. 1991) were predictable from tradeoffs in quality and quantity.

Further experiments also showed that moose perceive these tradeoffs between harvesting and digesting plants quickly, and modify their harvesting behavior as plant den-

sity changes. For example, moose consumed larger stem diameters as the size of patches of red maple (*Acer glabrum*) stems declined and the distance between patches increased (Shipley and Spalinger 1995), and consumed proportionately more birch as density declined (Vivås and Sæther 1987). Fast harvesting and digestion is particularly important for large herbivores like moose that spend on average >8 h/d each feeding and ruminating throughout the year (Table 1). Therefore diet choices that reduce the time spent in these activities allow moose more time for other life requisites such as raising young, avoiding predators, and thermoregulation.

Finally, many of the first spatially explicit individual-based foraging models (IBM) for large herbivores were built for moose (Roeser et al. 1991, Moen et al. 1997, 1998). For example, Moen et al. (1997) used IBM to examine how foraging rules affect emergent properties such as body mass and movement pathways of moose foraging across patchy and seasonally changing landscapes. Landscapes consisted of grids with 1 m² feeding stations containing bites of deciduous browse. Quantity and quality of browse was updated seasonally and with herbivory, and animals moved in nested time steps according to foraging rules. Moen et al. (1997) validated the emergent properties of their model with field and pen data, and found that simulated moose using optimal rules based, in part, on quantity and quality of forage had higher body mass and survival at the end of the year than moose foraging randomly. Although different in approach, these linear programming, optimal bite size, and IBM models indicate that when choosing diets, moose seem to weigh the value of fast harvesting and fast digesting and select the diet that gives them the highest digestible energy per day, and in many cases are more sensitive to the effects of plant morphology on intake rate than plant chemistry on digestion (Keilland and Osborne 1998).

POPULATION REGULATION: TOP-DOWN OR BOTTOM-UP?

Moose populations provide excellent case studies for investigating the classic question in population ecology of whether populations are regulated top-down by predators or bottom-up by food. The theoretical implications of this question have been recognized and debated for at least 100 years since the beginning of the field of ecology (Pimm 1991); however, the practical implications have become increasingly important as many large carnivores are either disappearing [e.g., lynx (*Lynx canadensis*) in northwestern USA; Koehler et al. 2008] or reappearing [e.g., successful recolonization of wolves (*Canis lupus*) in the northern Rocky Mountains of the USA; Oakleaf et al. 2006] on the landscape.

Almost 50 years ago, Hairston et al. (1960) argued that “the world is green” because plants are more abundant than animals, thus herbivore populations must be controlled top-down by carnivores. They suggested that carnivores should compete for food because they lack predators to limit their populations, whereas because herbivore populations are limited by predators, they should not compete for food. Assuming that herbivore populations are limited by predators, they should be unable to limit plant populations that in turn would compete for resources. Therefore, removing carnivores should have a strong effect on herbivores, but removing herbivores should have little effect on plant densities. Murdoch (1966) later suggested that the world is not green – instead plants are mostly “prickly and taste bad” – arguing that ecosystems are regulated bottom-up because physical and chemical defenses make plants largely inedible. Therefore, herbivores are scarce and compete intensely for limited nutrients available in plants. As a consequence, predators are limited by competing for scarce herbivores. Thus, removing either predators or herbivores has little effect on their food supply. Finally, Oksanen et al. (1981) suggested that whether

ecosystems are limited from the top down or bottom up depends on the productivity of the ecosystem. They argued that extremely unproductive systems like deserts and tundra do not produce enough forage to support herbivores, let alone carnivores. In moderately productive ecosystems, plants are limited by herbivores, but plants support insufficient herbivore populations to support large numbers of predators. In very productive systems, such as rainforests, herbivores are limited by predators, but plants are not limited by herbivores as Hairston et al. (1960) proposed originally.

Moose are considered a “classic textbook case” by ecologists for examining this debate (Peckarsky et al. 2008), both because many moose populations live in remote areas with relatively intact ecosystems in which their large predators are still present, and because of the availability of unique long-term datasets such as that collected in Isle Royale National Park for the last 50 years. On Isle Royale, bottom-up effects seem to predominate in the unique ecosystem of single plant (balsam fir, *Abies balsamea*), large herbivore (moose), and large predator (gray wolves) largely unaltered by humans. Vucetich and Peterson (2004) found that annual production of balsam fir was 3 times more important in models predicting moose density over the last 50 years than was wolf density. In turn, wolf density was predicted both by moose density and balsam fir production. In areas with more diverse plants, herbivores, and predators and those that have been modified by humans through harvest, both bottom-up and top-down effects have been observed. For example, moose range in south-central Alaska contains willow and other forage plants, an alternative large herbivore, and at least two abundant large carnivores [bears (*Ursus americanus*, *U. arctos*) and wolves; Testa 2004]. In a 4-year study, Testa (2004) found female moose in poor body condition, with low twinning rates and delayed age of first reproduction, and a negative relationship between raising a calf

successfully and producing twins the following year. These characteristics suggest that food (willow) plays a role in limiting the moose population. However, in the same study, Testa (2004) found high calf and adult mortality from predation, resulting in low recruitment indicating that predation had a greater influence on population dynamics than nutrition.

Whether a large herbivore might control an ecosystem as a top-down influence may depend on its ability to escape higher top-down control by carnivore populations through large size, migration, or availability of alternative prey or predators (Sinclair 2003). A vast body of literature (e.g., Bergström and Danell 1987, Lozinov and Kuznetsov 2002, Morris 2002, Persson et al. 2005, Siipilento and Heikkilä 2005, Stolter 2008) suggests that in areas where populations of large carnivores are naturally or artificially low, moose can control their food sources from the top-down. A review (Pastor and Danell 2003) of moose across their circumpolar range concluded that as moose select the most nutritious parts of hardwood browse, they damage or remove the photosynthetic and meristematic tissues. Many species of browse respond by growing more quickly and with less fiber and plant secondary metabolites. This, in turn, provides more high quality moose forage and an incentive for moose to re-browse the same plant. However, over the long term these plants grow more slowly, have lower survival, and are less competitive. Furthermore, Stolter (2008) found that browsed willows had fewer catkins and reduced reproductive output. It follows that in situations of overpopulation, preferred moose forages could be replaced with less nutritious plants, such as conifers, that grow and decompose more slowly and ultimately change the composition and reduce productivity of an ecosystem.

OVERVIEW

Moose are widespread, charismatic, and popular for recreation and subsistence, and thus have been the subject of much research

and even a dedicated scientific journal (Alces). Additional characteristics of moose and the habitats in which they reside have caused moose to emerge as a model herbivore for testing broad ecological principles. First, moose often reside in simple and/or intact ecosystems that facilitate basic research. For example, in many boreal systems moose select from fewer than 10 species of available plants during winter (Shipley et al. 1998, Vucetich and Peterson 2004). In addition, many habitats moose occupy have been protected by parks and reserves (e.g., Yellowstone National Park, Rocky Mountain National Park, Isle Royale, Denali National Park), or are protected *de facto* by their remoteness. Therefore, much of moose range still contains large carnivores and natural vegetation. Second, compared with many small and wary herbivores, moose have proven to be surprisingly easy to observe both in the field and captivity. For example, Risenhoover (1987), Van Ballenberghe and Miquelle (1990), and Dungan and Wright (2005) were able to count bites from wild moose that tolerated their presence, and researchers such as Renecker and Hudson (1986) and Shipley and Spalinger (1992, 1995) hand-reared moose for foraging studies in semi-natural conditions. Moose also leave conspicuous remnants of their foraging activity such as easy-to-see browsed twigs and fecal pellets. Finally, insights into food and foraging are often most lucrative when studying large herbivores like moose that must spend most of their time foraging to satisfy their high forage requirements. With these desirable characteristics, moose will continue to provide a model for examining ecological questions such as tolerances for plant chemistry, what governs animal movements over landscapes, and reciprocal interactions between predation and reproduction.

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