Managing multi-unqulate systems in disturbance-adapted forest ecosystems in North America

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Summary

Understanding how interactions among ungulate populations and their environmental dynamics play out across scales of time and space is a principal obstacle to managing ungulates in western North America. Morphological similarity, forage-base homogeneity and increasing animal density each enhance the likelihood of competitive interactions among sympatric populations. Competition is an interspecific relationship with mutually negative effects, and it is often confused with amensalism. Although competition or amensalism is commonly assumed, they have been very difficult to confirm in applied management settings, perhaps because field research has not typically examined relationships across temporal and spatial scales sufficient to linking short-term or small-scale interactions with longer-term reproductive performance. Perhaps by default, neutral coexistence has been concluded in many studies, and experimental research has suggested that facilitative relationships, in which resource overlap is actually beneficial, are possible as well. Forage-mediated relationships among ungulates can be strongly influenced by disturbance-induced landscape dynamics, through which forage composition (diversity), production, quality and pattern mosaics are modified. Unfortunately, different management entities are responsible for ungulate populations and landscapes, respectively, and these entities often approach their respective problems at differing temporal and spatial scales. These scales of management mayor may not align with the scales at which interactions between herbivores and plants play out. The overarching challenge facing managers is to develop information systems through which multi-species management can be planned so as to demonstrably contribute to long-term ecosystem sustainability while also maintaining its socio-economic viability.

Introduction

Landscapes in western North America are naturally complex due to rather extreme variations in climate, physiography, soils and disturbance regimes. This multifaceted variation creates landscape mosaics of heterogeneous plant communities comprised of many successional states. The vast majority of these mosaics require periodic disturbance for their maintenance. Native ungulates developed adaptations that facilitated coping with one another in the face of this environmental variability.

With European settlement, however, a broad suite of domestic herbivores has been introduced and historical regimes of landscape disturbance modified (Langston, 1995). Grazing in the late nineteenth and early twentieth centuries by domestic herbivores was very intense; the belief at the time being that any herbaceous vegetation left at the end of the grazing season was wasted. At the same time, old growth stands were commonly subjected to heavy logging pressure. Removal of over storey and understorey vegetation and active fire suppression dramatically altered natural fire cycles and successional dynamics at landscape scales. Suppression of fire and non-coniferous plants facilitated establishment of conifer seedlings, and these new forests often contained more trees per hectare than occurred historically and contained tree species that were not fire-adapted or adapted to the site conditions on which they were now growing (Quigley and Arbelbide, 1997). Such new forests in the western US developed unabated throughout the western US until late in the twentieth century when the combination of drought and insect attack provided a fuel source for large-scale stand replacement wildfires.

Historically, native ungulates may have had less impact on their environment than they do today. In some cases, populations were kept in check by intense year round Native American hunting (Kay, 1994, 1995, 1997b, 2003). Populations of ungulates had unlimited access to their environment and often migrated 300 km seasonally in response

Forestry, Vol. 83, No. 2, 2010. doi:10.1093/forestry/cpq004
Advance Access publication date 19 February 2010

to annual changes in weather and forage availability (Cole, 1971; Smith *et al.,* 2004). Animals were free to move from a food patch or a seasonal range where they had depleted the highest quality food available to one that was ungrazed and in the process may have provided opportunities for previously grazed areas to regenerate. Today, animals are forced to live in ecologically incomplete, compressed (Cole, 1971; Vavra and Sheehy, 1996) and homogenized habitats (Langston, 1995). Many seasonal ranges used historically by native ungulates have now been converted to agricultural uses, cities and recreational facilities, while historical fire suppression, logging and grazing practices have effectively homogenized habitats.

Modern managers are challenged to sort out the functional significance of these disruptions and to design strategies for management that can sustain both native species and the viability of domestic production systems, while also providing the ecological functions of ecosystem disturbance. Succeeding in these potentially conflicting endeavours demands an articulate understanding of the nature of ungulate interactions with one another and with landscape disturbance and of the scales at which those interactions become relevant to strategic management. Our central aim in this paper is to review the state of knowledge concerned with interspecific relationships and regional disturbance dynamics, with an eye to illustrating their interrelated nature and their relevance, while emphasizing some of the potential obstacles to reliable inference from applied research.

The hierarchy of foraging habitats

Ungulates must confront foraging in a descending hierarchy of habitats involving several scales from regional ecosystems to landscapes, communities and ultimately feeding stations. Animals implicitly make decisions at each scale (Senft *et al.,* 1987; O'Reagain and Schwartz, 1995), and those decisions can influence, and be influenced by, disturbance agents and other herbivores.

Regional ecosystems are large-scale assemblages of landscapes through which wild and domestic ungulate populations move (or are moved in the case of domestics) to efficiently exploit the broad-scale distribution of superior food resources (Vavra, 1986; Senft *et al.,* 1987; Coughenour, 1991). At this scale, movements and distributions of ungulate populations are motivated by spatially explicit differences in the availability of limiting resources. The extent to which populations interact with one another at this scale is largely a function of the extent of spatial similarity in their resource limitations.

Within regional ecosystems, landscapes are aggregates of localized plant communities that differ in species composition, vegetation structure and geophysical characteristics (O'Reagain and Schwartz, 1995). Landscapes are mosaics of communities that are controlled by interactions among climate and episodic disturbances such as fire, plant diseases, forest practices and herbivory (Starfield and Chapin, 1996; Butler *et al.,* 2007). Within these mosaics, the distribution of animal foraging at any particular time is largely based on spatial differences in the availability of preferred plants (Skovlin and Vavra, 1979; Senft *et al.,* 1987). Any ungulate population's spatial pattern of plant exploitation can be modified by a number of factors such as the accessibility of preferred plants, the relative security that plant communities provide because of their cover characteristics or topographic position, the relative comfort they provide to animals (e.g. shade) and/or their proximity to other limiting resources such as water, minerals or escape terrain (Risenhoover and Bailey, 1985; Stuth, 1991; Sheehy and Vavra, 1996; Holechek *et al.,* 1998). As a consequence of such complexities, ungulate foraging is almost never uniformly distributed within landscapes but rather tends to be concentrated in the best settings at particular times. Focal areas for foraging within landscapes shift over time as relative preferences among settings change. These spatial preferences change as plant phenology progresses, as the biomass of preferred plants is depleted by herbivores and as disturbance agents modify nutritional and non-nutritional attributes that contribute to their attractiveness.

Different authors have assigned the term 'patch' (O'Reagain and Schwartz, 1995) or 'plant community' (Senft *et al.,* 1987) to units of vegetation within a landscape, which can be further partitioned into feeding stations (Senft *et al.,* 1987). For clarity, we use the term 'community' for the larger of these scales and patch for the smaller. Ungulates face discrete choices among and within communities. Soil nutrients, moisture regime and topographic aspect largely determine the forage production potential for any given community. But, in forests, this potential can be strongly modified by succession and resulting overstorey dominance (by trees), episodic disturbances that periodically alter *over* storey dominance and also by chronic herbivory (Riggs *et al.,* 2000, 2004).

Once ungulates have selected a community in which to forage, the next unit of selection is the patch. Patches may be formed within plant communities by such micro site modifiers as dung and urine deposits, proximity to shrubs or trees (Belsky, 1994), past defoliation by herbivores (Ganskopp *et al.,* 1993) or by fine-scale patterns in disturbance such as fire (Riggs *et al.,* 1996), which variously contribute to differences in composition and nutritional content of plant tissues at fine scale. These modifiers may be positive or negative in their effects from a foraging *perspective,* are responded to by large herbivores to varying extents (Hobbs and Spowart, 1984) and influence diet *over*lap among sympatric species (Spowart and Hobbs, 1985).

Animal efficiencies

All ungulates have annual cycles of reproduction, lactation, periodic climate stress and nutritional deprivation. To meet these challenges, each herbivore species has *evolved* rather unique morphological characteristics (Hanley, 1982; Shipley, 1999) that govern the types of landscapes, communities and patches that each species can most efficiently exploit to meet its particular nutritional demands. Body

size largely dictates nutrient demand, while gut and mouth morphology largely influence diet selectivity (Shipley, 1999). Nutrient demand and diet selectivity interact with the composition, structure and biomass of forage to determine the communities or patches in which a given herbivore can be most efficient (Wickstrom *et al., 1984;* Hobbs and Swift, 1985; Canon *et al.,* 1987). These fine-scale nutritional efficiencies interact with landscape factors (Coughenour, 1991) and with cognitive and non-cognitive mechanisms of selection (Bailey *et al.,* 1996) to influence which particular communities or patches will indeed be preferred.

Scaling on body size and gut volume is common in assemblages of coevolved species (Owen-Smith, 1985; Mc-Fadden and Shockey, 1997), and it facilitates space and food partitioning among species for the sake of energetic efficiency (Bell, 1971; Houston, 1982; Austin *et al., 1983;* Vavra *et al.,* 1989; Sheehy and Vavra, 1996; Lindzey *et al.,* 1997). The partition is seldom 'clean'; however, in that some overlap in use of nutritional resources is typical (Owen-Smith, 1985), and thus, food-mediated interactions among ungulates expected and indeed are normal in interspecific relations. The functional significance of these interactions does not rest on their occurrence, however, but rather on whether their nature is competitive, amen sal, neutral or facilitative.

The theory of interspecific competition

Resource-mediated interactions are perhaps most often considered in the context of competitive exclusion (Wagner, 1969), whereby two species utilize a common resource that is limiting, and in so doing, each species reduces the other's reproductive performance. Mutually negative effects on performance of both populations have been generally accepted as being the key criteria for confirming competition in ecology (Odum, 1971; May, 1981). Nonetheless, it has not been uncommon to see arguments for relaxing these criteria to consider amensalism as equivalent to competition (in amensal relationships only one of the populations is negatively affected) or to infer competition from effects that are not clearly linked to reproductive performance (e.g. Schoener, 1983). **In** management, such relaxations usually are rationalized for convenience but at the same time represent a risk to clarity. Nevertheless, by any measure evidence for competition among species of ungulates is uncommon and using the rigid criteria of Odum (1971) and Wagner (1969) most research has concluded non-competitive coexistence rather than competitive exclusion (Lonner and Mackie, 1983 but see Hobbs *et al.,* 1996a, b).

Research scale is relevant to meeting the criterion that is crucial for concluding either competition or amensalism: the negative effect on a population must be significant to population performance. Timescale is important because the reproductive performance of any herbivore population is not merely a function of nutrient balances during gestation and lactation. Nutrient balance in the months prior to reproduction influence the likelihood of successful breeding (Wiltbank *et al.,* 1962; Cook *et al.,* 2004) and can also influence subsequent survival probabilities of adults and young (Hobbs, 1989; Cook *et al.,* 2004). Any negative effects of resource overlap are potentially played out over timescales that cross seasons and even years and are thus subject to confounding by other potentially limiting factors (Severson and DeBano, 1991). The detection of competition's consequences can also depend on the extent of time over which resource overlap persists between species (Ganskopp *et al.,* 1999). The spatial scale of research can be crucial to detecting competition as well, given that resource overlap between sympatric species can be expected to vary across landscapes. Variation in animal densities can, for example, introduce density-dependent variation in reproductive dynamics as well. Thus, space, time and density each influence how we perceived the nature and functional importance of resource overlap.

Applying competition theory to management

In their extensive search for evidence of competition between elk and mule deer, Lindzey *et al.* (1997) stated that competition might be the selective force that drives niche separation, and they provided an in-depth discussion of the opinions of Wiens (1977), Schoener (1982, 1983) and others in this regard. When managers have been concerned with potential competition, researchers have generally taken one of two principal approaches to hypothesis generation and inference: (1) base investigation on key species theory (Standing, 1938; Smith, 1965), which focuses on food overlap at the patch scale (e.g. Hobbs and Spowart, 1984; Spowart and Hobbs, 1985; Beck and Peek, 2005) or (2) focus principally on habitat partitioning among herbivore populations at landscape scale (e.g. Yeo *et al.,* 1993). It has not been common to see both approaches well integrated in a single investigation, and furthermore, because applied investigations have a tendency to enjoy short lifespans, the influences of persistence and animal density seldom receive the deserved attention that longer term research could provide. These constraints have often rendered the inferences of applied competition research to be reliant on assumptions that short-term or small-scale relationships observed during the course of study are indeed relevant to population biology at broader spatial and! or temporal scales. Ultimately, one reading Lindzey *et al.* (1997) might conclude that competition among North American cervids is still a matter of conjecture Mackie (1978) (although the authors did not state so specifically), principally because of an apparent inability of applied researchers to link various degrees of observed resource overlap to broader-scale reproductive performance.

Because interspecific competition and amensalism have been difficult to document definitively, managers are usually hampered by imperfect knowledge. An alternative to managing interspecific relationships directly is to manage them indirectly based on the density-dependent ecology of the respective species. Intra-specific competition increases

as the density of animals increases. Dominant individuals are likely to obtain the highest quality diets over time, forcing sub-dominants to subsist on inferior forage after dominants abandon feeding stations. Houston (1982) found that age of sexual maturity of female elk, pregnancy rates in 2-year-old elk and survival of young over the first year to be density dependent. Energy balance and winter mortality of mule deer are strongly influenced by food biomass with juvenile deer relatively more sensitive than adults (Hobbs, 1989). The probability of mortality increases as a function of time, over which juvenile deer expend a greater proportion of reserves than do adults, thereby predisposing juveniles to higher mortality, regardless of density. Deer populations at higher densities should experience a more rapid decline in forage biomass and quality during the course of the growing season, thereby reducing fitness at the onset of winter and increasing the probability of juvenile mortality in winter. Second, as an ungulate population increases in number, its influence on vegetation stability increases. Winter ranges, where herbaceous plants are consumed during their dormant period, may be relatively insensitive to increasing animal density (Houston, 1982; Wambolt *et al.,* 1998). On spring and summer ranges, however, herbaceous plants are consumed during their active growth cycle, and highly preferred forage species may be cropped to such extent that their reproduction and/or accrual of carbohydrate reserves is limited. Under this circumstance, herbivore-induced changes in composition are more likely to occur at relatively low densities (Austin *et al.,* 1983; Bowns and Bagley, 1986; Miller *et al.,* 1994; Riggs *et al.,* 2000). Trees and shrubs may react differently to seasonal defoliation, whereby winter defoliation has an impact on future growth (Kupferschmid and Bugmann, 2008).

In some cases, foraging habitats have been shown to improve with grazing (McNaughton, 1976), usually as a result of enhanced nutrient cycling, or induced growth stimulation (Peek *et al.,* 1978; Pastor and Naiman, 1992; Molvar *et al.,* 1993). Such studies usually view the forage substrate as being more or less homogenous at the patch or feeding station scale, whereas in reality, such substrates are rather heterogeneous in terms of their botanical composition and susceptibility of their constituent plant species to grazing. Where the substrate is heterogeneous, which it usually is, persistent selective foraging by a single herbivore species is likely to move plant succession in a direction that provides competitive advantage to those plants that are not preferred (Severson and Urness, 1994) and could lead to localized suppression or even the extinction of some of the most preferred species. Where this occurs, it represents a negative feedback, which has been demonstrated for both domestic livestock and wild ungulates (Chadde and Kay, 1991; Pastor and Naiman, 1992; Fleischner, 1994; Kay, 1997a; Riggs *et al.,* 2000). One might expect (hypothesize) that at comparable levels of grazing intensity (e.g. total forage demand per kilogram of total forage produced), wild selective herbivores (e.g. mule deer, roe deer *(Capreolus capreolus))* could influence forest succession to greater extent than larger domestic herbivores, which tend to be more general in their food habits. However, this hypothesis runs counter to the broadly accepted notion that native herbivores are more benign in their effects than that are domestics. Nevertheless, a caveat in western forests and woodlands is that certain disturbance-adapted plant species are often preferred by both generalist and by selective foragers, e.g. bitterbrush (Lesperance *et al.,* 1970), and thus, in landscapes occupied by both types of herbivore such comparisons are likely to be irrelevant. If landscape disturbance regimes (e.g. fires or surrogates like logging) are insufficient to ensure regeneration of these disturbance-adapted plant species over time, then the cumulative grazing pressure is likely to degrade their representation, sometimes even under low animal-density regimes (Lesperance *et al.,* 1970; Riggs *et al.,* 2000). When selective-grazing feedbacks are played out at landscape scale, animal carrying capacity can be degraded over time (deCalesta and Stout, 1997) even though obvious signs of 'overgrazing' are lacking. In western North America, aspen *(Populus tremuloides* Michx.), bitter brush *(Purshia tridentata* (Pursh) OC.) and mountain mahogany *(Cercocarpus* sp.) are commonly considered at risk from the combined effects of persistent herbivory and reduced episodic disturbance, but negative trends in status of these species have been so subtle as to be noticeable only after several decades.

Ungulates may influence their foraging habitats even when numbers are relatively low because reduced animal density facilitates a reduction in feeding patch size. This influence may be equally negative to the herbivore (as the density-dependent factors previously mentioned) but neutral or positive to the affected plants. Grazing herbivores are particularly sensitive to the presence of coarse standing herbaceous litter (Ganskopp *et al.,* 1993), and their selection of patches for feeding is negatively influenced by the presence of coarse, standing herbaceous litter (McNaughton, 1984; Ganskopp and Bohnert, 2006). There appear to be nutritional advantages to this selective behaviour for the grazer (Birrell, 1989; Ganskopp *et al.,* 2004) and implications for ecological condition of the range (McNaughton, 1984; Coughenour, 1991). Recently, burned areas are commonly preferred by ungulates due, at least in part, to the lack of standing litter (Riggs *et al.,* 1996). Periodic defoliation can have similar influences on shrubs by stimulating lateral budding and adventitious growth in the interior of the crown (Lesperance *et al.,* 1970; Peek *et al., 1978).*

Theory of facilitation

The theory of facilitation arises from observations that certain modifications of ecosystems by ungulates apparently facilitate improvement in the foraging substrate for syrnpatric species (e.g. Bell, 1971; Anderson and Scherzinger, 1975; McNaughton, 1976). Facilitation is thus an alternative to competition and amensalism in the consideration of interspecific interactions. Anderson and Scherzinger (1975) explain the facilitation hypothesis as it relates to structure. Specific methodologies to manipulate structure and succession are discussed by Severson and Urness (1994). Controlled livestock grazing, for example, can be used to enhance foraging conditions for wild ungulates in

several ways including: (1) modify the botanical composition of plant communities to favour plant species that are preferred by wild ungulates, (2) increase productivity of preferred species, (3) increase the nutritive quality of preferred species seasonally and (4) increase structural diversity in the landscape mosaic (Severson and Urness, 1994). Domestic herbivores (cattle, horses and sheep) can be used to seasonally improve foraging habitat for wild species (pronghorn, deer and elk). Some research shows that intensively managed grazing by sheep and/or goats can arrest or even reverse encroachment by invasive species (Walker *et al.,* 1994). However, research exploring facilitative grazing systems is usually conducted at relatively small spatial scales and under highly controlled regimes that may not have analogues in normal applied circumstances (Riggs *et al.,* 1990; Ganskopp *et al.,* 1999,2007).

Application of facilitation

The mismatch of scale between experimental research and applied management should motivate caution when attempting facilitative grazing management. Seasonal food preferences of the facilitative herbivore must be known because improperly timed or stocked grazing may negatively impact the plant species of interest. For example, cattle can be used to improve the productivity of a shrub species like bitterbrush because cattle usually focus on herbaceous plants early in the growing season. However, as herbs senesce cattle are more likely to gravitate towards this shrub as the season progresses (Lesperance *et al.,* 1970), and late defoliation can stimulate regrowth that cannot winter harden, thereby killing the plant. Thus, the time of the facilitative cattle grazing is crucial. Sheep may be marginal facilitators or require more intensive management in regard to season of use and stocking density if they are used to enhance shrubs because they are more inclined than cattle or horses to consume shrubs (Urness, 1990; Alpe *et al.,* 1999 but see Rhoades and Sharrow, 1990). Alpe *et al.* (1999) reported that sheep grazing had both negative and positive influences on browse quality and quantity but concluded that a carefully managed sheep-grazing programme could improve browse quality for wild ungulates in the following winter.

Generally speaking, large generalist ungulates (e.g. cattle) are more easily employed as facilitators than are smaller selective feeders (e.g. sheep). Large generalists are more likely to thrive on relatively poorer quality forage and in the process of grazing reduce the amount of obstructive litter (Bell, 1971). Smaller more selective herbivores are then more likely to take advantage of a residual sward that is low in biomass, but high in quality, and in particular if the sward regrows following the initial grazing treatment. Selective grazing by small herbivores is not likely to materially enhance forage swards for larger sympatrics in most circumstances, but there are exceptions (Riggs *et al., 1990).*

Facilitation has occurred in the western US, but documentation of its relevance at management scales is limited. The most-cited case studies have involved using cattle grazing to improve forage conditions for elk (Anderson and Scherzinger, 1975; Frisina and Morin, 1991; Frisina, 1992). Launchbaugh (2006) provides a how-to handbook for targeted grazing that includes using livestock to improve wildlife habitat. Likewise, Payne and Bryant (1994) describe several facilitative grazing systems for wildlife across a range of ecosystems. In Europe, Gordon (1988) reported that reintroduction of cattle increased calf crops for red deer hinds and speculated that cattle grazing could improve forage for red deer, and possibly sheep, over large areas of north-west Scotland.

Nevertheless, caution should be applied when attempting to facilitate forage enhancements for wildlife using livestock. In practice, facilitation usually involves modification of the forage sward through enhancement of the herbage layer and principally by stimulating grass regrowth or by making it more accessible (Anderson and Scherzinger, 1975; Severson and Urness, 1994). This type of facilitation is typically referred to as 'forage conditioning' and in practice usually involves using early season grazing by cattle to stimulate regrowth of grass that will subsequently senesce prior to maturity and thus be of higher nutritive value to wild herbivores later in the year. The caveat to this approach is that the realization of regrowth is dependent on there being sufficient soil moisture to support significant regrowth after cattle have been removed (Pitt, 1986). Judging the adequacy of soil moisture remains more art than science for most managers, and in arid or semi-arid regions or on thin soils, insufficient soil moisture will preclude realization of the facilitation. Ganskopp (1998) found an interacting effect of soil moisture and time of grass defoliation. Regrowth was 22 per cent of total herbage yield in a dry year and 50 per cent of total yield in an average precipitation year (but see Ganskopp *et al.,* 2004). When formulating the forage conditioning hypothesis, Anderson and Scherzinger (1975) did not address the relevance of soil moisture heterogeneity at landscape scale. Most western landscapes are heterogeneous in soil depth and type and are thus variable in their ability to retain moisture. Managers can expect the forage conditioning hypothesis to be operative on only part of the landscape.

The production of annual biomass from shrubs and trees may also be facilitated by livestock grazing. Cattle are primarily grass consumers particularly prior to maturation of grasses. Growing season defoliation affects the competitive ability of grasses, leaving them less able to compete for soil water and nutrient resources with neighbouring shrubs and/or trees that are not defoliated (Augustine and McNaughton, 1998). Ganskopp *et at.* (1999) found that early season grazing by cattle resulted in bitter brush that equalled or exceeded ungrazed control plants in volume for 3 years of study. However, cattle use of bitter brush increased as grasses matured (Ganskopp *et al.,* 1999) and negatively affected shrub volume compared with ungrazed controls.

Management considerations

Severson and Urness (1994) remarked that dynamic processes involved in plant community changes are a concern to

wildlife biologists when managing habitats and further that changes in plant composition, productivity and community structure will influence wildlife populations at the individual species and faunal assemblage levels. Improper livestock grazing has had tremendous negative effects in western North America (Fleischner, 1994), but livestock grazing systems nevertheless can be defined which will demonstrably benefit wildlife (Bryant, 1982; Severson and Urness, 1994).

Conversely, the managed growth and maintenance of high populations of wild ungulates in the twentieth century has also wrought dramatic and apparently negative effects in several ecosystems (Irwin *et al.,* 1994; Kay, 1997a; Riggs *et al.,* 2000), and in these circumstances, management goals for these wild populations could usefully be conditioned on larger ecosystem goals. The species of herbivore (wild or domestic) would seem less important to the ecological role of herbivory than the density and scale at which the herbivory is managed.

Succession

In the temperate coniferous forests, typical of western North America, late successional plant communities dominated by conifers or unpalatable shrubs seldom provide adequate foraging habitats for large ungulate populations. The bulk of the forage resource in forests is found in the 'transitory' habitats that develop following disturbance (e.g. timber harvest, fire). Transitory vegetations can provide diverse and productive forage arrays for large ungulates, but as succession progresses, the late-succession dominants regain status over time through resource competition and shading (Riegel *et al.,* 1991). On any given forest site, the transitory 'window' is often short, and while the decline of the forage sward is ultimately driven by closure of the forest canopy, it can also be accelerated by persistent grazing (Hobbs, 1996; Augustine and McNaughton, 1998; Riggs *et al.,* 2000). **In** some ecosystems, e.g. eastern US hardwood forests, white-tailed deer have altered regeneration in late successional forests and altered successions following disturbance (Tilghman, 1989). The changing US political climate has resulted in the near cessation of timber harvest and precommercial forest thinning on public lands, while fire regimes remain largely suppressed in managed landscapes. Timber harvest and thinning, if conducted with wild ungulates in mind, can facilitate understorey production (Rhoades and Sharrow, 1990; Visscher and Merrill, 2009). **In** more arid systems, Juniper *(Juniperus* sp.) and sagebrush *(Artemisia* sp.) communities exhibit similar declines in their herbaceous forage components during the course of their successions as well. Near monocultures of these species have developed over time across vast arid landscapes (Miller *et al.,* 1994). Carefully applied management practices such as cutting, fire or chaining can markedly enhance nutritional carrying capacities for both wild and domestic herbivores in these landscapes, but again, these management actions must be undertaken at the large scales meaningful to populations. Nevertheless, for any of these disturbance agents to be effective, they must be executed at scales that are relevant to the size (nutrient demand) of the herbivore populations in the landscape; large ungulate populations require large-scale disturbance regimes in these ecosystems (Riggs *et al.,* 1996). Along with relevant scale, forest managers should consider ungulate density, the composition of landscapes and herbivory effects on regeneration and composition of desired species (Horsley *et al.,* 2003), and ungulate populations may need to be adjusted to a threshold level (deCalesta and Stout, 1997).

Scale

The issue of scale is very important when considering management and planning of successional dynamics for habitats that cress-land ownerships. Private landowners tend to be more 'pasture oriented' as their livestock are restricted to fenced pastures. The largest scale relevant to private operators is usually that of their own ranch or if they graze public land the allotment area to which their grazing is restricted. State government agencies, however, plan and manage at rather large scales (multi-watersheds), which typically approximate the spatial extents of wild populations. These large planning units may contain several landscapes defined by watersheds, subwatersheds and/or political boundaries. Federal agencies increasingly conduct strategic long-range planning at scales approximating regional ecosystems, while nonetheless constraining their tactical management decisions to smaller scales on the order of watersheds or subwatersheds. The salient point is that these diverse entities do not share a common spatial-temporal basis for planning or management in most circumstances. Nonetheless, anyone entity's decisions at one scale can and does influence the options and outcomes for the others. Additionally, research-generated knowledge is often uniscalar and often not generated at the scale at which management must be undertaken.

Landscape

Despite growing evidence of density-dependent feedbacks resulting from high ungulate densities and reduced disturbance regimes, one can reasonably assume that public policy in western North America will continue to maximize herbivore population sizes (if not productivity). Big game herds are unlikely to be reduced except perhaps on some private lands, and livestock will continue on public as well as on private lands albeit somewhat reduced on the former. Most ecological assessments compare current vegetation with that perceived to have existed during the pre-settlement period, consider any deviations from historical conditions to be negative impacts, and champion management activities to return to those pre-settlement conditions (Quigley and Arbelbide, 1997). Nevertheless, it is widely recognized that pre-settlement conditions can only be approximated and never fully replicated, and restoration goals are commonly addressed in management documents as 'adaptive', 'ecosystem' or 'sustainable' end points. However, because ecosystems are dynamic, application of any of these should not be considered as particular states or

attainable end points but rather as trajectories with certain bounds (Fuentes, 1993).

Almost all North American ecosystems are disturbance adapted, with the main difference being the time interval between disturbances. In this context, management of ecosystems to accommodate multiple ungulates invariably involves periodic landscape-scale disturbance. Prescribed fire, conifer cutting and other similar tools can be used singly or in combination to develop mosaic patterns. The timescales or intervals at which disturbances repeat are specific to ecosystems as well as to goals for balancing early-succession and late succession vegetations. For example, natural fire cycles occurred every 8-15 years in many ponderosa pine types, 15-50 years in various sagebrush types and every 200-300 years in some conifer systems (Riggs *et ai.,* 1996). Such differences suggest strategies for anthropogenic management and for managing herbivore dynamics. It is probably unrealistic to expect to maintain high herbivore densities and meet strategic vegetation goals in most landscapes.

Livestock

Given that livestock grazing will continue on public lands, specialized programmes based on facilitation can enhance the utility of domestic grazing and should be considered by management agencies. Facilitative grazing provides foraging patches at larger scales within a given landscape. Wild ungulates in the absence of broad-scale forage removal by livestock may concentrate foraging on preferred areas and create grazing lawns. Adjacent areas may be ungrazed and contain persistent standing litter that essentially makes them 'grazing proof' (Ganskopp *et al.,* 1992; Ganskopp *et al.,* 1993). Changes in timing of livestock grazing should also be considered on landscapes where the potential for competitive interactions is possible. Ranges where shrubs are an important diet component of wild ungulates should not be grazed by livestock after maturity of grass species, or if grazed at the time, at low density and carefully monitored. In these cases, livestock grazing reduces the availability of concentrated forage patches to areas not preferred by livestock (scale reduction). Wild ungulates are forced to disperse in search of scarce nutrient concentrations. Likewise, livestock use should be deferred until after fawning where herbaceous cover is an important structural component of fawning habitat (Barrett, 1981) because livestock grazing reduces structure by utilization.

Pastor *et al.* (1997) provide an important cautionary note. When managers intentionally alter the spatial and temporal dynamics of habitat, a poor understanding of how heterogeneity arises in ecological systems sometimes leads to management techniques causing the opposite effects of those intended. Failure is always a risk of action. A prescribed fire that is designed to burn 60 per cent of the prescription area but actually burns 100 per cent serves as an example. Lack of a regenerating shrub component on that same area would compound the problem, particularly if the area was a mule deer winter range. However, no action may result in a fuel build-up and increasing risk of conflagration fire with the same end result.

Research needs

Cooperative efforts between research and management agencies must be undertaken to test research results at management-relevant scales. Facilitative grazing has been addressed at the plant community level (Ganskopp *et al.,* 1999) but it has not been applied at the landscape scale with appropriate monitoring protocols to evaluate its effectiveness. Following disturbance in forests, transitory ranges exist until canopy closure occurs, but thus far, our research has not adequately addressed how the size and frequency of episodic disturbances could interact with variations in the populations of multiple herbivore species to influence ecosystem stability. Thus, researchers are challenged to 'scale up' the focus of their research, in terms of temporal and spatial scale and in terms of the complexity of disturbance agents and their regimes.

Conclusions

We have tried to convey the complexity involved in managing heterogeneous landscapes for multiple species of ungulates that often include wild and domestic counterparts. To say that our knowledge is incomplete would be an understatement. If it is in the interest of the public to simply have only wild ungulates on western landscapes without regard to the vigour of those ungulate populations and then the extent of anthropogenic management of those lands could be minimal. However, anthropogenic management is necessary given continuation of livestock grazing or given that production goals are in the Public interest for even wild ungulates alone.

To be effective, anthropogenic management must be based on planning that crosses all scales.

Disparate species of ungulates require complex habitats. Almost all ecosystems are disturbance based, but disturbances rarely consume entire landscapes and thus contribute to the development and maintenance of mosaics. In most areas of western North America, habitats have been homogenized through direct action like fire suppression or indirectly through succession caused by overgrazing with livestock and/or by maintenance of large unproductive herds of big game. These landscapes will support fewer ungulates over time if intervention does not occur. Mule deer declines may be in part caused by changes in successional stages that no longer favour mule deer (Urness, 1990). There is also some evidence of a similar decline in some elk populations (Irwin *et al.,* 1994).

Unfortunately, habitat management for ungulates or integrating them in landscape management paradigms appears to be a low priority on public lands. In the 1950s and 1960s, alteration of landscapes reached its zenith on public lands (Heady and Bartolome, 1977). Most of these improvements were directed at rectifying degraded conditions and providing improved livestock forage. Improvements to wildlife habitat were mostly fortuitous. Today, typically, where wild ungulate conflicts occur with private lands, state wildlife agencies acquire nearby land. Intensive

management of that land is initiated to ensure that animals will be attracted from conflict areas. Reseeding, fertilization, facilitative grazing, water development, road closure, feeding and weed and brush control are often employed (Anderson and Scherzinger, 1975; Meresczak *et al., 1981;* Frisina and Morin, 1991; Frisina, 1992). Yet, these same intensive habitat management tools are seldom applied to the general landscape on public lands.

Weisberg and Bugmann (2003) noted that we still may not know enough to be able to derive the generalizations needed to scale up to ungulate vegetation interactions over multiple species and heterogeneous landscapes. But, as Fuentes (1993) pointed out, if we consider management actions as setting a trajectory rather than establishing a static end point and if that trajectory is based on learning from action and science, a direction of constructive change should result. Lee (1993) stated that if we wait for all the data to come in so that a final conclusion can be made, it will take too long and it may be too late to do anything about it.

Funding

Pacific Northwest Research Station, USDA, Forest Service, Managing Disturbance Regimes Program.

Conflict of Interest Statement

None declared.

References

Alpe, M.J., Kingery,J.L. and Mosley, J.C, 1999 Effects of summer sheep grazing on browse nutritive quality in autumn and winter.]. *Wildl. Manage.* 63, 346-354.

Anderson, E.W. and Scherzinger, R. J. 1975 Improving quality of winter forage for elk by cattle grazing. J. *Range Manage. 28,* 120-125.

Augustine, D.]. and McNaughton, S. J. 1998 Ungulate effects on the functional species composition of plant communities: herbivore selectivity and plant tolerance. J. *Wildl. Manage. 62,* 1065-1083.

Austin, D.D., Urness, P. J. and Fierro, L.C. 1983 Spring livestock grazing affects crested wheatgrass regrowth and winter use by mule deer. J. *Range Manage.* 36,589-593.

Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B. and Swift, D.M. *et al.* 1996 Mechanisms that result in large herbivore grazing distribution patterns. J. *Range Manage.* 49, 386-400.

Barrett, M.W. 1981 Environmental characteristics and functional significance of pronghorn fawn bedding sites in Alberta. J. *Wildl. Manage.* 45,120-131.

Beck, J. and Peek, J.M. 2005 Diet composition, forage selection, and potential for forage competition among elk, deer, and livestock on aspen-sagebrush summer range. *Rangeland Ecol. Manage.* 58, 135-147.

Bell, R.H.V. 1971 A grazing ecosystem in the Serengeti. *Sci. Am.* 225, 86-93.

Belsky, A. J. 1994 Influences of trees on savanna productivity: test of shade, nutrients, and tree-grass competition. *Ecology.* 75, 922-932.

Birrell, H.A. 1989 The influence of pasture and animal factors on the consumption of pasture by grazing sheep. *Aust. J. Agric. Res.* 40, 1261-1267.

Bowns, J.E. and Bagley, C.F. 1986 Vegetation responses to long-term sheep grazing on mountain ranges. *J Range Manage. 39,* 431-434.

Bryant, F. C. 1982 *Grazing, Grazing Systems, and Wildlife. Technical Article T-9-297 of the College of Agricultural Science.* Texas Tech University, Lubbock, TX, p. 15.

Butler, L.G., Kielland, K., Rupp, TS. and Hanley, TA. 2007 Interactive controls by herbivory and fluvial dynamics on landscape vegetation patterns on the Tanana River floodplain, Interior Alaska. J. *Biogeogr.* 34, 1622-1631.

Canon, S.K., Urness, P,J. and Debyle, N.V. 1987 Habitat selection, foraging behavior, and dietary nutrition of elk in burned aspen forest. J. *Range Manage.* 40,433-437.

Chadde, S.W. and Kay, C.E. 1991 Tall-will communities on Yellowstone's northern range: a test of the "natural-regulation" paradigm. Pages 231-262. In *The Greater Yellowstone Ecosystem: Redefining America's Wilderness Heritage.* R.B. Keiter and M.S. Boyce (eds). Yale University Press, New Haven, CT, p.428.

Cole, G.F. 1971 An ecological rationale for the natural or artificial regulation of native ungulates in parks. *Trans. North Am. Wildl. Conf* 36,417-425.

Cook, J.G., Johnson, B.K., Cook, R.e., Riggs, R.A., DelCurto, T. and Bryant, L.D. *et al.* 2004 *Effects of Summer-Autumn Nutrition and Parturition Date on Reproduction and Suruiual of Elk.* Wildlife Monographs, No 155. 61 pp.

Coughenour, M.B. 1991 Invited synthesis paper: spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems. J. *Range Manage.* 44, 530-542.

deCalesta, D.S. and Stout, S.L. 1997 Relative deer density and sustainability: a conceptual framework for integrating deer management with ecosystem management. *Wildl. Soc. Bull. 25,* 252-258.

Fleischner, TL. 1994 Ecological costs of livestock grazing in Western North America. *Conseru. Bioi.* 8,629-644.

Frisina, M.R. 1992 Elk habitat use within a rest-rotation grazing system. *Rangelands.* 14,93-96.

Frisina, M.R. and Morin, F.G. 1991 Grazing private and public land to improve the Fleecer Elk Winter Range. *Rangelands. 14,* 93-96.

Fuentes, E.R. 1993 Scientific research and sustainable development. *Ecol. Appl.* 3, 576-577.

Ganskopp, D. 1998 Thurber needlegrass: seasonal defoliation effects on forage quantity and quality. J. *Range Manage. 51,* 276-281.

Ganskopp, D. and Bohnert, D. 2006 Do pasture-scale nutritional patterns affect cattle distribution on rangelands? *Rangeland Ecol. Manage.* 59, 189-196.

Ganskopp, D., Angell, R. and Rose, J. 1992 Response of cattle to cured reproductive stems in a caespitose grass. J. *Range Manage.* 45,401-404.

Ganskopp, D., Angell, R. and Rose, J. 1993 Effect of low densities of senescent stems in crested wheatgrass on plant selec-

tion and utilization by beef cattle. *Appl. Anim. Behav. Sci. 38,* 227-233.

Ganskopp, D., Svejcar, T., Taylor, F., Farstvedt, J. and Paintner, K. 1999 Seasonal cattle management in 3 to 5 year old bitterbrush stands. J. *Range Manage.* 52, 166-173.

Ganskopp, D., Svejcar, T. and Vavra, M. 2004 Livestock forage conditioning: blue bunch wheatgrass, Idaho fescue, and bottlebrush squirreltail. J. *Range Ivumage.* 57,384-392.

Ganskopp, D., Aguilera, L. and Vavra, M. 2007 Livestock forage conditioning among six northern Great Basin grasses. *Rangeland Ecol. Mange.* 60,71-78.

Gordon, I.J. 1988 Facilitation of red deer grazing by cattle and its impact on red deer performance. J. *Appl. Ecol.* 25,1-10.

Hanley, T.A. 1982 The nutritional basis for food selection by ungulates. J. *Range Manage.* 35, 146-15l.

Heady, H.F. and Bartolome, J. 1977 *The Vale Rangeland Rehabilitation Program: The Desert Repaired in Southeastern Oregon. U.S.D.A. Forest Service Resource Bulletin PNW-70.* Pacific Northwest Forest and Range Experiment Station, Portland, OR, p. 132.

Hobbs, N.T. 1989 *Linking energy balance to survival in mule deer: development and test of a simulation model.* Wildlife Monograph No 101, 39 pp.

Hobbs, N.T. 1996 Modification of ecosystems by ungulates. J. *Wildl. Manage.* 60,695-713.

Hobbs, N.T. and Spowart, R.A. 1984 Effects of prescribed fire on nutrition of mountain sheep and mule deer during winter and spring. J. *Wildl. Manage.* 48, 551-560.

Hobbs, N.T. and Swift, D.M. 1985 Estimates of habitat carrying capacity incorporating explicit nutritional constraints. J. *Wildl. Manage.* 49, 814-822.

Hobbs, N.T., Baker, D.L., Bear, G.D. and Bowden, D.e. 1996a Ungulate grazing in sagebrush grassland II: mechanisms of resource competition. *Ecol. Appl.* 6, 200-217.

Hobbs, N.T., Baker, D.L., Bear, G.D. and Bowden, D.C. 1996b Ungulate grazing in sagebrush grassland II: effects of resource competition on secondary production. *Ecol. Appl.* 6,218-227.

Holechek, J.L., Pieper, R.D. and Herbel, C.H. 1998 *Range Management: Principles and Practices.* Prentice-Hall, Inc., Upper Saddle River, NJ, p. SOL

Horsely, S.B., Stout, S.L. and deCalesta, D.S. 2003 White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* 13,98-118.

Houston, D.B. 1982 *The Northern Yellowstone Elk.* MacMillan Publishing Co., Inc., New York, p.474:

Irwin, L.L., Cook, J.G., Riggs, R.A. and Skovlin, J.M. 1994 *Effects of Long-term Grazing by Big Game and Livestock in the Blue Mountains Forest Ecosystems. U.S. Forest Service General Technical Report PNW-GTR-325.* Pacific Northwest Research Station, Portland, OR.

Kay, CE. 1994 Aboriginal overkill: the role of Native Americans in structuring western ecosystems. *Hum. Nat.* 5, 359-398.

Kay, C.E. 1995 Aboriginal overkill and native burning: implications for modern ecosystem management. *West.* J. *Appl. For.* 10,121-126.

Kay, C.E. 1997a Condition and trend of aspen, *Populus tremuloides,* in Kootenay and Yoho National Parks: implications for ecological integrity. *Can. Field Nat.* 111,607-616.

Kay, CE, 1997b Aboriginal overkill and the biogeography of moose in western North America. *Alces.* 33, 141-164.

Kay, CE, 2003 Lewis and Clark, aboriginal overkill, and the myth of once abundant wildlife. Pages 103-109. In *A Confluence of Cultures: Native Americans and the Expedition of Lewis and Clark. Proceedings of the Symposium.* University Printing and Publication Services, University of Montana, Missoula, MT. ISBN-O-972 7122-4-0.

Kupferschmid, A.D. and Bugmann, H. 2008. Ungulate browsing in winter reduces the growth of Fraxinus and Acer saplings in subsequent unbrowsed years. *Plant Ecol.* 198,121-134.

Langston, N. 1995 *Forest Dreams, Forest Nightmares.* University of Washington Press, Seattle, WA, p.368.

Launchbaugh, K. (ed.). 2006 *Targeted Grazing: A Natural Approach to Vegetation Management and Landscape Enhancement.* American Sheep Industry Association, Denver, CO, p. 199.

Lee, K.N. 1993 Greed, scale mismatch, and learning. *Ecol. Appl.* 3,560-564.

Lesperance, A.L., Tueller, P.T. and Bohman, V.R. 1970 Symposium for maximum production in beef cattle: competitive use of the range forage resource. J. *Anim. Sci.* 30, 115-12l.

Lindzey, F.G., Hepworth, W.G., Mattson, T.A. and Reese, A.F. *1997 Potential for Competitive Interactions between Mule Deer and Elk in the Western United States and Canada: A Review.* Wyoming Cooperative Fisheries and Wildlife Research Unit, Laramie, WY, p. 82.

Lonner, T.N. and Mackie, R.J. 1983 On the nature of competition between big game and livestock. Pages 53-58. In *Proceedings of the Forestland Grazing symposium.* B.F. Roche' and D.M. Baumgartner (eds). Washington State University, Pullman, WA, p.114.

Mackie, R.J. 1978 Impacts of livestock grazing on wild ungulates. *Trans North Am. Wildl. Nat. Resour. Conj.* 43,462-476.

May, R. 1981 Models for two interacting species. Chapter 5. In *Theoretical Ecology.* R. May (ed.). Blackwell, Oxford.

McFadden, B.J. and Shockey, B.J. 1997 Ancient feeding ecology and niche differentiation of Pleistocene mammalian herbivores from Tarija, Bolivia: morphological and isotopic evidence. *Paleobiology.* 23, 77-100.

McNaughton, S.J. 1976 Serengeti migratory wildebeest: facilitation of energy flow by grazing. *Science.* 191, 92-94.

McNaughton, S.J. 1984 Grazing lawns: animals in herds, plant form and co-evolution. *Am. Nat.* 124, 863-886.

Meresczak, I.M., Krueger, W.e. and Vavra, M. 1981 Effects of range improvement on Roosevelt Elk winter nutrition. J. *Range Manage.* 34, 184-187.

Miller, R.F., Svejcar, T.J. and West, N.E. 1994 Implications of livestock grazing in the intermountain sagebrush region: plant composition. Pages 101-146. In *Ecological Implications of Livestock Herbivory in the West.* M. Vavra, W.A. Laycock and R.D. Pieper (eds). Society for Range Management, Denver, CO, p.297.

Molvar, E.M., Bowyer, R.T. and Van Ballenberghe, V. 1993 Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. *Oecologia.* 94, 470-472.

Odwn, E.P. 1971 *Fundamentals of Ecology.* 3rd edn. W.B. Sanders, Philadelphia, PA, p.546.

O'Reagain, P.J. and Schwartz, J. 1995 Dietary selection and foraging strategies of animals on rangeland. Coping with spatial and

temporal variability. In *Recent Developments in the Nutritin of Herbivores. Proceedings of the IVth International Symposium on the Nutrition of Herbivores.* M. Journet, E. Grenet, M.-H. Farce, M. Theriez and e. Demarquilly (eds). INRA Editioons, Paris, France, pp. 407-423.

Owen-Smith, N. 1985 Niche separation among African ungulates. Pages 167-171. In *Species and Speciation. Transvaal Museum Monograph No.4.* E.S. Vrba (ed.). Transvaal Museum, Pretoria, South Africa.

Pastor, J. and Naiman, R.J. 1992 Selective foraging and ecosystem processes in boreal forests. *Am. Nat.* 130,691-705.

Pastor, J., Moen, R. and Cohen, Y. 1997 Spatial heterogeneities, carrying capacity, and feedbacks in animal-landscape interactions. *J Mammal.* 78, 1040-1052.

Payne, N.F. and Bryant, F.C. 1994 *Techniques for Wildlife Habitat Management of Uplands.* McGraw-Hilllnc., New York, p.840.

Peek, J.M., Johnson, F.D. and Pence, N.N. 1978 Successional trends in a ponderosa pine/bitterbrush community related to grazing *by* livestock, wildlife, and to fire. *J Range Manage. 31,* 49-53.

Pitt, M. 1986 Assessment of spring defoliation to improve fall forage quality of blue bunch wheatgrass *(Agropyron spicatum). J Range Manage.* 39, 175-181.

Quigley, T.M. and Arbelbide, S.J. 1997 (eds). *An Assessment of Ecosystem Components in the Interior Columbia Basin and Portions of the Klamath and Great Basins: Volume II. U.S.* USDA Forest Service, Washington, DC, 1055 pp. Forest Service General Technical Report PNW-GTR-405.

Rhoades, B.D. and Sharrow, S.H. 1990 Effect of grazing by sheep on the quantity and quality of forage available to big game in Oregon's Coast Range. *J Range Manage.* 43, 235-237.

Riggs, R.A., Urness, P.J. and Gonzalez, K.A. 1990 Effects of domestic goats on deer wintering in Utah oakbrush. *J Range Manage.* 43, 229-234.

Riegel, G.M., Miller, R.F. and Krueger, W.e. 1991 Understory vegetation response to increasing water and nitrogen levels in a *Pinus ponderosa* forest in northeastern Oregon. *Northwest Sci.* 65,0-15.

Riggs, R.A., Bunting, S. and Daniels, S.E. 1996 Prescribed fire. Pages 295-319. In *Rangeland Wildlife.* P.R. Krausemann (ed). *Society* for Range Management, Denver, CO, p. 440.

Riggs, R.A., Tiedemann, R.A., Cook, J.G., Ballard, T.M., Edgerton, P.J. and Vavra, M. *et al.* 2000 *Modification of Mixed-Conifer Forests by Ruminant Herbivores in the Blue Mountains Ecological Province.* U.S. Forest Service Research Paper PNW-RP-527.77 pp.

Riggs, R.A., Cook,].G. and Irwin, L.L. 2004 Management implications of ungulate herbivory in Northwest Forest Ecosystems. *Trans. North Am. Wild/. Nat. Resour. Conf* 69, 759-784.

Risenhoover, K.L. and Bailey,].A. 1985 Foraging ecology of mountain sheep *(Ovis Canadensis):* implications for habitat management. *J Wildl. Manage.* 49, 797-804.

Schoener, T.W. 1982 The controversy over interspecific competition. *Am. Sci.* 70,586-595.

Schoener, T.W. 1983 Field experiments on interspecific competition. *Am. Nat.* 122,240-285.

Senft, R.L., Coughenour, M.B., Bailey, D.W., Rittenhouse, L.R., Sala, O.E. and Swift, D.M. 1987 Large herbivore foraging and ecological hierarchies: landscape ecology can enhance traditional foraging theory. *Bioscience.* 37, 789-799.

Severson, K.E. and DeBano, L.F. 1991 Influence of Spanish goats on vegetation and soils in Arizona chaparral. *J Range Manage.* 44,111-117.

Severson, K.E. and Urness, P.J. 1994 Livestock grazing: a tool to improve wildlife habitat. Pages 101-146. In *Ecological Implications of Livestock Herbivory in the West.* M. Vavra, W.A. Laycock and R.D. Pieper (eds). *Society* for Range Management, Denver, CO, p. 297.

Sheehy, D.P. and Vavra, M. 1996 Ungulate foraging areas on seasonal rangeland in northeastern Oregon. *J Range Manage.* 49, 16-23.

Shipley, L.A. 1999 Grazers and browsers: how digestive morphology affects diet selection. Pages 20-27. In *Grazing Behavior of Livestock and Wildlife. Idaho Forest, Wildlife and Range Experiment Station Bulletin No.* 70. K.L. Launchbaugh, K.D. Sanders and J.C, Mosley (eds). University of Idaho, Moscow, ID, p.147.

Skovlin, J. and Vavra, M. 1979 *Winter Diets of Elk and Deer in the Blue Mountains, Oregon. U.S. Forest Service Research Paper PNW-260.* Pacific Northwest Forest and Range Experiment Station, Portland, OR, p.21.

Smith, A.D. 1965 Determining common use grazing capacities *by* application of the key species concept. *J Range Manage. 18,* 196-201.

Smith, B., Cole, E. and Dobkin, D. 2004 *Imperfect Pasture: A Century of Change at the National Elk Refuge in Jackson Hole, Wyoming.* Grand Teton Natural *History* Association, Moose, WY, p.149.

Spowart, R.A. and Hobbs, N.T. 1985 Effects of fire on diet overlap between mule deer and mountain sheep. *J Wildl. Manage.* 49, 942-946.

Standing, A.R. 1938 Use of key species, key areas, and utilization standards in range management. *Ames Forester.* 29, 9-19.

Starfield, A.M. and Chapin, F.S. 1996 Model of transient changes in arctic and boreal vegetation in response to climate and land use change. *Ecol. Appl.* 6, 842-864.

Stuth,].W. 1991 Foraging behavior. Pages 65-83. In *Grazing Management an Ecological Perspective.* R.K. Heitschmidt and J.W. Stuth (eds). Timber Press, Inc., Portland, OR.

Tilghman, N.G. 1989 Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *J Wildl. Manage.* 53, 524-532.

Urness, P.J. 1990 Livestock as manipulators of mule deer winter habitats in northern Utah. Pages 25-41. In *Can Livestock Be Used As a Tool to Enhance Wildlife Habitat?* E.K. Severson (ed.). U.S. Department of Agriculture General Technical Report RM-194.123 pp.

Vavra, M. 1986 Manipulative grazing of plant communities. Pages 167-178. In *Grazing Research at Northern Latitudes.* O. Gudmundson (ed). Plenum Publishing Corporation, New York and London, p. 374.

Vavra, M. and Sheehy, D.P. 1996 Improving elk habitat characteristics with livestock grazing. *Rangelands.* 18, 182-185.

Vavra, M., McInnis, M. and Sheehy, D. 1989 Implications of dietary overlap to management of free-ranging large herbivores. *Proc West. Sect. Am.* Soc. *Anim. Sci.* 40, 489-495.

Visscher, D.R. and Merrill, E.H. 2009 Temporal dynamics of forage succession for elk at two scales: implications of forest management. *For. Ecol. Manage.* 257, 96-106.

Wagner, F.H. 1969 Ecosystem concepts in fish and game management. Pages 259-307. In *The Ecosystem Concept in Natural Resource Management.* G.M. Van Dyne (ed.). Academic Press, New York.

Walker, J.W., Kronberg, S.L., AI-Rowaily, S.L. and West, N.E. 1994 Comparison of sheep and goat preferences for leafy spurge. J. *Range Manage.* 47,429.

Wambolt, C.L., Fraas, W.W. and Frisina, M.R. 1998 Bitterbrush *(Purshia Tridentata* Pursh) growth in relation to browsing. *Great Basin Nat.* 58, 28-37.

Weisberg, P.J. and Bugmann, H. 2003 Forest dynamics and ungulate herbivory: from leaf to landscape. *For Ecol. Manage.* 181, 1-12.

Wickstrom, M.L., Robbins, C.T, Hanley, TA., Spalinger, D.E. and Parish, S.M. 1984 Food intake and foraging energetics of elk and mule deer. J. *Wildli. Manage.* 48, 1285-130l.

Wiens, J.A. 1977 On competition and variable environments. *Am. Sci.* 65,590-597.

Wiltbank, J.N., Rowden, W.W., Ingalls, J.E., Gregory, K.E. and Koch, R.M. 1962 Effect of energy level on reproductive phenomena of mature Hereford cows. J. *Anim. Sci.* 21,219-225.

Yeo, J.J., Peek, J.M., Wittinger, W.T and Kvale, C.T 1993 Influence of rest-rotation catrle grazing on mule deer and elk habitat use in east-central Idaho. *J Range Manage.* 46,245-250.

Received 25 March 2009