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# Evolution and Wildlife Management

All ecosystems contain multiple layers of information. These layers may coincide with trophic levels, or they may coincide with human usage patterns in the system. Additional layers are provided by the organisms living within the system as they interpret information concerning resource availability, mating opportunities, etc. When we manage an ecosystem, we place values on different forms of information. Some are extraneous to our management goals and are therefore considered to be unimportant. Other information may be used in various ways and interpreted differently depending on our management goals. However, managers must take great care not to dismiss information that may be critical to the survival of components of the ecosystem other than those directly affiliated with their management goals (e.g., non-target species).

This paper examines the role that information about vegetation plays in ecosystem management, when the goal of that management is the production of wildlife species. Frequently, "wildlife" is narrowly defined as being mammalian species, rather than including birds and fish. In this paper, this definition is narrowed even further to allow us to examine what role vegetation information has played in the management of herbivorous wildlife species. Four primary types of vegetation data have historically been considered to be critical in the management of wild herbivores. These include whether or not the system is overgrazed, the effects of grazing on community structure (usually defined as species diversity), information on exotic plant species and spread, and the effects of management on endan-gered plant species or habitats (e.g., riparian areas). I will examine each of these briefly and will conclude by encouraging managers to add a new data layer to their arsenal: that of the evolutionary responses of vegetation to herbivory.

## Overgrazing and Wildlife Management

Implicit within the term "overgrazing" is the concept that ecosystems have an equilibrial level to which they will return if left unperturbed by humans. Different definitions of overgrazing exist depending upon the definition of this equilibrium (Coughenour and Singer 1991). The most relaxed definitions assume that ecosystems have multiple stable states (Caughley 1979) or exhibit chaotic behavior. The definitions which are least relaxed assume that there is a defined equilibrial

point for ecosystems, and that reductions of plant vigor, extinctions of species, and reductions in herbivore biomass can result in an irrevocable change in the system. This is analogous to the terminology introduced by Lauenroth et al. (1978) when they found certain combinations of perturbations to the shortgrass prairie that resulted in the formation of a new community structure that would not return to shortgrass prairie. This new structure was termed a "basin of attraction."

A great deal of interest has focused on the idea of irreversible ecosystem change in the management literature, particularly as it applies to the idea of carrying capacity (Caughley 1979). Strictly defined, carrying capacity is the number of organisms a given environment can support at a given time in a sustainable manner. This definition does not consider climatic variability. Climate is extremely important in regulating variance of biomass production between years, while shorter-term factors such as grazing are more important in regulating biomass production (both mean and variance) within a given year. In a meta-analysis of grazing literature, Dyer and Wallace (in prep.) found that grazers tended to increase mean production of monocots while reducing the coefficient of variation (CV) around that mean within a given year, resulting in a more stable or predictable mean. Dicots responded in a very different manner, with no general response in either mean or CV. Thus in monocot-dominated systems (e.g., grasslands), it appears that grazers tend to control the mean biomass production and the stability of that mean within a year. To date, only one field test of this finding has taken place (Bell 1997), in which grazers were found to increase mean production and decrease its CV for monocots at the landscape scale. However, grazers had no significant effect on mean production and its CV for dicots, or for monocots at the community or individual-plant scales. Climate was found to be important for regulating the variability of biomass production between years. Of several factors examined, grazing had the greatest influence on production variability, decreasing it significantly at the landscape scale for both years of the study. Thus, our definition of carrying capacity has to be modified to realize that the interaction between herbivores and their forage base may be under different controls than we previously imagined. This does not come under our typical overgrazing definitions, but rather views grazing as having effects that may differ at different spatial and temporal scales (Brown and Allen 1989; Hendon and Briske 1997).

## Grazing and Community Structure

Volumes have been written concerning the effects of grazing on plant

community structure (for reviews see Vallentine 1990; Heitschmidt and Stuth1991; Wallace and Dyer 1995, 1996). Much of the management literature describes the "climax" stage of a community and states that any change from this stage due to herbivory constitutes range degradation. Numerous examples have been found in which managed grazing by both wild and domestic herbivores has caused reductions in species diversity. Again, depending on the definition of ecosystem stability used, some of these changes could be due to the combined effects of climate and grazing and could be well within the natural range of variation experienced by the system and its multiple stable states or chaotic behavior (van de Koppel et al. 1997). Although there is considerable controversy surrounding the diversity–stability issue (Tilman and Downing 1994; Huston 1997), the potential for change in ecosystem functioning due to alterations in community structure is of great concern to managers.

## Grazing and Exotic Plant Species

Grazing opens plant canopies (Heitschmidt and Stuth 1991; Escos et al. 1997) thereby increasing the amount of bare ground in many communities (Wallace and Dyer 1996). These openings can increase the relative availability of light and nutrients, both critical resources in grazed systems (Tilman 1990). Invasion of exotic plant species appears to be enhanced when such openings exist. Once such a foothold is gained, further movement of the exotic throughout the system can occur, either with or without the mediation of grazing. Examples of such invasions include Russian and spotted knapweeds, leafy spurge, Canadian thistle, cheatgrass, ox-eye daisy, and more. These exotics further their spread into communities primarily where they are not consumed by wildlife herbivores, while many of the native species are grazed. This sets up asymmetric competition in which the native species are at a disadvantage (Keddy 1989; Law et al. 1997). Exotic species may alter ecosystem function sufficiently to force the system into a new basin of attraction (Chapin et al. 1997). One example of this is cheatgrass invasion, in which the phenology of *Bromus tectorum* has altered the fire regime of much of the sagebrush grasslands of the intermountain western USA, causing the loss of many native species (Mack 1981; Brandt and Rickard 1994). It is interesting to note, however, that current livestock grazing is not always a prerequisite to the invasion by exotic species. Brandt and Rickard (1994) found that exotic species still readily invaded areas which had been grazed several decades prior to their study.

## Grazing and Endangered Species or Habitats

Riparian areas and other critical habitats are particularly susceptible

to degradation by herbivore use (see Naiman and Rogers 1997 for a review). Large-bodied animals create paths, which increase soil erosion into waterways, compact the soil, and can greatly decrease vegetation growth in these sensitive areas. Browse species can be negatively affected either directly (through heavy browsing) or indirectly, due to animal effects on soils, overstory vegetation, hydrology, etc. When regulating animal usage of these areas, it is important to separate direct and indirect effects so that managers know whether solutions lie in reductions of animal numbers or some form of habitat modification to ameliorate damage. Other habitats which have been critically affected by wildlife grazing include arid grasslands. These grasslands can easily be shifted from a grass stable-state to a woody vegetation state (van de Koppel et al. 1997). If wildlife movements are restricted, or wildlife are somehow forced into these environments, or wildlife and domestic grazers both utilize the same area, desertification can occur.

Any wildlife management plan for a region including such habitats needs to take rare and endangered species into consideration. The primary cause of species being listed as threatened or endangered is loss of habitat. Wildlife grazing in fragile areas such as riparian sites or tundra may place unique species at risk. For example, *Philippsia algida* (icegrass)

is a rare species that grows in wet alpine gravel below melting snowbanks (Clark et al. 1989) and is threatened by livestock grazing.

## Shortcomings of Past Usages of Vegetation Information by Wildlife Managers

Wildlife managers are frequently faced with the issue of ecosystem management as well. If one was assigned the task of managing a typical engineering system, the task would be much more straightforward. Such systems typically have one or more definable inputs and equally definable outputs which not only need to be maximized in terms of the input variables, but also usually operate at only one spatio-temporal scale. On the other hand, wildlife managers are frequently faced with managing systems that do not have a simplistic input–output relationship. If a wildlife manager is to maximize the production of wildlife, would this place another portion of the ecosystem at risk? The typical usage of vegetation information in the past has been to yield data about ecosystem health. However, we are now finding that this issue is not as readily understood as we previously thought. Ecosystem health must be defined at many different spatial and temporal scales (Brown and Allen 1989; Allen and Hoekstra 1992; Dobson et al. 1997; Herendon and Briske 1997; von de Koppel et al.1997). Examining vegetative characteristics as static snapshots may lead to erroneous in-

terpretations in terms of the system's state relative to its long-term dynamics.

An additional, philosophical question that also depends on an understanding of system functioning at different scales is the idea of whether or not the system is "natural." Human influences on ecosystems are somehow considered to be "unnatural" or are felt to transform an ecosystem from its "natural" state to an "unnatural" one. Given that grazing ecosystems can have multiple stable states (von de Koppel et al. 1997), it is important to know what past ecosystem dynamics may be and whether or not human influences have pushed an ecosystem out of range of those preceding dynamics into a new basin of attraction. Complicating this further is the notion that potentially stable states may vary continuously with changing climate. Hence, wildlife managers striving to maintain a "natural" ecosystem that is defined according to some static ideal may not be allowing the ecosystem to express its full range of dynamic responses.

This lack of long-term knowledge of ecosystem dynamics can also lead to unrealistic expectations of herbivore behavior. Just as we have developed the myth concerning the role of Native Americans in "pristine" ecosystems (Schullery 1997), we also have a myth which states that free-ranging wildlife grazers will never have negative effects on an ecosystem. If these animals are constrained to stay in one area for any reason, if climatic variables change, or if the herd population age structure is altered, the effects of wild herbivores on the system may change over time. Again, this must be placed in context of long-term ecosystem dynamics to interpret just how seemingly novel grazing behaviors may fit within the realm of ecosystem behavior.

## Grazing and Evolutionary Biology

The evolutionary history of most forage species in North America is not extremely long (Axelrod 1985; Gottlieb and Jain 1988; MacFadden 1997). The post-Pleistocene rise of the North American flora and fauna has led to some species being tightly coupled to grazing as an important disturbance element in their physiological, morphological, and reproductive development. By examining the responses of species to grazing intensity, frequency, and seasonality, we may be able to understand their evolutionary history more fully. This history then can tell us more about long-term ecosystem dynamics in ways which would be extremely informative to wildlife management.

Milchunas et al. (1988) eloquently express how the evolutionary role of grazing in a system may influence vegetation response to herbivory. In arid systems, plant community diversity will suffer with increased grazing intensity. However, this effect is more moderate in a system with an evolutionary history of grazing than

one in which there has been little grazing over evolutionary time (Mack and Thompson 1982). Similar responses are noted for ecosystems in more mesic climates, with those systems with a long grazing history showing responses to herbivory similar to what would be predicted by the intermediate disturbance hypothesis (Connell 1978).

How long does a system need to be grazed in order to have a "long evolutionary history"? A subset of this question might be, "How quickly can plant genotypes adapt to grazing?". This has been the subject of research examining the development of grazing ecotypes. Detling and his coworkers have found that the time frame for the "development" of ecotypes showing grazing-adaptive traits can be quite short. In studies in northern mixed grass prairie, differential responses were found in as short a time as 31 years (Detling and Painter 1983; Polley and Detling 1988).

Thomas and Wallace (in prep.) found that differential responses to clipping mimicking grazing could be found in a very short time in tallgrass prairie. *Andropogon gerardii* (big bluestem) showed different morphological growth patterns between clones growing either within a 25-year-old exclosure or outside of it (Figure 1). Interestingly, *Schyzachrium scoparium* (little bluestem) showed no such response. However, this species is seldom grazed by large-bodied herbivores (e.g., bison, cattle, elk).

These types of studies show that there is sufficient genetic variation in grazed systems (even those in which vegetative reproduction predominates) such that grazing-adaptive ecotypes can exist. Tonielli (1995) found sufficient genetic diversity (Table 1) between two populations of *Phleum pratense* (timothy), an exotic grass species growing in Yellowstone National Park, to correlate with the differential response of these two populations to the combined effects of grazing and drought (Figures 2 and 3). The population from the more mesic, deeper soil location was unable to maintain high rates of gas exchange in the face of drought and grazing while the population from the drier, shallow-soil site was unaffected by drought and grazing (Figure 2). Greenhouse experiments on the two populations indicate differential responses of biomass accumulation in dry rather than moist conditions as well (Figure 3). This, again, points to the critical role played by climate variability in vegetation responses.

Therefore, grazing ecosystems can maintain a wide range of genetic variability, capable of different responses to different levels of herbivory. Given this, it is an important source of information to wildlife managers in terms of what the long-term history of the system in question may be. For example, carefully
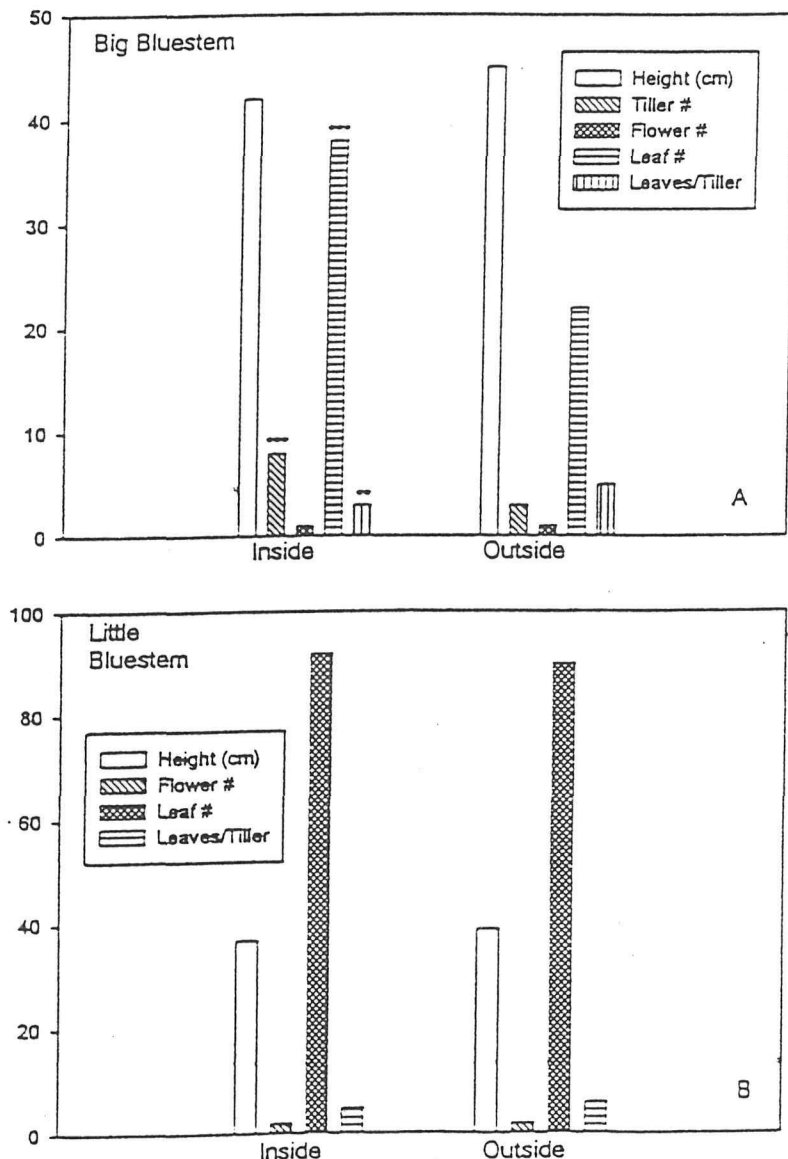
Figure 1. Morphology of *Andropogon gerardii* (big bluestem) (A) and *Schizachyrium scoparium* (little bluestem) (B) populations collected originally from inside and outside a 25-year-old exclosure in the Wichita Mountains Wildlife Refuge, southwestern Oklahoma. *Schizachyrium scoparium* is not usually grazed, while *A. gerardii* is a preferred forage species. Therefore, we can see significant differences between clones exposed to or protected from grazing in the latter species, but not the former.

Table 1. Indices of genetic variation in two populations of *Phleum pratense* in Yellowstone National Park. Means are given for each population with standard errors in parentheses, where applicable. Between-population indices (I and D) are also presented (Tonielli 1995).

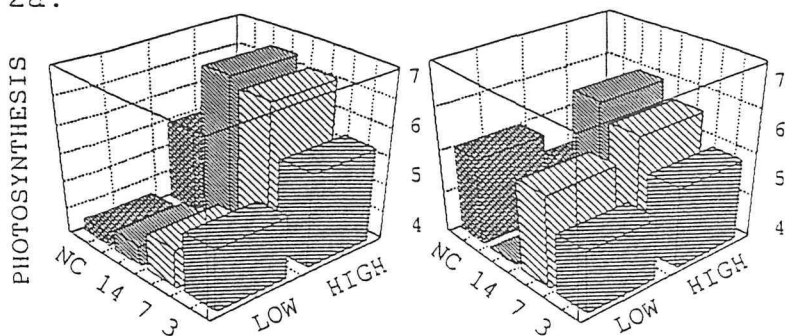| | *Upper Norris* | *Lower Cache Calfee* |
|---|---|---|
| Mean sample size / locus | 23.6 (0.6) | 53.7 (0.4) |
| Mean number of alleles / locus | 1.4 (0.3) | 1.4 (0.3) |
| Proportion of polymorphic loci | 21.4 | 21.4 |
| Mean number of alleles / polymorphic locus | 3 | 3 |
| Mean observed heterozygosity | 0.068 (.038) | 0.061 (.035) |
| Mean expected heterozygosity | 0.087 (.052) | 0.094 (.054) |
| Nei's (1978) genetic identity (I) | 0.997 | |
| Genetic distance (D) | 0.003 | |

crafted experiments can show which frequencies and intensities of grazing could optimize the growth of different genotypes (Oesterheld and McNaughton 1988, 1991). These studies could also be coupled with timing of precipitation, and different soil types (Georgiadis et al. 1993; Hicks and Reader 1995; Tonielli 1995; Varnamkhasti et al. 1995), to show what seasonal levels of grazing may have resulted in optimal growth in the past and how these levels interact with soil types (Molvar et al. 1993). These data could be collected from clones located across a landscape or across resource gradients on the landscape. Then, by taking this information and organizing it within a spatial and temporal model of the landscape, the manager could develop an evolutionary model of herbivore grazing intensities. If the movement patterns and grazing in-

tensities found in the extant landscape do not fall within these bounds (allowing for interannual variability), the manager may wish to take additional actions to modify herd movements, herd size, etc. The choice of forage species to study is extremely important. Both currently dominant species as well as rare species need to be examined, because rare species may be rare due to their response to herbivory, rather than a response to competitive pressures (Hartnett 1989; Hulme 1996).
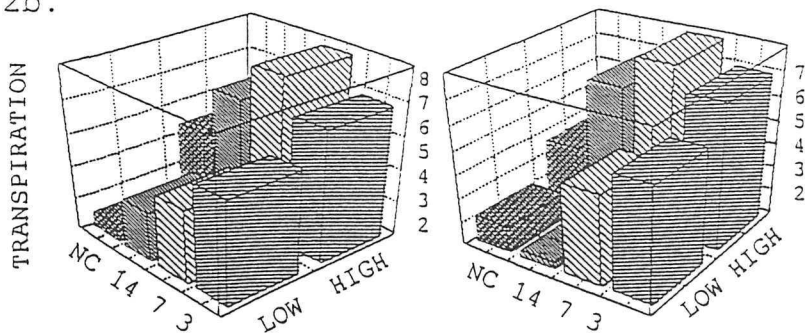
Experiments such as those described above examine the evolutionary history of the entire ecosystem. They do not discern the mechanism for the range of responses shown by either the herbivores or the plants. This has been an area of great controversy (e.g. Brown and Stuth 1993; Cebrian and Duarte 1994; Post and Klein 1996). How-
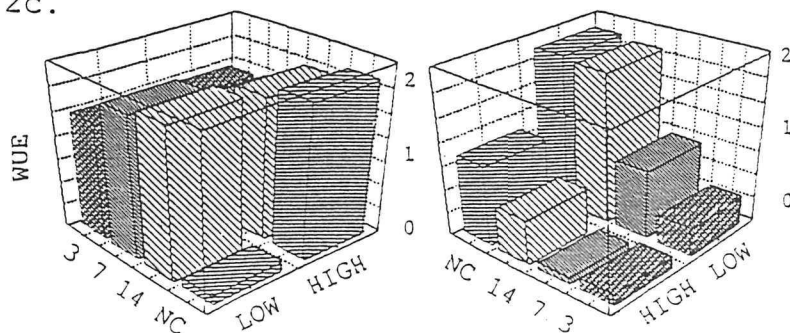
Figure 2. Physiological responses of two populations of *Phleum pratense* from Yellowstone National Park. The populations were collected at two sites, Upper Norris (UN) and Lower Cache Calfee (LCC) and were exposed to daily watering (HIGH) or weekly watering (LOW) and different clipping frequencies. NC = not clipped, 3 = clipped every 3 days, 7 = clipped weekly, 14 = clipped every other week. Data for UN are shown in the left column and for LCC are shown in the right column. Note that the population from the LCC site shows little difference in responses between high and low watering regimes. Large differences are noted for the other population.
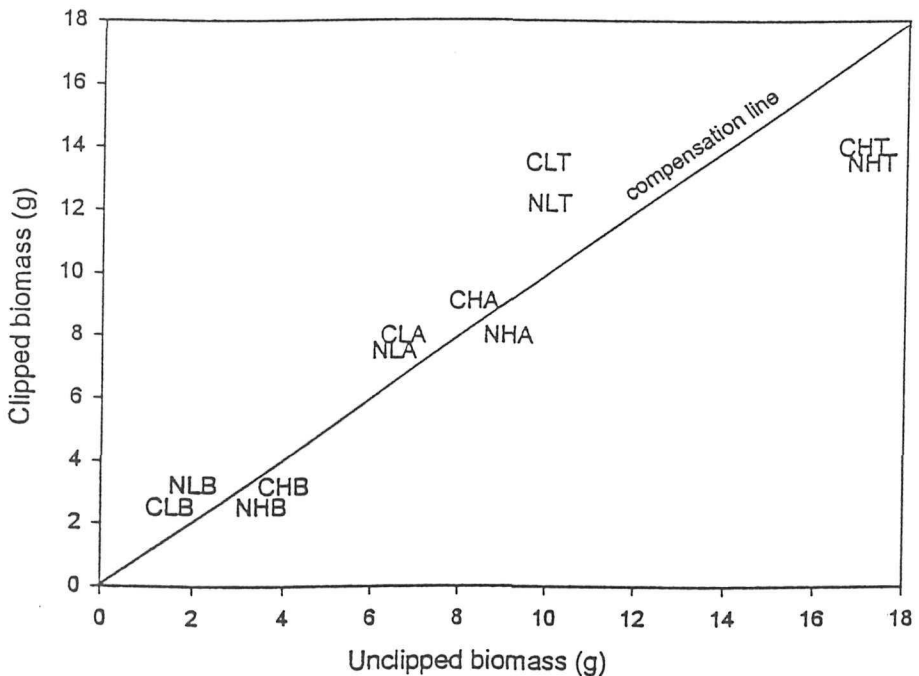
Figure 3. Comparison of clipped and unclipped treatments at the end of the experiment described in the legend of Figure 2. Legends for the points on the graph contain three sets of information. The first letter designates which site plants are from (N=Upper Norris, C=Lower Cache Calfee); the second letter describes the watering regime (L=low water, H=high water); the third letter describes which plant component was weighed (T=total biomass, A=aboveground biomass, B=belowground biomass). Note that plants which received less water tended to overcompensate regardless of the site of origin. This is important evidence for the differential effect of climate on ecosystem response to herbivores.

ever, in terms of understanding if the extant dynamics are sustainable, this question is not immediately germane. If it is determined that grazing levels are indeed not sustainable, then determining the causal agent will become critical to the manager's response.

In summary, ecosystems are dynamic entities which are capable of maintaining multiple stable states. Rather than manage for a static entity, it is critical that wildlife managers use the vegetation response to different frequencies, intensities, and timing of grazing to understand what the long-term dynamics of the system may have been. Given these boundaries of system behavior, the manager can then monitor the system to de-

termine if those boundaries have been exceeded and whether or not this excess may lead to system degradation. It is critical to attempt to do this analysis in a predictive rather than in a *post hoc* manner so that predictive models of ecosystem behavior can be developed (Nichols et al. 1995). Integrative models would also allow managers to use the large number of data layers available to them, rather than focusing on only a few output parameters. These models would, I hope, reflect the evolutionary history of the system in question more than short-term economic considerations or the biases of the system's political constituents.

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