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## *Invited Paper:*

### **MODIFICATION OF ECOSYSTEMS BY UNGULATES**

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**Abstract:** Ecosystem ecologists traditionally have focused their attention on direct interactions among species, particularly those interactions that control flows of energy and materials among trophic levels. Emerging evidence suggests that indirect interactions may be more important than direct ones in determining ecosystem patterns and processes. Here I review indirect effects of ungulates on nutrient cycling, net primary production, and disturbance regimes in terrestrial ecosystems. Ungulates influence the nitrogen (N) cycle by changing litter quality, thereby affecting conditions for N mineralization, and by adding readily available N to upper levels of the soil in urine and feces. As a result of these additions, natural heterogeneity in the spatial distribution of N within landscapes is amplified by ungulate selection of habitats and patches. The magnitude of returns of plant N to the soil in urine and feces is a function of animal body mass and characteristics of the diet, particularly N content and levels of tannin. Effects on N cycling can cascade throughout the ecosystem, and can stabilize or destabilize the composition of plant communities. Net primary production can increase or decline in response to ungulate grazing. The direction of this response depends on the intensity of grazing or browsing, the evolutionary history of the ecosystem, and the opportunity for regrowth. Opportunity for regrowth is determined by physiological and morphological characteristics of the plant as well as environmental conditions, particularly the extent and timing of moisture availability. Ungulates influence fire regimes by altering the quality and quantity of fuels available for combustion. In grasslands, ungulates often reduce the extent, frequency, and intensity of fires, while in shrublands and forests, their effects can increase the likelihood of crown fires, while reducing the likelihood of surface fires. I develop the case that the way that ungulates influence ecosystem process is contingent on historical context, in particular the long-term context provided by plant-animal coevolution and soil development and the short-term context created by climate and weather. I show that ungulates are important agents of change in ecosystems, acting to create spatial heterogeneity, modulate successional processes, and control the switching of ecosystems between alternative states.

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Understanding the ways that organisms interact with each other forms the central challenge of ecology. Historically, a prevailing approach to meeting this challenge has focused on trophic relations among species, for example, on predator/prey interactions (Hassel and Anderson 1989), resource competition (Tilman 1982, Keddy 1989, Law 1989), the structuring of food webs (Pimm et al. 1991), foraging behavior (Stephens and Krebs 1986), and decomposition (Swift et al. 1979). This emphasis has simplified the many complexities of ecological systems by allowing ecologists to focus on direct interactions (Pastor et al. 1988).

In keeping with the trophic approach, ecologists traditionally have viewed ungulates as consumers of plants and as food for predators. Thus, ungulate populations have been seen as

outputs of plant communities; plants as inputs to ungulate populations (Sinclair 1974, McCullough 1979, Botkin et al. 1981, Caughley 1982). In contrast to the trophic view, a recent approach has focused on the consequences of changes in environments induced by ungulates, changes that modify conditions for other organisms above and belowground. A growing set of examples illustrates that the indirect effects of such modification may exceed the direct consequences of flows of energy and materials from plants to ungulates (Dublin et al. 1990, Hobbs et al. 1991, Pastor and Naiman 1992, McNaughton 1992). It follows from this perspective that ungulates are not merely outputs of ecosystems, they may also serve as important regulators of ecosystem processes at several scales of time and space.

Here, I review the role of native ungulates in modulating ecosystem processes. I focus on their effects in 3 related areas: alteration of nutrient cycles, influences on net primary production, and modification of abiotic disturbance, particularly fire regimes. Using these effects as examples, I develop the idea that ungulates are important agents of environmental change, acting to create spatial heterogeneity, accelerate successional processes, and control the switching of ecosystems between alternative states (Wilson and Agnew 1992). I show that the ways that ungulates modify ecosystem patterns and processes often depend on selectivity—the choices ungulates make among landscapes, patches, and plants (Senft et al. 1987, McNaughton 1989, Coughenour 1991, Seagle et al. 1992). I also make the case that the effects of ungulates depend on historical context, particularly the long-term context provided by soil development and plant/herbivore coevolution, and by the more proximate context created by climate and weather.

Throughout this article, I will emphasize work on native ungulates over studies of livestock because native species tend to have a longer evolutionary history with the habitats they occupy and because the dynamics of populations of native ungulates are coupled more tightly to other ecosystem processes (McNaughton 1986). However, I will selectively include studies of domestic ungulates when those studies offer insight relevant to understanding the role of native ungulates in similar ecosystems.

## EFFECTS OF UNGULATES ON NUTRIENT CYCLING

In most undisturbed, terrestrial ecosystems, external inputs of nutrients provide a tiny proportion of the nutrient supply required by the biota, while the preponderance of needed nutrients comes from internal cycling (Horner et al. 1988, Aber and Melillo 1991). Often, decomposition processes limit the rate of nutrient recycling and, in so doing, limit availability of nutrients to plants. Nutrient availability, in turn, affects primary production and influences the composition of plant communities (Aber and Melillo 1991). It follows that processes affecting nutrient availability to plants can have far-reaching effects on ecosystem dynamics (Horner et al. 1988, Vitousek 1982).

Ungulates affect nutrient availability to plants in 2 general ways. They accelerate nutrient

turnover directly by excreting nutrients in a form readily available for uptake by microbes and plants. Moreover, they can influence nutrient turnover indirectly by modifying the quality and quantity of plant litter available for decomposition. In reviewing these effects, I will focus on N dynamics because N frequently limits productivity of terrestrial ecosystems (Vitousek 1982) and because several recent studies have shed light on the role of ungulates in N cycling.

## Nitrogen Returns in Dung and Urine

A substantial portion of plant N consumed by ungulates is returned to the soil in urine and feces (Ruess and McNaughton 1987, Frank et al. 1994). Excretion of N in dung and urine is important to N recycling because it offers a much accelerated alternative to decomposition of litter as a pathway for N turnover (Ruess and McNaughton 1987, McNaughton 1992, Pastor et al. 1993, Frank et al. 1994). Additions of urinary and fecal N are believed to contribute to higher levels of soil nutrients and microbial biomass in patches grazed by ungulates relative to ungrazed patches (Floate 1970, Ruess and McNaughton 1987, Seagle et al. 1992; but also see Tiedemann and Berndt 1972, Pastor et al. 1993).

Dung and urine contain high levels of soluble ammonium and urea (Floate 1970). Following deposition, urea is hydrolyzed to ammonium, which after several weeks is nitrified to nitrate (Doak 1952). Thus, urine offers N in mineral form that can be used readily by plants and microbes to meet N requirements for growth (Ruess and McNaughton 1987, Seagle et al. 1992). Plants with an evolutionary history of grazing show elevated growth responses to urea and ammonium relative to other inorganic forms of soil N, particularly when subject to defoliation (Ruess 1984, Ruess and McNaughton 1987).

In addition to direct fertilizing effects of urine and feces, excretion by ungulates promotes decomposition of organic matter and release of mineral N. Ungulate feces contain more N relative to carbon (C) than does plant litter (Ruess 1987, Seagle et al. 1992, Pastor et al. 1993) and as a result, are less resistant to microbial breakdown. Thus, urinary and fecal excretion promotes mineralization of N by providing a substrate that is decomposed more readily than plant litter and by enhancing conditions for decomposition of soil organic matter by increasing availability of N relative to C (Floate 1970, Ruess

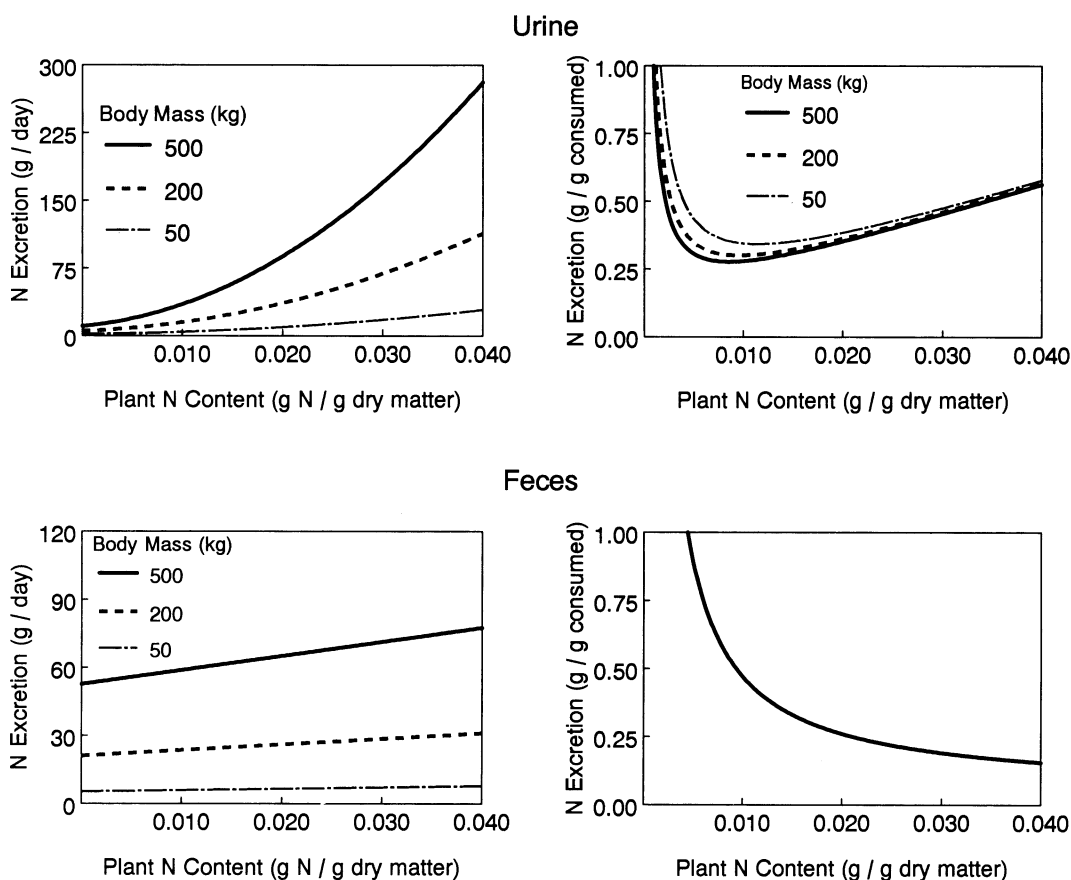


Fig. 1. Dynamics of nitrogen excretion in ungulates. Excretory returns of nitrogen to the soil depend on animal body size and dietary N. Other influences on excretion rates not represented in this figure include dietary tannin levels and the digestible energy content of the diet.

and McNaughton 1987, McNaughton 1992, Seagle et al. 1992, Pastor et al. 1993). Empirical studies show that soils amended with ungulate dung have higher rates of N mineralization than do unamended soils (Ruess 1987, Ruess and McNaughton 1987, Pastor et al. 1993) and simulations have predicated strong fertilizing effects of dung and urine on microbial biomass and mineralization rates (Seagle et al. 1992).

Urinary and fecal returns of N to ecosystems vary with animal body size and respond to dietary levels of N, digestible energy, and tannins (Fig. 1, Appendix A; Robbins 1983, Robbins et al. 1974, 1987; Mould and Robbins 1981, Hanley et al. 1992). Nitrogen excretion increases substantially with increasing levels of dietary N (Fig. 1, Appendix A) because the biological value of plant protein declines as N concentrations increase. This simply means that more N is excreted in the urine when dietary N levels are

high because the animal is not able to use fully the proteins it consumes for growth and maintenance. In this case, proteins are deaminated; their C skeletons are used for energy, and N must be excreted (Rodwell 1977). It follows that urinary N becomes a much larger fraction of total N excreted as plant N levels increase (Fig. 1). For example, as the levels of plant N in the diet increase from 1 to 3, the proportion of N returns in urine rises by roughly 4-fold, from less than half of fecal returns to more than double fecal returns.

As a rule of thumb, total N excreted exceeds N consumed when dietary N falls below about 0.07 gN/g dry matter. In this case, most excreted N originates from animal tissue. Thus, N returns as a percentage of plant N consumed increase dramatically at low levels of dietary N because endogenous losses exceed intake (Fig. 1).

If N were excreted uniformly across an animal's home range (i.e., Appendix A, Eq 11), then excretory additions of N to the soil would be trivial, on the order of  $10^{-2}$  kg ha<sup>-1</sup> yr<sup>-1</sup>, less than 1% of wet deposition from the atmosphere, and many times less than N mineralized in most terrestrial ecosystems (Aber and Melillo 1991). However, empirical measurements of N deposition can exceed the theoretical average deposition rate based on home range size (Appendix A, Eq 11) by several orders of magnitude. This occurs because urine and feces are concentrated in space at several scales. At the scale of the landscape (10<sup>3</sup> km<sup>2</sup>), Frank and McNaughton (1992) estimated that elk and bison populations on the northern winter range of Yellowstone National Park excreted 0.811–4.600 g N m<sup>-2</sup> yr<sup>-1</sup>, an amount that is roughly 4 times greater than the amount of N in senescent plants and almost 1/3 of the total N mineralized. At the scale of the patch (10<sup>-4</sup> km<sup>2</sup>), deposition of sheep dung doubles the levels of soil phosphorous relative to other patches on the landscape (Rowarth and Gillingham 1989). At the scale of the plant (10<sup>-6</sup> km<sup>2</sup>), additions of N can be as high as 50–100 g m<sup>-2</sup> yr<sup>-1</sup> (Saunders 1984).

Nutrients in dung and urine become concentrated in space because ungulates do not use their environment uniformly (Hilder and Mottershead 1963, McNaughton 1983, 1985; Senft et al. 1987, Cougenhour 1991, Ward and Saltz 1994). Selection between landscapes and among landscape positions amplifies nutrient returns in areas preferentially selected by ungulates. For example, elk migrate to low elevation to avoid snow during winter and to pursue emerging green plants during spring (Frank and McNaughton 1993). These migrations result in net movement of N from summer ranges to winter ranges (Frank et al. 1994). African ungulates seek shade when they rest, depositing a disproportionate amount of urine and feces under trees than in the open (McNaughton 1992). Domestic sheep prefer level areas for bedding and this preference results in 60% of dung being deposited on 15% of pasture area (Rowarth and Gillingham 1989). Bison tend to feed selectively on patches of plants that have been fertilized previously by urine (Day and Detling 1990), increasing the likelihood that patches fertilized by urine will be refertilized. In each of these cases, ungulates act as "conduits" for nutrient movement—N consumed over large areas is concentrated spatially as a result of selective use of

landscape positions (Ruess 1987). This selection is reinforced by positive feedback between areas of past deposition of dung and urine and the likelihood of future use by ungulates because urine and fecal deposition enhances conditions for grazing by increasing plant biomass and nutrient concentrations (Day and Detling 1990).

Excretion of N in dung and urine does not translate directly into additions to the soil because urinary N is subject to loss from the system via volatilization (Denmead et al. 1974, Vallis et al. 1982, Schimel et al. 1986, Hatch et al. 1989). Although Woodmansee (1978) surmised that volatile losses could be a large fraction of urinary N returns, recent work suggests this is not the case. Vallis et al. (1982) found that <15% of urinary N is lost to volatilization. Moreover, Schimel et al. (1986) revealed that volatilization of N from urine patches depended strongly on season and on soil properties associated with landscape position. Urinary N returns in lowland soils were not affected by volatilization; losses from upland soils were 12% of returns during winter, 27% during summer (Schimel et al. 1986). Thus, selection for landscape position by ungulates exerts strong effects on the extent of N volatilized.

However, these are gross losses and do not account for the volatile losses that would occur from plants in the absence of grazing (Detling 1988). Such losses could equal or exceed volatile losses from urine (Schimel et al. 1986), in which case, urinary losses would be balanced by conserving effects of grazing on volatilization from plants. Such conservation appears to occur in East African grasslands where total volatile losses of N were inversely correlated with grazing intensity at any given site, suggesting that grazing by abundant, native ungulates results in retention of nutrients that would otherwise be lost from the system (Ruess and McNaughton 1988).

## Effects on the Soil Environment

Although urinary and fecal additions of soluble N to the soil can be large, the direct effects of these additions on availability of N to plants may be less important than the indirect effects of ungulate grazing and browsing on decomposition (Holland and Detling 1990, Holland et al. 1992). The amount of N available in the soil solution for uptake by plants represents the balance between the incorporation of N in microbial bodies (immobilization) and the release of

N resulting from decomposition of soil organic matter (mineralization). The availability of N and the form and amount of C present in the soil determine whether microbes immobilize or mineralize N (Melillo et al. 1984, Pastor et al. 1987).

The primary substrates for decomposition are plant roots and aboveground plant litter. If feeding by ungulates affects the quantity or chemical composition of these substrates, it can modulate the balance between mineralization and immobilization. In so doing, ungulates can influence availability of N to plants either by reducing competition with microbes or by increasing N release from organic matter (Holland et al. 1991, Merrill et al. 1994). These effects, in turn, can cascade through the ecosystem, affecting the structure and distribution of plant communities over large areas (Pastor and Naiman 1992). Here, I review 2 general cases of modification of the soil environment by ungulates and the influence of these modifications on N cycling. These cases illustrate the extreme divergence of effects that ungulates can exert on nutrient cycling.

*Case 1: Grasslands in East Africa.*—Migratory ungulates concentrate their feeding activities on shortgrass plains during the wet season in the Serengeti Mara region of East Africa. These grasslands have been heavily grazed by native ungulates for centuries; 60–94% of aboveground net primary production is consumed annually (McNaughton 1985). The grasses in this region have evolved a variety of responses promoting rapid regrowth of leaves following defoliation by ungulates (see section on Effects of Ungulates on Net Primary Production).

Grazing-induced regrowth of grasses has 3 important consequences for decomposition processes determining N availability to plants. First, rapidly growing plants contain high levels of N relative to their levels of C, and the C that is present is in a form that tends to be more decomposable than C in mature plant tissue (McNaughton 1983, Seagle et al. 1992). Moreover, because grazing intensity is high, the amount of litter returned to soil is relatively low (instead, N is returned in dung and urine as described above). Finally, C in roots is allocated to shoots following defoliation (Detling et al. 1979, 1980; Caldwell et al. 1981, Osterheld and McNaughton 1988). The net effect of these changes is that the ratio of C to N (C:N) in the substrates available for decomposition exceeds the C:N of de-

composition substrates in the absence of ungulate grazing. Reduced C:N means that microbes are more likely to be limited by the availability of C than by the availability of N (i.e., there is a greater “N surplus”). As a result, immobilization of N declines, mineralization accelerates, and more N becomes available in the soil solution for uptake by plants (Ruess 1987, Holland and Detling 1990, Holland et al. 1992, Seagle et al. 1992).

During the dry season, ungulates migrate to tallgrass plains of the Serengeti Region, where grass production is much higher than on the shortgrass plains. As a result of this elevated productivity, a relatively small proportion of plant biomass is consumed, and although regrowth may be stimulated, the standing crop fails to attain the concentrations of N seen in the shortgrass case. This failure results in part from the relatively nutrient deficient, sandy soils of the tallgrass plains, and in part from dilution of regrowth by a large standing crop of mature grass (Seagle et al. 1992). Consequently, large quantities of litter containing high levels of C are added to the soil. Moreover, because grazing increases production, these quantities exceed those that would be expected in the ungrazed case (Seagle et al. 1992). The large additions of high C:N substrate means that C is relatively more abundant than N in the soil environment; microbial growth becomes limited by N more than C, and competition for N between microbes and plants intensifies. Increased immobilization of N in microbial biomass reduces availability of N to plants as the system becomes “clogged” by litter.

Thus, ungulate grazing can accelerate or retard mineralization in African grasslands. The direction of the influence of ungulates on N mineralization depends on context. Although grasses throughout the region appear to be highly adapted to withstand intense grazing, the availability of moisture as well as the properties of the soil environment create contingencies that determine whether ungulates expand availability of N to plants or constrain it.

*Case 2: Moose browsing in the boreal forest.*—Moose populations have browsed in Isle Royale National Park during the last 80 years. They feed in early successional plant communities dominated by deciduous species—aspens (*Populus tremuloides*) and paper birch (*Betula papyrifera*). Although moose consume less than 10% of the annual plant production, their feed-

ing has fundamental effects on nutrient cycling and plant succession (Pastor et al. 1988).

These effects result from effects of ungulates on N availability to plants. The deciduous communities selected for browsing by moose tend to grow rapidly and produce biomass that contains relatively high N concentrations (Pastor and Naiman 1992). These high N levels promote rapid decomposition, and, as a result, N in litter is rapidly returned to the soil solution where it can be absorbed by plants (Pastor and Naiman 1992). This rapid turnover is necessary for maintaining deciduous species on a site because their high growth rates can be sustained only if availability of soil N is high (Pastor and Naiman 1992).

Deciduous communities eventually succeed to coniferous ones dominated by white spruce (*Picea glauca*) and balsam fir (*Abies balsamea*). These species grow slowly and have low N requirements, characteristics that are associated with low levels of N and high levels of digestion inhibiting secondary plant compounds in leaves. As a result, conifer leaves are poor food for moose. Moreover, the attributes of coniferous leaves that inhibit digestion by moose also retard decomposition by soil microbes (Horner et al. 1988). It follows that increases in the contribution of conifers to litter tends to diminish N availability by retarding decomposition.

Moose feed selectively, consuming deciduous leaves and rejecting coniferous ones. An important consequence of this selection is an increase in the proportion of coniferous leaves in plant litter, which, as described above, reduces N availability to plants (McInnes et al. 1992, Pastor et al. 1993). These reductions in availability of N offer a competitive advantage to coniferous species because their slow growth rate allows them to grow on N-poor sites while the relatively high N requirements of deciduous species prevent them from growing there. These relations produce a series of positive feedbacks mediated by moose browsing, feedbacks that accelerate the succession of deciduous plant communities to coniferous ones (Pastor et al. 1988, Pastor and Naiman 1992).

However, there are also conditions resulting from moose browsing that could retard succession (Pastor and Naiman 1992). If moderate browsing by moose stimulated shoot and leaf production by deciduous trees (Dutoit et al. 1990, Bergstrom 1992), then moose could enhance the quality of litter by increasing the contribution

of deciduous leaves, thereby enhancing N turnover and availability to plants. This would convey a competitive advantage to deciduous species over conifers and would slow the rate of succession. Thus, it appears that population dynamics of moose and their feeding behavior can stabilize plant community structure and or destabilize it. Community composition is stabilized when moderate intensity browsing retards succession; it is destabilized when high intensity browsing accelerates succession (Pastor and Naiman 1992).

The operation of this switch is likely to depend on landscape structure (Pastor et al. 1988). Patches of deciduous plant communities are established following disturbance. Small disturbances (beaver dams, windfall) create small patches; large disturbances (fire) create large ones. Browsing intensity depends on patch size—small patches may be heavily browsed even when moose populations are low, while large patches may offer so much food that they are never browsed intensely, even in the face of expanding moose populations (Pastor et al. 1988). It follows that selective foraging by moose mediates a complex interaction among disturbance regimes, plant succession, and nutrient cycling. The outcome of this interaction has fundamental consequences for the structure and composition of boreal forest landscapes (Pastor and Naiman 1992).

## EFFECTS OF UNGULATES ON PRIMARY PRODUCTION

### Compensatory Growth and the Grazing Optimization Hypothesis

In a series of seminal papers, McNaughton proposed that consumption of plants by native ungulates could elevate annual net primary production (ANPP) in grassland ecosystems as a result of grazing-induced feedbacks among individual plants, plant communities, and the soil environment (McNaughton 1976, 1979, 1983). These feedbacks are believed to produce a biphasic response of ANPP to increasing grazing intensity (Dyer et al. 1993), a response that has become known as the "grazing optimization hypothesis." The grazing optimization hypothesis predicts that plants can compensate for effects of defoliation such that grazed plant communities produce more biomass than ungrazed ones. This prediction has been verified empirically in several ecosystems (McNaughton 1979, 1985;

Table 1. Mechanisms contributing to compensatory growth following defoliation.

Level of organization	Mechanism	Source
Individual plant	Increased allocation of photosynthate to leaves	Detling et al. 1979
		Detling et al. 1980
	Increased photosynthetic rate	Caldwell et al. 1981
		Osterhead and McNaughton 1988
		Painter and Detling 1981
		Parsons and Penning 1988
	Increased uptake of nutrients by roots	Wallace 1990
		Ruess 1984
	Increased allocation of nitrogen to leaves	Ruess and McNaughton 1984
		McNaughton and Chapin 1985
Jarmillo and Detling 1988		
Polley and Detling 1988		
Jarmillo and Detling 1988		
Plant community	Reduced transpiration	Polley and Detling 1988
	Increased water use efficiency	Whicker and Detling 1988
	Increased light penetration	Wraith et al. 1987
	Increased soil moisture	McNaughton 1985
	Increased mineralization of nitrogen	Monsi et al. 1973
Ecosystem	Reduced immobilization of nitrogen	Archer and Detling 1986
		Ruess 1987
		Ruess et al. 1987
		McNaughton et al. 1988
	Rapid return of mineral nitrogen to plants via excretion of urine and dung	Seagle et al. 1992
		McNaughton et al. 1988
		Holland and Detling 1990
		Frank et al. 1994
		Ruess et al. 1987

Page and Whitham 1987, Dyer et al. 1991, Frank and McNaughton 1993, Turner et al. 1993).

Although the interpretation of empirical results showing increased ANPP in response to grazing has been questioned (Belsky 1986, 1987; Verkaar 1986), there is nonetheless a large body of evidence documenting mechanisms responsible for compensatory growth in individual, grazed plants as well as grazing-induced increments in productivity in grazed plant communities (Table 1). Moreover, in a recent, comprehensive review of literature on effects of grazing on ecosystems, Milchunas and Lauenroth (1993) found that 17% of studies showed elevated ANPP in areas that were grazed relative to areas where grazing was excluded. This is a particularly strong result because the preponderance of work reviewed by Milchunas and Lauenroth (1993) studied effects of domestic ungulates. Grazing by livestock tends to be more intense than grazing by wild ungulates simply because livestock densities can be higher and spatially constant as a result of fencing, water improvements, predator control, veterinary care, and mineral supplementation (McNaughton 1993). Thus, domestic grazing systems are probably biased toward heavier grazing intensities than would be

seen in native ones, and such bias may tend to underestimate the prevalence of compensatory responses in plants, which are predicted to occur only at moderate grazing intensities. The findings of Milchunas and Lauenroth (1993) contrast with previous conclusions that grazing-induced increments in ANPP were rare and were limited to African systems (Detling 1988, Lacey and Van Poolen 1981).

Models of plant animal systems (Hilbert et al. 1981) as well as empirical studies (McNaughton 1983, Coughenour 1985, Wallace et al. 1985, Georgiadis et al. 1989) reveal conditions under which grazers and browsers can enhance ANPP in the plants they eat. These conditions include 2 components—capacity and opportunity. The capacity to regrow after defoliation is a result of the evolutionary history of plants and the ungulates that eat them (Mack and Thompson 1982). Adaptations providing the capacity for regrowth include low stature, deciduous leaves, linear leaf elongation from intercalary meristems, rhizomatous growth, high shoot density, below ground nutrient reserves, and rapid transpiration and photosynthetic rates (Coughenour 1985).

The capacity for compensatory growth can



be expressed only if environmental conditions provide the opportunity for regrowth following defoliation. This opportunity depends in large measure on the extent and timing of moisture availability and the availability of soil nutrients. For example, Georgiadis et al. (1989) found that total aboveground production of potted plants of *Sporobolus kentrophyllus*, an African grass, was maximized under conditions of moderate defoliation if plants were limited by water availability at the time of clipping, and if the period between waterings was at least 24 days. Under other conditions of moisture availability, effects of defoliation had no effect on plant growth or reduced growth.

The net effect of grazing or browsing on plant production is a balance between growth-simulating and growth-inhibiting effects. The way in which this balance is expressed depends on the environmental context (Noy-Meir 1993). Thus, it should be expected that the full range of growth responses to defoliation by ungulates, from negative to positive increments, might be seen even in plants of the same species under different environmental conditions (Noy-Meir 1993). It follows that substantial temporal variability in compensatory responses occurs within ecosystems as a result of variation in weather and climate (Huntley 1991). Moreover, some ecosystems are more likely to allow compensatory responses of plants to grazing and browsing than other ecosystems are simply because of differences in the evolutionary history of plants and animals in these systems and because of differences in characteristics of their soils (Mack and Thompson 1982).

### Grazing Lawns: Spatial Variability in Regrowth

Variability in plant production over space results in part from soil conditions and in part from selection of plant patches by ungulates—some patches are grazed or browsed heavily, some not at all (Wiens 1985, Lundberg and Dannel 1990, Hobbs et al. 1991, Ward and Saltz 1994). When feeding by ungulates in a patch increases the likelihood that animals will feed in the patch again, the patch is known as a “grazing lawn” (McNaughton 1984, Dutoit et al. 1990). Grazing lawns are patches within the landscape that contain plants maintained in a juvenile, rapidly growing state as a result of the effects of feeding by herbivores. Such patches may be composed of graminoids (McNaughton

1984) or shrubs (Dutoit 1990). Frequently, these areas contrast sharply with ungrazed areas of the landscape (Hobbs et al. 1991).

For example, in African grasslands, grazing lawns contain plants of lower stature with higher bulk densities (i.e., g/m<sup>3</sup>) of leaves, and higher leaf N concentrations (McNaughton 1984). As a result, the amount of N per unit volume in the patch is several fold higher than in an ungrazed patch. Because N and other nutrients are concentrated in grazing lawns, feeding by herds of ungulates acts to enhance the conditions for future feeding as plants regrow (McNaughton 1976, 1984).

In contrast to the positive feedback between grazing and regrowth observed in native ungulate systems in Africa, there is evidence from studies of livestock that increasing herd densities acts to harm rather than to enhance food supplies (rev. by Westoby 1985). Moreover, browsing may induce production of secondary defensive compounds in trees and shrubs (Haukioja 1991, Bryant et al. 1991, Bergstrom 1992) and grazing can increase silification in grasses (McNaughton and Tarrants 1983). Thus, intense herbivory can result in a grazing lawn or a patch of low palatability, and grazing-induced enhancements in forage quality may be more than offset by grazing-induced reductions in the quantity of forage available (Hobbs et al. 1996a).

Hobbs and Swift (1988) defined thresholds specifying when patches offer food supplies that accelerate energy gain by ungulates relative to the ungrazed condition. In short, this threshold occurs when the increases in nutrient concentration within the patch are directly offset by a reduction in eating rate resulting from a diminished amount of food relative to the ungrazed condition (Hobbs and Swift 1988). Thus, in systems where regrowth of plants is slow or absent, there is a negative feedback between present and future grazing—grazed patches are unlikely to be grazed again. When regrowth is rapid, the feedback is positive—grazing enhances the conditions for future grazing.

These feedbacks have important implications for landscape structure. Positive feedback increases landscape heterogeneity by heightening the contrast between areas that are grazed and those that are not. Negative feedback achieves the opposite—landscape heterogeneity is reduced or fails to change because grazing intensity tends to become uniform. Which feedback prevails depends on environmental limits on pri-

mary production, the intensity of herbivory, and the response of plants to defoliation (see rev. in Huntly 1991, Bergstrom 1992).

## EFFECTS OF UNGULATES ON FIRE REGIMES

Fire is an important source of disturbance in many of the world's grasslands, forests, and shrublands (Aber and Melillo 1991). Because grazing and browsing by ungulates modifies the type and amount of vegetation available for burning, ungulates can exert important controls over the spatial and temporal dynamics of fire.

### Ungulates and Fire in Grasslands

Fire and grazing by large ungulates occur together in grasslands throughout the world. Because grazing by ungulates reduces the standing crop biomass of plants available for burning, ungulates can reduce the frequency, extent, and intensity of grassland fires (Frost and Robertson 1987, Stronach and McNaughton 1989). For example, McNaughton (1992) showed that the proportion of grasslands in the Serengeti that burned annually was asymptotically related to the population size of wildebeest. At populations <600,000, most of the Serengeti Plains were consumed by fire, but when populations exceeded 600,000, only 20% of the region burned. Thus, ungulate population dynamics provided a switch between 2 alternative states for the ecosystem: fire prone and fire resistant.

The effect of ungulates on regional flammability depends on environmental factors controlling net primary production (Frost and Robertson 1987). In dry, shortgrass savannas with low productivity, grazing and fire do not interact strongly because fuels are rarely sufficient to support large fires; while in moist, tallgrass savannas, productivity is so great that annual fires occur despite ungulate grazing (Frost and Robertson 1987). Mesic, midgrass systems provide the greatest opportunity for interaction between ungulates and fire. In these systems fires are frequent and extensive in the absence of grazing, and are infrequent and confined when grazing is intense.

Thus, it appears that ungulates exert meaningful control over the flammability of large areas of grassland ecosystems. This control has important implications for nutrient cycling and for additions of C to the atmosphere (Hobbs et al. 1991). In grazed grasslands, nutrients con-

tained in aboveground biomass are consumed by ungulates and are transferred to the upper levels of the soil in urine and feces. Some of these nutrients are also incorporated into ungulate bodies. Both of these transfers result in conservation of nutrients that would be volatilized when litter or aboveground biomass burns (Ruess 1987, Hobbs et al. 1991). Such conservation can determine whether the system's nutrient budget is positive or negative. Hobbs et al. (1991) estimated that cattle grazing in the tallgrass prairie resulted in net conservation of about  $0.1 \text{ g N m}^{-2} \text{ yr}^{-1}$ . Such conservation was sufficient to determine whether the ecosystem gained or lost N, and appeared to play an important role in sustaining soil fertility in burned tallgrass prairie (Hobbs et al. 1991). Again, ungulates offer a switch controlling the trajectory of the ecosystem, from a system where N accumulates, to one where N is continually lost.

Ecosystem level effects of ungulates on fire regimes in grasslands depend on the aggregate influence of selectivity by ungulates at patch scales. Ungulates feed selectively in grasslands, and this selection often creates a mosaic of heavily and lightly grazed patches (Hobbs et al. 1991, McNaughton 1992, Jefferies et al. 1994). Fire intensity is inversely related to standing crop biomass (Stronach and McNaughton 1989) and as a result, grazed patches burn less completely and intensely than burned ones do (Hobbs et al. 1991). Because the susceptibility of any given patch in the landscape depends on the flammability of surrounding patches (Knight 1987), the mosaic created by patchy grazing can provide natural "firebreaks" that prevent small fires from becoming large (McNaughton 1992, but also see Turner and Bratton 1987).

Fire also influences the effects of grazing on spatial heterogeneity within grasslands. At the landscape scale, fire can interrupt the positive feedback that develops between grazing in patches and the probability of regrowth (see section on Grazing Lawns). For example, in unburned tallgrass prairie grazed patches are more likely to be regrowth (Hobbs et al. 1991). As a result, standing dead tends to accumulate in ungrazed patches, while grazed patches typically contain new growth. This produces a high contrast between ungrazed patches and grazed ones in unburned prairie. Fire eliminates this contrast by removing standing dead from ungrazed patches (Hobbs et al. 1991). Thus, fire has a "homogenizing" effect; it reduces the het-

erogeneity created by grazing at the scale of the landscape.

At the regional scale, grazing by ungulates increases the heterogeneity created by fire. Sites that are grazed and burned are more dissimilar than sites that are only burned (Glenns et al. 1992). This occurs because grazing promotes colonization of burned areas by creating space among dominant species. Species colonizing a site vary depending on the composition of the surrounding communities. Thus, the interaction between grazing and random processes of immigration can create high levels of heterogeneity at a regional scale (Glenns et al. 1992). Burning in the absence of grazing enhances growth of a few species of dominant grasses, and thereby promotes regional homogeneity.

### Ungulates and Fire in Shrublands and Forests

Ungulates consume a relatively small fraction of net primary production in forests and shrublands (Gessaman and MacMahon 1984, Pastor et al. 1988). Consequently, their direct effects on accumulation of plant biomass and hence, fuel amount, would appear to be minor. However, herbivory by ungulates could affect the interval between crown fires. This is the case because browsing by ungulates can significantly retard regeneration of forest and shrublands following disturbance (Cowan 1945, Hough 1949, Stoeckeler et al. 1957, Davis 1967, but also see Webb et al. 1956). Consumption rates of 30–60% of the mass of emerging woody sprouts are not uncommon following crown fires (Cowan 1945, Legee 1969, Philleo et al. 1978, Wolff 1978, Basile 1979) and reduced fire frequency has been attributed to removal of fine fuels by herbivores in forests (Madany and West 1983) and shrublands (Zimmerman and Neuenschwander 1984).

Discontinuity in fuels causes boundaries between grasslands and woody plant communities to be relatively impermeable (Wiens et al. 1985) to the spread of fire. In chaparral, ungulates may accentuate this boundary impermeability by creating a “bare zone,” an area essentially denuded of vegetation, between grass and shrub patches (Bartholomew 1970, Halligan 1973). This zone offers a natural fire break, reducing the likelihood that surface fires will spread from highly flammable grasslands to the crown of shrubs. These effects of feeding by ungulates modulate the effects of fire on spatial pattern.

Disturbances that spread within the same habitat type increase diversity of spatial pattern (e.g. fire within chaparral), while disturbances that spread between habitat types (e.g. fire in grassland spreading to forest) may reduce diversity (Turner 1989, Turner et al. 1989). Thus, ungulates may affect the boundary dynamics of crown fires, and in so doing, act to increase diversity in spatial patterns resulting from them.

Understanding effects of ungulates on fire regimes in woody plant communities requires differentiating between conditions that favor fires on the surface and those that favor fires in the crown. In addition we need to separate the immediate, direct effects of herbage removal from longer term, indirect effects of ungulates on plant succession. The immediate consequences of consumption of plant tissue by ungulates opposes the accumulation of a spatially continuous fuel supply. However, by influencing plant competition and mortality, the indirect effects of herbivory by ungulates may change the nature of the fuel in complex ways that favor fire in shrublands and forests. Such indirect effects can be seen in browsing-induced changes in plant life form and chemical composition.

Plant life forms play a crucial role in determining the flammability of forests and shrublands. Fires burning on the surface can spread to the crown when the energy output rate per unit of flame front exceeds a critical intensity (Van Wagner 1977). For this to occur, there must be enough vertical continuity in fuels to bridge the gap between the surface and the canopy; that is, “. . . bridge fuels must presumably be present in sufficient quantity to intensify the surface fire appreciably as well as to extend the flame height” (Van Wagner 1977:30). It follows that initiation of crown fires is opposed by large gaps between surface fuels and the overstory. Thus, if herbivores influence the vertical structure of surface vegetation, they can affect the likelihood of initiation of crown fire by controlling the spread of fire from the surface to the canopy above.

The influence of ungulates on the accumulation of “bridge” fuels (sensu Van Wagner 1977: 30) in forests is vividly illustrated in Madany and West (1983:663, Fig. 2). Heavy grazing by livestock shifted the composition of the understory of ponderosa pine (*Pinus ponderosa*) communities from palatable perennial grasses to unpalatable trees and shrubs and changed the physiognomy of the vegetation from open sa-

vanna to dense thicket. Although grazing caused a reduction in the frequency of surface fires by reducing fine fuels (grasses), it favored conditions necessary for fires to crown by providing abundant vegetation of intermediate height (shrubs and tree seedlings). In contrast, browsing by ungulates in East Africa prevents trees from reaching large size, and thereby allows fire to maintain grassland conditions (Belsky 1984, Frost and Robertson 1987, Bergstrom 1992). In the absence of such browsing, trees reach large size, escape the effects of surface fires, and outcompete grasses (Dublin et al. 1990, Scarpe 1992) causing a conversion from grassland to forest. Thus, although fire may initiate a transition from forest to grassland, browsing by ungulates maintains the grassland state (Dublin et al. 1990). This shows how removal of a small component of the biomass of the ecosystem by ungulates can control the switching of the system between alternative states.

Effects of herbivores on the accumulation of flammable chemicals in plant communities amplify their influences on plant life form. Volatile compounds found in the leaves and stems of woody plants can profoundly influence fire regimes in forests and shrublands (Mutch 1970). Although the frequency of occurrence of natural fire is directly related to frequency of lightning strikes, increases in fuel flammability increase the probability that a given strike will initiate a fire, and the probability that a fire will spread once initiated (Rundel 1981). Volatile chemicals in plant tissue affect the fire regime directly by increasing flammability of plant tissue (Rundel 1981). They influence it indirectly by retarding decomposition of litter (Horner et al. 1988) and accelerating accumulation of fine fuel.

Many of the volatile compounds that increase flammability of trees and shrubs are also important deterrents for herbivory (Christensen 1985). For example, concentrations of ether extracts in woody vegetation are positively related to flammability and negatively related to palatability. Although the evolutionary significance of these chemicals is debatable (Christensen 1985), it is clear that they are ecologically significant in increasing the chances that woody plant tissue will burn (Mutch 1970, Rundel 1981), and in reducing the chances that it will be eaten (Bryant and Kuropat 1980). As a result, ungulates may offer a competitive advantage to plants containing volatile chemicals (Pastor et al. 1988,

Pastor and Naiman 1992). In so doing, they favor development of woody plant communities that are more flammable, more resistant to decomposition, and less palatable. Thus, herbivores increase the likelihood of crown fires by accelerating succession toward plant communities that are more likely to support such fires.

An excellent example of these effects can be seen in the interactions between herbivores and shrubs in chaparral (Mills 1983, 1986). Two species of shrubs, chamise (*Adenostoma sparsifolium*) and ceanothus (*Ceanothus greggii*), are prominent in the emerging plant community following crown fire in chaparral. Deer and small mammals prefer to eat seedlings of ceanothus over those of chamise. This preference appears to be influenced by concentrations of ether extracts in the 2 shrubs. When browsing is intense, chamise predominates in the post-fire community, but when herbivores are excluded, ceanothus seedlings outcompete those of chamise. Thus, by controlling the outcome of competition and altering early stages of succession, the activities of browsers regulate whether the emerging community is dominated by flammable, unpalatable shrubs, or less flammable palatable ones. This illustrates that by influencing colonizing species and thereby affecting the initial conditions of a successional sequence, ungulates may exert a disproportionate influence on the course of succession (MacMahon 1981) and the development of fuels.

The effects of ungulates on fire regimes in forests and shrublands depend on the relative size of burned areas (Main 1981) and the juxtaposition of burned and unburned habitat (Turner and Bratton 1987). If relatively small areas burn, then ungulates are likely to have major effects on patterns of post-fire succession (Pastor et al. 1988) and consequently, on the development of fuel complexes. If the same number of animals are attracted to burned patches differing only in size, the smaller patches will experience greater effects as a result of concentration of animals on a smaller area. In this case plant mortality may be high and palatable plant species can be eliminated (Main 1981). Burns that offer a flush of new growth over large areas allow palatable plant species to escape effects of herbivores (Cowan 1945, Main 1981, Pastor et al. 1988) in much the same way that synchronous reproduction of prey dampens the effects of predation (Dauphine and McClure 1974, Rutberg 1987). Moreover, small patches are more likely

to be used uniformly by ungulates than large ones are because of the proximity of the unburned matrix that offers vegetative structure needed to meet the shelter requirements of ungulates (Peek et al. 1982, Urness 1989).

Most fires create relatively small burned patches in forests and shrubland, but most burned areas result from a few large fires (Houston 1973, Arno 1980, Minnich 1983, Bonan and Shugart 1989, Romme and Despain 1989). Thus, ungulate herbivores frequently may have the opportunity to influence the accumulation of fuels at landscape scales. However their effects are probably minor over regional scales, because most of the area burned in forests and shrublands can be traced to extensive but infrequent fires that occur as a result of severely dry weather (Bonan and Shugart 1989, Romme and Despain 1989) or as a consequence of accumulation of fuel due to fire suppression (Minnich 1983). The sheer magnitude of these events reduces the chance for ungulates to affect the fire regime.

### CONCLUSIONS: SELECTIVITY, CONTEXT, AND "SCALING-UP"

I have made the case that ungulates are important agents of change in ecosystems ranging from grasslands to forests. Ungulates modify nutrient cycling, influence primary production, alter patch dynamics, and affect abiotic disturbance. Their roles in these processes can be usefully assigned to 3 general modes of feedback to plant communities: they regulate process rates, they modify spatial mosaics, and they act as switches controlling transitions between alternative ecosystem states. In all of these cases, the type of feedback (positive or negative) depends on the environmental context in which it occurs.

I described several examples of the ways that ungulates can accelerate or retard net primary productivity, nutrient turnover, and plant community succession. In all of these cases, the influence of ungulates on system rates depended on a complex interaction among their population dynamics, their responses to landscape pattern, and attributes of soil and climate controlling plant community structure and productivity. Understanding and predicting the effect of ungulates on rates of ecosystem processes is not possible without knowing all 3 of these dimensions of context. For example, moose browsing can affect plant succession in boreal forest because N availability for plants is sensitive to litter

quality, and because the rate of succession is sensitive to N availability (Bryant et al. 1991, Pastor and Naiman 1992, Pastor et al. 1993). These conditions allow the feedback to occur. However, whether the feedback is positive or negative, whether moose accelerate or retard forest succession, depends on their population density, their patch choices, and landscape pattern.

It has long been recognized that herbivores can modify spatial pattern of landscapes over several spatial scales (Wiens 1976, 1985; Huntly 1991). Their modifications may increase spatial heterogeneity, or they may act to make landscapes more homogenous in pattern. At patch scales, the direction of effects of ungulates on spatial pattern appears to depend on the production response of plants to grazing or browsing, the nature of competition between palatable and unpalatable plant species and the effects of abiotic sources of disturbance, such as fire. If the intensity of herbivory promotes regrowth that maintains or enhances the palatability of plants within grazed or browsed patches, then positive feedback between current and future selection of patches leads to high contrast in the landscape (Hobbs et al. 1991). This contrast can be expressed in a variety of ways, including the spatial distribution of nutrients, patterns of plant phenology, and composition of plant communities. Alternatively, if foraging by ungulates reduces the attractiveness of grazed or browsed patches, then this negative feedback causes animals to select patches more evenly across the landscape, and effects on spatial pattern are dampened (Hobbs et al. 1991). At regional scales, the effects of ungulates appear to depend on the ways that grazing influences the balance between colonizing plants and established ones. The opportunity for increases in spatial heterogeneity depend on the responses of dominant plants to large scale disturbance (i.e., fire) and the responses of colonizers to small scale disturbance (i.e., grazing) (Glenns et al. 1992).

Although ungulates may exert minor effects on the structure and function of ecosystems years after disturbance, their effects immediately following the disturbance can determine the trajectory of the system among alternative states. In forests, browsing by ungulates may provide competitive advantage to plants containing high levels of volatile secondary compounds, which increase the flammability of the ecosystem. Thus,

dietary selection by herbivores immediately following disturbances, e.g. fire, may control whether the forest and shrub systems that emerge are prone to frequent fires, or are fire resistant. Moreover, although fire can initiate transitions from forest to grassland, selectivity by ungulates can play a key role maintaining the grassland state by maintaining trees in a state that preserves their sensitivity to the effects of fire (Dublin et al. 1990).

Being able to fully understand and predict the ways that ungulates modify ecosystems remains a large task, despite the excellent science reviewed here. A predictive ability depends on the extent to which ecologists can integrate and "scale-up" findings obtained in a wide range of studies, from physiological and behavioral studies conducted at the level of the individual animals, to studies of populations, communities and whole ecosystems. Plant ecologists offer a valuable illustration of such scaling-up—whole canopy models of ecosystem function rely in a fundamental way on understanding physiological responses controlling photosynthesis, water balances and nutrient flux at the level of the leaf (Aber and Melillo 1991). There is no parallel to this hierarchical understanding in ungulate ecology, and I believe this notable absence of multi-scale synthesis can be traced to 2 fundamental challenges that have yet to be met successfully.

The first challenge is the integration of behavior into predictive, ecosystem models. Many of the connections between ungulates and ecosystems are behavioral rather than physiological. As I showed above, volition and its manifestation in selection of diets, patches, and habitat selection plays a fundamental role in determining the ways that ungulates interact with their environment and often shapes the outcomes of those interactions. Selectivity by ungulates is particularly important in ecosystems because it operates at multiple scales, from the plant to region (Senft et al. 1987, Coughenour 1991, Seagle et al. 1992), and because it is extremely rapid in its response to environmental variation (Bryant et al. 1991). Scaling-up is made difficult because our understanding of the behavioral responses of ungulates to their environment is nowhere near as well developed as, for example, our understanding of the physiological response of plants to their environment.

The second unresolved challenge is to understand the relations between population dynam-

ics of ungulates and ecosystem processes. By far, most studies of ungulate populations have been substantially introspective—variation in population density was seen as a way to understand populations (Sinclair 1977, McCullough 1979, Houston 1982, Coughenour and Singer 1996). Rarely have population experiments with ungulates been used to understand ecosystems. There are notable exceptions, and the natural experiment caused by the release of ungulates in East Africa from control by rinderpest is an outstanding one. Much has been learned about the role of ungulates in ecosystems from this experiment (Sinclair and Norton-Griffiths 1982, McNaughton 1992). Studies that have controlled ungulate densities and observed ecosystem level response have documented striking, non-linear relations (Hobbs et al. 1996a, b). However, studies such as these remain the exception, and future progress in understanding how ungulates modify ecosystems and respond to ecosystem change will require experiments that manipulate density.

For many years, managers of natural resources focused their attention on a few outputs of ecosystems. For example, forest ecosystems produced trees, watersheds, wildlife, and recreation. The emerging ethic of ecosystem management (Grumbine 1994, Kaufmann et al. 1994, Knight 1996) has broadened that focus to include the importance of a wide range of ecosystem properties and processes. Many managers now appreciate the fundamental importance of maintaining the integrity of whole systems. An important consequence of this change in focus is the realization that the components of ecosystems that were once viewed as outputs or products must now be seen as entry points or opportunities for management action. Ungulates offer such opportunity because they play an important role in many ecosystem processes and because managers can influence their abundance and distribution by harvest. This opportunity allows managers of natural resources to alter the state and trajectory of ecosystems.

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## APPENDIX A: ESTIMATION OF NITROGEN RETURNS TO ECOSYSTEMS BY UNGULATES

Nitrogen (N) excreted in urine and feces consists of 2 components. The first component is endogenous nitrogen ( $N_e$ ) resulting from the breakdown of body tissues and N excreted during digestion (i.e., enzymes, mucosal sloughings). The second component is N of plant origin that is not absorbed and metabolized by the animal. These components can be estimated for an individual ungulate as follows.

Dietary N intake ( $N_i$ , g/day) can be estimated as function of body mass ( $W$ , kg) (Cordova et

al. 1978), and dietary concentration of N in plants consumed ( $N_p$ , gN/g dry matter),

$$N_i = 25 \cdot W \cdot N_p \quad (1)$$

Assuming that animals are not catabolizing lean body to meet energy demands, endogenous N in urine (EUN, g/day) can be approximated as

$$EUN = 0.1 W_{kg}^{0.75} \quad (2)$$

based on the data in Robbins (1983: Table 8.3). Endogenous fecal N (EFN) can be estimated using (Robbins 1983: Table 8.1),

$$EFN = 4.21 \cdot 0.025 \cdot W_{kg} \quad (3)$$

Nitrogen of plant origin (PFN) excreted in the feces (g/day) can be estimated from dietary N content and the true digestibility of plant N (TDN, decimal percent),

$$PFN = (1 - TDN) \cdot N_i \quad (4)$$

For plants that do not contain protein precipitating compounds, we can assume that TDN  $\approx$  0.95 (Robbins et al. 1974, Van Soest 1982, Mould and Robbins 1981). Nitrogen of plant origin (PUN, g/day) in the urine is determined by N intake ( $N_i$ ), by true N digestibility (Van Soest 1982), and by the biological value (BV, decimal percent) of protein in the diet,

$$PUN = N_i \cdot TDN - (N_i \cdot BV). \quad (5)$$

Biological value can be estimated from Mould and Robbins (1981: Fig 6) as

$$BV = 0.781 - (11.6 \cdot N) \quad (6)$$

Combining these expressions and simplifying, we obtain values for urinary N returns ( $N_u$ , g/day),

$$N_u = 289.06 \cdot N^2 \cdot W + 1.9625 \cdot N \cdot W + 0.1 \cdot W^{0.75} \quad (7)$$

and for fecal returns,

$$N_f = W(1.25 \cdot N + 0.10525). \quad (8)$$

These can be expressed as a proportion of plant N consumed,

$$\frac{N_f}{N_i} = 0.05 + \frac{0.00421}{N} \quad (9)$$

$$\frac{N_u}{N_i} = 11.56 \cdot N + \frac{0.004}{N \cdot W^{0.25}} + 0.078 \quad (10)$$

With an allometric relation for home range size for mammalian herbivores ( $A_{km}^2 = 0.032W_{kg}^{0.98}$ , Harestad and Bunnell 1979), and assuming year-

round occupancy of the home range, we can calculate net returns of N ( $N_i$ , kg ha<sup>-1</sup> yr<sup>-1</sup>),

$$N_i = \frac{N_u + N_f}{0.032 \cdot W_{kg}^{0.75}} \cdot 1 \frac{\text{kg}}{1,000 \text{ g}} \cdot \frac{100 \text{ ha}}{1 \text{ km}^2} \cdot \frac{365 \text{ day}}{\text{yr}} \quad (11)$$

There are 2 important sources of error in these approximations. First, they do not account for urinary excretion of N resulting from catabolism of lean body required to meet energy demands. Such excretion can be substantial (Mould and Robbins 1981: Fig. 3) and probably contributes to excretory returns of N whenever plants are senescent. Because plant N content tends to be correlated with digestible energy levels, this

source of error will be particularly problematic when plant N levels are low. Thus, the estimates provided above will tend to underestimate N at low levels of plant N.

In addition, I assumed above that true N digestibility is static and high. This assumption is reasonable for grasses and some dicots. However, when plants contain tannin or other protein precipitating compounds as is the case for many browses, N digestibility can be variable and low (Robbins et al. 1987). In this case, N digestibility will need to be adjusted by measures of protein precipitation (Hanley et al. 1992) to compensate for these effects in equations 3 and 4.

## ESTIMATING FAT CONTENT OF CARIBOU FROM BODY CONDITION SCORES

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**Abstract:** Body condition scores provide a subjective measure of body fatness. We scored the condition of 64 barren-ground caribou (*Rangifer tarandus granti*) and 10 reindeer (*R. t. tarandus*) that were later killed and analyzed for chemical composition. A body reserve index (product of body condition score and body mass) was superior to either body mass or body condition score as a predictor of fatness for older calves and adults. The probability of pregnancy for adult female caribou was significantly related to both body condition score ( $n = 107$ ,  $P = 0.017$ ) and body reserve index ( $n = 103$ ,  $P < 0.001$ ).

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**Key words:** arctic, body condition score, body mass, body reserves, body weight, caribou, fat, pregnancy, *Rangifer*, reindeer.

The condition of an ungulate is principally a reflection of its fat reserves. Those reserves, in turn, are generally assumed to determine an individual's reproductive potential. Determination of fat content in live animals is often difficult, time consuming, and expensive (Franzmann 1985). Precise measurements of fatness often require sacrifice of the study animal, effectively precluding research clarifying the effects on subsequent fecundity or survival.

Body condition scoring is a reasonable alter-

native to direct measurement of chemical composition. It provides an index of the energy stored as fat and muscle and is a quick, reliable means of identifying extremes of nutritional status (Franzmann 1985). In the livestock industry, condition scores have been widely applied as measures of nutrition, reproductive potential, and herd health or productivity (Wildman et al. 1982, Ruegg 1991). For instance, such scoring systems have been used to investigate the effects of fatness on activity and secretion of repro-