# Invited Synthesis Paper

The Editorial Board of the *Journal of Range Management* invited Michael B. Coughenour to prepare this synthesis paper.

MICHAEL B. COUGHENOUR has offered important insights into processes regulating responses of plants to grazing by large herbivores. He has often applied a clear understanding of the physiology of individuals to explain mechanisms operating at higher levels of ecological organization.

Michael received Bachelor and Master of Science degrees in biology from the University of Illinois and his Doctor of Philosophy in systems ecology from Colorado State University. His doctoral work focused on impacts of SO_2 emissions on the sulphur cycle in grassland ecosystems. During 1978–1983, he was a post-doctoral fellow in the laboratory of Sam McNaughton at Syracuse University, where he developed simulation models of primary production of east African grasses. Since then, Michael has been a research scientist at the Natural Resource Ecology Laboratory at Colorado State University, and has worked on a variety of ecosystem studies in east Africa and in Yellowstone National Park.

Michael has published many influential papers. The hallmark of his writing is an unusual ability to assemble knowledge from diverse sources—from experiment, from scholarship, and from simulation. He brings this information to bear in revealing ways on important questions in contemporary ecology.

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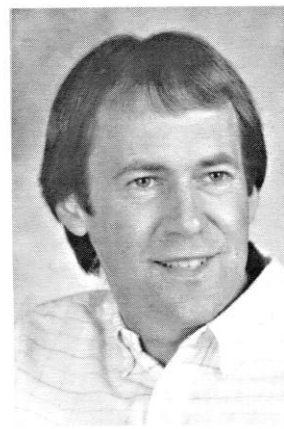
Spatial components of plant-herbivore interactions in pastoral, ranching, and native ungulate ecosystems

MICHAEL B. COUGHENOUR

Abstract

The spatial component of herbivory remains enigmatic although it is a central aspect of domestic and native ungulate ecosystems. The effects of ungulate movement on plants have not been clearly established in either range or wildlife management. While livestock movement systems have been implemented to cope with increases in livestock density, restrictions on movement, and overgrazing, a large number of studies have disputed the effectiveness of different livestock movement patterns. Traditional pastoralism, particularly nomadism, has been perceived as irrational and even destructive, but many studies have documented features of traditional pastoral land use that would promote sustainability. Disruptions of wild ungulate movements have been blamed for wildlife overgrazing and population declines, but actual patterns and mechanisms of disrupted movement and population responses have been poorly documented.

Models that integrate plant growth, ungulate movement, and foraging are suggested as a way to improve analyses of spatial plant-herbivore systems. Models must give due attention to non-forage constraints on herbivore distribution, such as topography. Models should assess the significance of movement as a means of coping with local climatic variation (patchy rainfall). Models that distribute an aggregate population over a landscape in relation to the distribution of habitat features deemphasize aspects of ungulate movements and population responses that inevitably cause nonideal distributions, particularly in natural ecosystems. Individual based models describe movement and foraging processes more accurately, but these models are difficult to apply over large areas. Both top-down and bottom-up approaches to spatial herbivory are needed. To model plant responses to movement, it is important to account for small scale phenomena such as tiller defoliation patterns, patch grazing, and grazing lawns as well as large scale patterns such as rotation and migration. Herbivory patterns at these different scales are interrelated.

Managers of wildlife and domestic livestock populations confront similar problems as they attempt to interpret ungulate spatial distribution patterns and their effects on plants. Overgrazing and subsequent ecosystem degradation on rangelands or pastoral grazing areas are often attributed to inappropriate management of livestock spatial distributions. Overabundances of ungulates in wildlife preserves, and consequent overgrazing, are often attributed to human interference with natural ungulate migrations or dispersal patterns. These management problems are analogous in that ungulate spatial utilization patterns determine how grazing impacts are distributed in space and in time. Ecosystem sustainability is affected by interactions among animal movement and abundance, plant growth, plant response to grazing, and the physical structure of the landscape.

The consequences of herbivory for ecosystems depend, of course, upon herbivore abundance. However, herbivore abundance is expressed in terms of numbers of animals per unit of land, per unit of plant production, or per unit of land per unit time. These measures have been distinguished as stocking density, grazing pressure, and stocking rate, respectively (Heitschmidt and Taylor 1991). Until recently, research and management of ungulate herbivores have treated the denominators of these expressions as homogeneous. The aim of this paper is to explore heterogeneities in these denominators that are normally averaged out.

Although livestock spatial distributions have been manipulated in relation to forage availability for thousands of years, a meager amount of scientific attention has been devoted to the spatial components of herbivory. Spatial management is often based on tradition, trial and error, subjective judgements, or poorly defined

conceptual models. Although spatio-temporal distribution patterns apparently affect plants and livestock productivity and explain wildlife overabundances and overgrazing, a stronger scientific foundation is needed to support these perceptions.

The difficulty of uniting a wide range of disciplines has undoubtedly slowed progress in the science of spatial plant-herbivore interactions. Synthetic studies are needed which link landscape ecology, geography, anthropology, plant ecology, and ungulate biology and behavior. Plant responses to herbivory must be integrated with ungulate spatial distributions. Effects of ungulate behavioral processes on movement must be considered, as well as effects of culture and human behavior in pastoral systems. Population dynamics come into play in native ungulate ecosystems.

Spatial heterogeneity has not been included in the mathematical models of plant-herbivore systems that have had the greatest impacts on wildlife management (e.g., Caughley 1976b, Walker et al. 1981, Crawley 1983). The quest for mathematical simplicity and analytical tractability in models has, unfortunately, also precluded considerations of the spatial components of plant-herbivore interactions. However, computer models have recently become sophisticated enough to simulate realistic spatial interactions. Large amounts of information are involved in spatial analyses but computerized techniques for spatial data storage and analysis have advanced greatly.

The principal aim of this paper is to reexamine the spatial elements of herbivory in both domestic and native ungulate ecosystems, synthesizing knowledge from a wide range of disciplines. I assess what is known about effects of ungulate movements and distributions on their interactions with plants and propose elements of a framework for analyses of spatially extensive plant-ungulate ecosystems. The first element of this framework is quantification of the effects of nonforage factors on ungulate distributions. Models of ungulate distributions and movements and plant responses to resultant grazing regimes are additional components. The final element draws from theory of the consequences of spatial heterogeneity for ecosystem stability.

Spatial Herbivory Patterns in Ranching Ecosystems

When livestock numbers increased dramatically in the western U.S. in the late nineteenth century, there was little management of livestock numbers or distributions to prevent overgrazing. Early American cattle and sheep herders exploited space in a nomadic manner. But the open ranges were greatly restricted from 1912 to 1925 with the influx of homesteaders (Cole et al. 1927). Early cattlemen looked upon settlers with disfavor because their fences prevented open range herds from "drifting with the storms" (Vass 1926). When fences were encountered, stock simply "walked back and forth along them until they became exhausted".

Large numbers of livestock were imported from the midwest by rail and from the south along cattle trails. The carrying capacity of the open range was quickly exceeded. The loss of flexibility in nomadic movement, increasing competition, and associated problems of overgrazing were reasons for early implementations of grazing systems. Seasonal adjustments in livestock distribution were imposed to compensate for lack of freedom of movement (Bell 1978).

Jared Smith, who was the first to advocate seasonal or deferred grazing (Smith 1895), saw that many grasslands had evolved under intermittent grazing by native migratory ungulates. He alluded to the state of affairs of only 30 years prior, when millions of bison roamed and moved naturally, permitting alternating periods of pasturing and rest (Smith 1899). Severe livestock overgrazing from 1885 to 1899 prompted him to suggest "partial resting", a system of alternating grazing among smaller subdivided pastures.

Many early grazing schemes were developed in mountainous terrain (e.g., Cotton 1907). Jardine (1912) suggested that mountain ranges should not be close grazed in the first half of the year every year, so he designed a deferred rotation system. Some of Sampson's first tests of deferred grazing were in the mountains of Oregon (Sampson 1913), and in the high summer range in Utah (Sampson and Weyl 1918).

A parallel chain of events occurred in the eighteenth and nineteenth centuries in S. Africa. First, trekboers established ranches, used them exhaustively, and then moved on. Later, trek farming arose as a transhumant system of seasonal movements between sourveld (tall grass) in summer and sweetveld (short grass) in winter (Rowland 1937). Land settlement and livestock disease put an end to the practice of trek farming; thus deferred grazing systems were developed.

Widespread changes of S. African range from grassveld to dwarf shrub and bare soil by 1950 were thought to be a result of continuous grazing (Howell 1978). A three-camp rotation system (1950-61) failed to reverse the trend, and caused patch grazing problems. Multi-camp nonselective grazing began in 1961, wherein stock were concentrated onto small areas to prevent selective grazing. Grazing bouts were short, to prevent overgrazing of regrowth.

Grazing systems were later touted as a way to increase production. Grazing systems enforce more even distribution and thereby achieve fuller utilization of the land. As water points, salt licks, and fencing are installed in stages, the landscape becomes more fully, and thus efficiently, utilized (Ares 1936a,b, Anderson 1967). Livestock can be forced to utilize less preferred forage species when they are confined in a given pasture. Management costs can be reduced because animals can be more easily controlled as tight herds (Kennedy 1963).

The benefits of grazing systems have since been called into question. Many grazing systems have had no effect and where they have, the impacts have been less significant than those resulting from simple changes in stocking rate (Van Poollen and Lacy 1979). Grazing systems proved ineffective in annual grasslands (Ratliff 1986). Grazing systems have also proven ineffective in Australia (L. Myers 1972). A large number of experiments have shown maximal animal production under simple continuous grazing (Gammon 1978, Wilson et al. 1984).

Forage quality and quantity on a short duration grazing (SDG) system were not different from quality and quantity under longer rotation systems (Heitschmidt et al. 1987a,b,c). Harvest efficiency was not improved by SDG (Heitschmidt 1987a). Recent studies comparing SDG with other grazing systems have failed to show any benefits (Pitts and Bryant 1987, Hart et al. 1988, Willms et al. 1990, Ralphs et al. 1990, Gillen et al. 1990). Many tests of SDG effects on soil properties and seedling establishment have failed to show any positive effects (Balph and Malechek 1985, Warren et al. 1986, Thurow et al. 1986, Weigel et al. 1990). Rigorous tests of SDG impact on range that is degraded, subject to patch grazing and sealing soil are lacking.

Additional confusion arises from coincident plant responses to climate. The notion that overgrazing was the original cause of a change from grassveld to dwarf shrubland (karoo) in S. Africa has little scientific basis (Hoffman and Cowling 1990). The country experienced drought during 1925-1933 and 1944-1953. Most of the theory of karoo invasion originated during 1947-1953. Thorough examination of evidence suggests that vegetation change has been influenced more by climatic change than by mismanagement (Hoffman and Cowling 1990). The effects of good rainfall from 1968-77 (Howell 1978), could have confounded the original tests of SDG. Unfortunately, there was no appropriate control treatment (Gammon 1984, cited by Heitschmidt 1987a).

Confusion and even dispute have arisen regarding plant responses to these movement patterns, suggesting that hypotheses of the

effects of herbivore movement on plants must be more explicitly stated and tested.

Traditional Pastoral Movement Patterns

It is yet more difficult to understand how ungulate movements affect plants in pastoral ecosystems. Pastoral ecosystems involve movements over large spatial scales, in poorly understood patterns. The movement patterns, or the effects of movement patterns on plants, have rarely been studied. The causes and ramifications of nomadic pastoral land use, in particular, are poorly understood (e.g., Darling and Farver 1972, Widstrand 1975). Traditional nomadic pastoralism is commonly perceived as a wandering form of land use that is devoid of any systematic management and thus prone to induce range degradation. When understood, however, nomadic pastoralism often proves to be a rational and sustainable system for exploiting rangeland plant resources.

Bedouin herders in Saudi Arabia move opportunistically among very large areas of land in response to random, patchy rainfall (Perevalotsky 1987). Forage is communally owned. It is more beneficial for a pastoral group to grant neighbors access to forage when it is available than to exclude them, as the neighbors will reciprocate. It is impossible for a single pastoral group to use all the forage on its patch of land during the brief period that it is available. Settlement of Bedouins around permanent watering points near oil-producing facilities has only promoted yearlong grazing and vegetational destruction (Heady 1972).

The Phala nomads of the Tibetan Plateau (Goldstein et al. 1990) rotate between a multipasture encampment used in winter, spring, and summer and an encampment used in fall and early winter. This system allows the nomads to utilize growing foliage during summer. It provides an ample supply of ungrazed forage reserve for use in fall and early winter, which prepares animals for subsistence through the long winter. A feudal lord (Lama) periodically reallocated pasturing rights to groups in proportion to their herd sizes.

Nomadic pastoralists in Turkana, Kenya (McCabe 1983; Coughenour et al. 1985b; Coppock et al. 1986, 1988; McCabe and Ellis 1987) are most densely aggregated during the wet season. The pulse of annual grass growth on the wet season range is brief and senescence is rapid (Coughenour et al. 1990). It is difficult for livestock to fully exploit all facets of the wet season range during the brief growing season. As the dry season progresses, the pastoralists disperse throughout the higher rainfall areas in the region. In late dry seasons, or in drought, pastoralists utilize the high mountains and plateaus where there is little water and difficult terrain. Dry season ranges are consequently rested during the growing season.

It is not exactly clear why the more productive dry season ranges of Turkana are used little in the wet season. These areas may be avoided because of cooler temperatures, which are bad for camels, and lack of mineral springs, which are good for camels. Ticks are more prevalent. But if pastoralists failed to concentrate on the less productive wet season area, a great deal of nutritious (though transient) plant productivity would be lost to decomposition, termites, and abiotic weathering. Pastoralists who move to the wet season areas would thus gain a competitive advantage. Pastoralists who remained on the dry season range year around would experience competition from the influx of pastoralists as they return from the wet season range.

The Jie of Uganda move in an opposite pattern (Gulliver 1965). Camps are widely dispersed on the wet season ranges. As the dry season progresses, the Jie shift to the west and become progressively concentrated around permanent water sources. There is intense public disapproval of those who camp on dry season ranges during the wet season as these pastures are recognized as a necessary dry season reserve.

Different dispersal-convergence movement patterns arise in response to the spatial dispersions of the most limiting resources (Baker 1978). When water is available all year, or widely distributed, then dispersal should occur during the dry season to exploit widely scattered patches of plant growth. Grazers should be concentrated on patches of favored or transient forage in the wet season. Where water is clumped in the dry season, then there should be wet season dispersal to plants that are far from water.

Pastoralists of the Niger delta of the Sahel traditionally moved into the Northern drylands in the wet season to exploit the transient pulse of plant growth (Breman et al. 1978). Overgrazing of the wet season range was prevented by movement responses to scarce water distributions. In the dry season, the herders returned to the more productive Niger delta. It would otherwise be relatively disadvantageous to remain in the delta during the wet season due to wet ground, poor forage quality, and tsetse when there is an abundant supply of high quality forage in the north.

A much larger and longer-term pattern of movement has been associated with African pastoralists. Until 4,000 years ago the only pastoralists in Africa were on the west coast of the Red Sea, but by approximately 2,000 years ago, pastoralism had spread to East Africa (Lamprey 1983). Approximately 1,300 years ago, Fulani pastoralists in Senegal were spreading east (Baker 1978). The Masaii occupied northwest Kenyan lowlands (present Turkana) 400 years ago (Talbot 1972). They continued to move south until about 1640. Talbot (1972) thus hypothesized that Masaii probably overgrazed their land, abandoned it and moved on fairly frequently. Lamprey (1983) also hypothesized that intra-regional movements were part of a large scale pattern of overgrazing and abandonment. However, there is little evidence that environments were actually degraded by overgrazing or that this was the cause of dispersal. Changes in climatic patterns as well as the general trend of human population growth and expansion over the continent must also be considered.

Nomadic pastoralists have been associated with the "tragedy of the commons" (Hardin 1968) syndrome. As rangelands appear to be open for free access, pastoralists would seem to have little or no personal incentive for conservation. However, it is doubtful that any pastoral system operates under true "open access" (McCabe 1990). In East Africa, for instance, forage can be used by any member of a tribe or tribal section but well water rights are owned and this limits foraging. Tribal or sectional territories are also defended from use by outsiders: evidence of a form of livestock density regulation (McCabe 1990).

Traditional pastoralism has often come into conflict with other forms of land use. Settled agriculture and other forms of economic development often restrict traditional movements or preclude the traditional grazing pattern altogether. Interestingly, when these disruptions do occur, a common result is some form of overgrazing. Thus, inappropriate pastoral livestock movement patterns are particularly likely to arise in the early stages of economic development. Economic development imposes boundaries that preclude traditional strategies of dispersal migration (Talbot 1972, Lamprey 1983). Authoritarian systems of supervised grazing management have been advocated to compensate for the inadaptation of the traditional system to the new situation (Lamprey 1983).

In the Sahel, there is a widespread pattern of localized overgrazing around developed watering areas (Sinclair and Fryxell 1985). Eventually locally degraded areas fuse across the region. When watering points are developed on wet season ranges it becomes more likely that grasses will be grazed during their growth cycle. When settled agriculture promotes year-around use of traditional dry season grazing areas, the grasses there are never rested. The inadvertent consequence is the removal of mechanisms which prevent overuse.

Development efforts in Masailand, Kenya, in the 1950's included water point development, fencing, and veterinary services (Talbot 1972). These improvements led to great increases in livestock numbers, accelerated by imports of livestock into some areas. A series of dry years occurred, culminating in 1961. Areas that were most developed, and probably most heavily stocked, suffered the most during this drought.

Group ranching, first implemented in Kenya as early as 1969, is a system wherein a parcel of tribal land is allocated to a group of pastoral households. A committee oversees its subsequent development. However, sedentarization and restrictions on cattle migration have favored increased holdings of closer-ranging sheep and goats (King et al. 1984). Livestock populations have increased in response to more watering points, better veterinary service, and large development loans. This has probably increased grazing pressures on plants and the likelihood of overgrazing after drought.

African pastoralists and open range ranchers have repeatedly rejected fenced ranching schemes (Behnke 1984). Botswana pastoralists believed that this would trap herds on ranches that were periodically untenable due to local drought, fire, or borehole breakdowns. The Masaii have stressed problems of spatially erratic rainfall and periodically insufficient resources on particular ranches.

Unfortunately, economic development efforts have usually failed to calculate the effects of long-standing spatial constraints on livestock abundance and spatial distributions, and effects of movement on plant-animal interactions. Effects of developmental changes which override constraints such as water limitations on livestock distributions must be better anticipated. Developmental planners should: (1) specify appropriate stocking rates using knowledge of plant and soil responses to specific grazing regimes; (2) determine how stocking rates should vary in response to climatic variation; (3) consider the distributions of nonforage resources (such as water) on the landscape and their impacts on spatial and temporal herbivory patterns; and (4) develop options for redistributing livestock over larger spatial scales in response to changing patterns of rainfall and forage availability. It is important to consider the effects of intra-regional spatial redistribution patterns on plants in any determination of regional carrying capacity.

Wild Ungulate Movements and Interactions with Plants

The idea that wild animals move in a manner that conserves forage and prevents overgrazing can be traced at least back to Smith's (1895) reference to bison. More recently, Bell (1978) recounted that bison and wild horses migrated, by coincidence, in a pattern that was beneficial to both plants and animals. Summer elk grazing has been likened to a complex deferred rotation grazing system in which plants grazed one year may go unused in following years (Gruell 1973, cited by Houston 1982). However, the idea that migratory movements would evolve to conserve forage would probably not be accepted by evolutionary theorists because it would require altruistic sacrifices by individual animals. This does not rule out the possibility that other proximal causes of migration (such as patchy rainfall and snow distributions) might create a situation in which forage is conserved, however.

In most regions bison moved nomadically in response to variable local and regional rainfall patterns. Although bison movements were highly erratic, large-scale patterns were observed in some regions (Roe 1951). Southern herds generally moved north in summer to escape heat. Some herds were observed to utilize eastern grasslands in the spring because they initiated regrowth before western grasslands. Canadian herds moved north in winter into the scrub belt for shelter and south onto the plains in summer. Thus, extreme southern grasslands were probably little grazed in mid-

summer. Many eastern grasslands could have not been grazed in summer while many western grasslands could have avoided herbivory in the early spring. Grass in the north Canadian scrub belt would have been rested in the summer. Erratic movements at small and large scales would have imposed a deferred rotation in that a given area would not likely be grazed at the same time every year. Return movements would have taken time, thus providing deferment during early season regrowth.

Saiga antelope in southwest Asia are essentially nomadic but they also move regularly between summer and winter ranges (Bannikov et al. 1967). Summer and winter range distinctions are blurred in mild winters. Summer movements are mainly responses to unpredictable rainfall patterns while winter movements are responses to snow distributions. Movement and searching would give some grasslands a chance for regrowth. Productive grasslands of lakeshores and riverbanks areas are apparently avoided during good years. This is fortuitous because these areas then act as dry season grazing reserves.

Wildebeest in the Serengeti (Pennycuik 1975, Inglis 1976) and the Kalahari (Williamson et al. 1988) and kob in southern Sudan (Fryxell and Sinclair 1988) make long-distance treks to areas of low annual rainfall at the beginning of the wet season. These are areas where grasses are typically shorter in stature and available for only a short period of time. Serengeti short grasslands are probably favored over taller grasslands because soils and plants are much richer in mineral nutrients (Kreulen 1975, McNaughton 1990). Mineral pans in the Kalahari wet season area are used as licks prior to calving (Williamson et al. 1988). Forage quality of taller grasses is also inherently lower than that of short grasses due to a higher degree of lignification.

What explains the low number of resident ungulates in the higher rainfall areas of the Serengeti? It would seem these productive areas could support many more grazers during the wet season. A few resident herds of wildebeest and many water buffalo stay on the more productive area year around, but clearly they do not exploit all the forage that is available to them. Migrants gain access to a transient, though expansive and nutrient-rich, resource on the shortgrass plains. Migrants consequently would increase in number relative to residents. The migratory strategy would increasingly prevail over the resident strategy. At the end of the wet season when the huge herds of migrants return to the taller grasslands they remove large quantities of forage, to the disadvantage of the residents. Competition from large numbers of returning migrants at the height of the dry season (Sinclair 1983) would also reduce numbers of residents. The ratio of residents to migrants should be dictated by the ratio of net benefits of each strategy (Sinclair 1983).

The exodus of migrants provides a period of rest for grasses in the more mesic areas in the wet season, although certain areas are heavily grazed by residents, even forming grazing lawns. During the wet season wildebeest and other ungulates chase patchy rainfall and waves of nutritious regrowth on the shortgrass plains (McNaughton 1985, Durant et al. 1988). Possibly, shortgrasses exhibit a short burst of intense production before they are "discovered", but wildebeest have been noted to arrive at areas of rainfall within three days (McNaughton 1985). At the end of the wet season tremendous "grazing fronts" pass through transition grasslands dominated by *Themeda triandra* and other midgrasses. Spatially separate short grasslands lure herbivores away from the transition grasslands during the growing season by virtue of higher plant nutrient content and reduced predator danger. *T. triandra,* a grazing sensitive species, consequently thrives in the presence of the large free-ranging herbivore population (Coughenour et al. 1985a).

When Wildlife Movements are Disrupted

Fencing has negatively affected wild ungulate numbers in the

Kalahari. Wildebeest have declined due to restricted migration to surface water (Williamson et al. 1988). One of three subpopulations of wildebeest in Kruger National Park declined after fencing restricted access to summer grazing areas (Whyte and Joubert 1988). Large herds initially built up on the remaining summering area within the fence. This resulted in overgrazing and the herd was consequently culled. A second fence was erected to exclude animals from the overgrazed area. Now, only sedentary animals remain on scattered patches of suitable habitat.

In contrast, ungulate overabundance and overgrazing in wildlife preserves has also become a serious problem. It often appears that animal populations are confined or compressed and that their dispersal is prevented (see Caughley 1976a), but this is often against a background of declining populations outside reserves. Presumably, ungulates normally disperse in search of better conditions when forage supply is reduced by drought or grazing. According to the compression hypothesis, regional scale systems of movement that are necessary for system persistence are disrupted by humans, thus causing ecosystem degradation (Cahalane 1943, Buechner and Dawkins 1961, Pengelly 1963, Lamprey et al. 1967, Laws 1969, N. Myers 1972). Long life spans of large herbivores could prevent rapid readjustment of the compressed population to its food supply if the compression occurs abruptly.

For example, there has been historic concern that there are too many elk on Yellowstone's northern winter range because movements out of the park have been restricted (Cahalane 1943, Pengelly 1963, see Coughenour and Singer 1991). Land areas north of the park have been occupied by ranches and agriculture, and it seems clear that hunting pressure outside the park could suppress emigration. Aside from the lack of firm evidence, the situation is not this simple. If elk regain access to ranch and farmland, as they now are, it seems reasonable to expect that the population will increase in response to a greater forage base. Elk numbers would likely increase if hunting were eliminated. A mechanism must be proposed that would force elk off park areas that have ample forage. One possibility is that greater snow depths within the park would drive elk downhill, particularly in severe winters. Yet, elk have historically coped with snow depths on the park's winter range.

Much controversy arose over elephant in Tsavo National Park, Kenya, in the 1960's and early 1970's (Laws 1969, Glover 1972, Sheldrick 1972, N. Myers 1972, Croze et al. 1981). Elephant numbers had gradually increased within the park under a policy of no culling. Substantial numbers of elephant likely immigrated into the park during 1960–70 (Corfield 1973). At the same time, dispersals were thought to have been inhibited by human populations surrounding the park. A drought occurred in 1970–1971. Due to lack of browse in proximity to water, many elephants died from starvation (Corfield 1973).

Tree populations declined considerably between 1970–74 (Leuthold 1977), which was attributed to elephant damage. Yet, bone isotope composition indicates that browse was not used more heavily during drought (Tieszen et al. 1989). Possibly, elephant were highly dependent on annual browse growth, which was reduced by the drought. As a result, elephant may have harvested accumulated browse standing crop. The relative effects of drought and browsing, and their interactive effects on woody plants, have not been clearly distinguished.

The elephant die-off was perceived to be a result of overpopulating and over-browsing (N. Myers 1972). Blame for the die-off was placed on the interference of humans with natural elephant dispersal patterns. It was asserted that elephants historically migrated to alternative grazing areas when drought, or their own utilization, reduced the local forage supply.

Possibly, rainfall patterns in this region are patchy at the scale of elephant movements, which would induce a large-scale shifting mosaic of plant growth. This could promote plant-herbivore stability. As spatially separated resource levels vary nonsynchronously, then time required for searching and movement among these areas would provide time for plant regrowth. Studies of elephant movements after the 1970–71 drought in Tsavo (Leuthold and Sale 1973) demonstrated that elephant move over long distances during the wet season in response to changes in the distribution of rainfall and resultant vegetation growth. However, studies have also suggested the possibility of spatially fixed dry-season ranges. Nearly all of the mortality during the 1970–71 drought occurred in dry-season concentration areas near rivers in the more arid half of the park (Corfield 1973).

Possibly there are ecological or evolutionary advantages of dispersing to marginal habitats or "sink areas" (Owen-Smith 1981). Natural selection could favor competitive exclusion or territoriality that would force surplus animals to disperse to less favorable habitats before overgrazing occurs.

The phenomenon of fencing-induced population increases has been called the Krebs effect (MacArthur 1972, Krebs et al. 1969, Stenseth 1983). Krebs et al. (1969) observed a population of field mice increased to unnatural densities within a small fenced area until food eventually limited population growth. This effect has not yet been explained, although it has been theorized that fencing may override a natural tendency towards intraspecific aggression and consequent dispersal (Stenseth 1983).

Application of a frustrated dispersal hypothesis to ungulates in parks requires that several difficult questions about traditional movement patterns be answered. To where would ungulates have dispersed? What level of forage or population density would trigger the dispersal? Would the trigger have been conservative enough to prevent overgrazing? Why? In some cases suggested dispersal sinks are actually areas of ample resources. Why would such habitats be underutilized? Functional relationships between dispersal, competitively controlled density, and relative plant availability are very poorly known.

Good explanations of overabundance and overgrazing in wildlife preserves require much better analyses of the spatial component of the plant-herbivore system. Synthetic quantitative analyses of climatic driving variables, herbivore movements, plant responses, and system dynamics are needed. While experimentation provides the strongest support, this is difficult or impossible at these very large spatial and temporal scales.

The Importance of Scale for Analyses of Plant-Herbivore Interaction

Specific ecological interactions are limited to specific domains of scale (Senft et al. 1987, O'Neill et al. 1988, Weins 1989, Kotliar and Weins 1990). Complex problems can be decomposed into more manageable pieces by identifying which plant-herbivore interactions occur over which spatial scales. Problems of confusing causes at one scale with responses at another are also avoided.

Although grazing may appear to be relatively uniform at coarse levels of resolution, this may only be because significant pattern at finer scales is blurred. In reverse, apparently uniform grazing can actively comprise a patch of grazing at larger landscape or regional scales.

Hierarchy theory (Allen and Starr 1982, O'Neill et al. 1986) states that the details of finer scale processes at lower levels of organization become insignificant at higher levels of organization: only the emergent behavior of the fine scale processes is significant at larger scales. Conversely, processes at higher levels of organization change too slowly or vary over too large a spatial scale to be perceptible at lower levels; yet the large scale provides the context within which the finer scaled system must operate.

Perceived plant response to herbivory depends on the scale and level of organization at which the response is measured (Brown and Allen 1989). Detrimental grazing impacts on plants are more likely to be measured at smaller spatial and temporal scales. Over a period of several days or several weeks grazed plant growth can prove to be less than ungrazed plant growth. Over a year, however, the grazed plants could compensate for their losses because limiting nutrients are recycled at a faster rate by herbivores (e.g., McNaughton 1979, 1984; Coughenour 1984; Ruess and McNaughton 1984; Detling 1988). Water to support regrowth may be retained in the soil. If a single plant is defoliated in a patch of 3 plants, the patch response is not necessarily simply one-third of a typical defoliated plant response plus two-thirds of a typical nondefoliated response. The 2 nondefoliated plants in the patch can grow at a faster rate due to defoliation of their neighbor and reduced competition for limiting resources (e.g., Mueggler 1972).

The landscape scale plant response to herbivory cannot be assumed to be equivalent to an average grazing pressure that is applied continuously and uniformly to an average plant. The aggregate response of a sward that is uniformly defoliated by 50% can be quite different from the aggregate response if 50% of the plants are 100% defoliated. If grazing is highly patchy, it will be unlikely that any plant will have experienced the fictitious average of grazed and ungrazed patches. Thus, individual plant responses can only be translated to the landscape scale response by incorporating information about patch and community scale patterns.

Grazing Patterns at Tiller, Patch, and Community Scales

Herbivory patterns at tiller through patch scales cause unique responses at higher levels of organization. Two types of patch scale patterns in particular cause ecosystem responses that would not occur if herbivory was spatially uniform: grazing lawns and patch grazing.

Grazing lawns are an alteration in plant form and function in response to frequent close grazing, characterized by a drastic reduction in height and activation of an increased number of tillers with few short stems and more horizontal leaf angles (Vesey-Fitzgerald 1973, McNaughton 1984). Forage quality is usually greater on a grazing lawn than off.

It has been hypothesized that grazing lawns are a unique benefit of herd formation (McNaughton 1984). While an individual animal could form a small grazing lawn, it would be more susceptible to predation (Estes 1974). In a dense herd animals have few opportunities to be selective, particularly when the herd is moving slowly. This imposes relatively uniform grazing intensity. Competitive advantage normally afforded to nonpreferred plants or tillers is consequently eliminated. Therefore, herds are more likely than individual animals to exert consistent grazing pressures required to shift dominance towards lawn forming species or genotypes. Ungulates probably have to move as herds to form large lawns. But when they do so, the nutritional advantages of feeding on lawns may be offset by lower intake rates (Hobbs and Swift 1988).

When forage quality is greater on grazed areas, total nutrient flow to herbivores can be accelerated even when total net primary production is lower. This has been documented, for example, on prairie dog towns (Jaramillo and Detling 1988). Grasses on young dog towns have more prostrate morphologies (Detling and Painter 1983, Jaramillo and Detling 1988) and higher rates of nutrient uptake (Polly and Detling 1988, Jaramillo and Detling 1988). This could be why these areas are used preferentially by bison (Coppock et al. 1983).

Patch grazing (Stobbs 1970, Bakker et al. 1983, Ring et al. 1985) is initiated when forage supply exceeds demand (Spedding 1971). Regrowth on grazed patches becomes higher in quality than the surrounding ungrazed matrix. As time passes grazers continue to select the regrowth and the grazed patches diverge further from the ungrazed matrix in terms of forage quality and plant form, and a mosaic pattern develops in the pasture. It has been hypothesized that patches form a dynamic mosaic, with grazed patches being formed from nongrazed patches of previous years. While patches persist for 4 or more years (Willms et al. 1988), use of grazed patches has been shown to decay over time (Hobbs et al. 1991). While net primary production on grazed patches is sometimes lower than that on ungrazed patches, there are more available nutrients in the soil of grazed patches (Willms et al. 1988). Ungrazed patches provide emergency forage in years of poor rainfall (Willms et al. 1988).

Patch grazing can lead to ecosystem degradation (Mott 1987). Once selective grazing of patches begins, continued grazing pressure can lead to rapid death of individual plants. Areas of plant death form "scalds", which result from soil surface sealing (Bridge et al. 1983). Removal of the vegetation and litter cover exposes the soil to direct raindrop impact. In soils of intermediate texture the raindrops can defloculate soil aggregates, glance off finer soil particles and deposit them in the form of crusts on the soil surface (see Shainberg and Singer 1985). Also, reduced carbon inputs to the soil can accelerate degradation of soil structure (Mott et al. 1979). In subsequent seasons new patches are formed, expanding the degradation. Dry-season fires can be used to remove the patches, thus increasing the stability of the pasture as a whole (Andrew 1986, Coppock and Detling 1986, Hobbs et al. 1991).

Importantly, large scale movements of grazers in grazing systems impose particular smaller scale patterns of defoliation among individual tillers. Continuous and rotation grazing system effects on tiller-scale defoliation patterns were compared by Gammon and Roberts (1978). Under continuous grazing some tillers were repeatedly utilized (thus showing a tendency towards patchy grazing at tiller scales). Intermittent grazing reduced the number of tillers that were defoliated three or more times. A greater percentage of tillers was grazed under a heavier stocking rate (Briske and Stuth 1982). In a short duration rotation system, higher stocking rate also increased the percentage of tillers regrazed at least 2 or 3 times (Pierson and Scarneccia 1987).

When livestock were rotated more rapidly among 8 pastures, they defoliated a smaller percentage of the tillers in a given area in each grazing episode (Gillen et al. 1990). Rotation rate had no effect on the cumulative number of tillers that were defoliated over a season, but faster rotation increased the number of tillers that were defoliated repeatedly. When stocking rate was increased under a given rotation rate, a greater percentage of tillers was grazed repeatedly, and tillers of the more preferred species were grazed to a lower height. Here, duration was shortened by faster rotation of a fixed number of animals among a fixed number of pastures so rotation rate was not confounded with altered herd density. Usually when SDG is implemented, grazing duration is shortened by increasing the number of pastures, which also increases herd density. The results suggest that if higher stocking rates can be supported under SDG, as often claimed, it is likely a result of greater herd density and fuller use of available tillers, rather than a result of altered duration.

While paddock scale grazing systems are imposed to achieve a certain grazing regime, livestock may create smaller scale grazing systems of their own within paddocks. Consequently, the grazing regime experienced by plants is not necessarily predictable solely from rate and intensity of herbivore rotation among pastures. Obviously, livestock movements are not controlled under continuous grazing, but individual animals or groups can nevertheless rotate. Theoretically, any system of movement that can be implemented by fencing can be implemented by the livestock themselves (Spedding 1970). Livestock move, and they cannot occupy the

entire area all at once. They may form a concentrated area of grazing or they may create numerous scattered grazed sites (Spedding 1970). Of course, the more intensely animals are managed, the less likely it is that animals will be able to create their own small-scale grazing system.

If grazing ungulates do impose deferred rotation or short duration grazing patterns of their own within pastures, then the need for grazing systems cannot be argued on the basis of a need to rest plants. Rest is provided by livestock movements within pastures. Unfortunately however, the natural grazing system of the animals is often in balance with plant growth at an undesirably low stocking rate: livestock may only prefer to use parts of the landscape, some of the patches or some of the plant species.

The Need to Consider Landscape Physical Constraints on Ungulate Distributions

Analyses of spatial plant-herbivore interactions requires knowledge of physical constraints upon ungulate distribution on the landscape. Spatial distributions of landscape physical factors, climate, and herbivores can be used to estimate spatio-temporal patterns of herbivory and plant growth. Patterns of herbivory on the landscape are constrained by spatial distributions of topography, cover, water, and minerals. Effects of habitat structure on wild and domestic ungulate distributions have been documented in a great number of studies. A sample of these is provided here to illustrate their potential effects on spatial patterns of herbivory.

Topographic effects can be broken into five different types: (1) effects on herbivore movement and foraging; (2) effects on microclimate experienced by herbivores, (3) effects on interactions with predators; (4) effects on social grouping; and (5) effects on plant growth.

Topography affects movement by either imposing physical barriers or by increasing the time and energy required to move a certain distance. Slopes can simply be too steep for travel. For example, cattle avoid slopes of greater than 30% and horses avoid slopes greater than 50% (Ganskopp and Vavra 1987). Elk spend far more time on gentle than on steep slopes (Houston 1982). Slope amplifies other distance functions. The costs of travel to water are increased on steeper slopes such that vertical distance above water affects cattle distributions (Roath and Krueger 1982).

Topography defines movement pathways across the landscape. For instance, landscape form determines the locations of cattle trails (Weaver and Tomanek 1951, cited by Arnold and Dudzinski 1978). Use of plants on the landscape is influenced by their proximity to these trails. Regular deer migration routes are often along corridors defined by topographic features such as ridges and canyons (Thomas and Irby 1990), with preferential foraging in open areas along the route. Locations of mountain passes affect the accessibility of entire landscapes and the use of plants within those landscapes.

Regional topographic characteristics have had an influence on the geographic distribution of bison (Van Vuren 1987). Much of the terrain west of the Rockies is a disjunct mosaic of habitats separated by physiographic barriers to movements such as mountains and canyons. This inhibited movements of local populations out of areas which are periodically impacted by drought, heavy snow, or predation. Over time, resultant local extinctions depressed the regional population, which may in turn, have affected the coevolutionary relationship between herbivores and plants (Mack and Thompson 1982).

Topographic influence on snow depth affect ungulate movement and foraging. Winter ranges of horses in some areas are characteristically on or near wind-swept ridges (Miller 1983). Wind-blown ridges are important snow-free areas for pronghorn (Ryder and

Irwin 1987) and elk (Houston 1982). Elevation effects on snow depth determine the sizes and configurations of elk winter ranges (Houston 1982, Wambolt and McNeal 1987).

Topography affects the microclimate that is experienced by animals through effects on orientation to sun and prevailing winds, as has been demonstrated for cattle (Senft et al. 1985b) and wintering pronghorn antelope (Ryder and Irwin 1987). Pronghorn prefer habitats with sites that provide shelter from prevailing winds and sites that are warmed by the sun.

Topography provides escape from predation for ungulates that can exploit rugged terrain (Krausman and Leopold 1986). Bighorn move to their summer range long before good forage is present, apparently to find terrain needed for predator avoidance during lambing (Festa-Bianchet 1988). Mountain goats and other caprids also use topography for predator avoidance (Hutchins and Geist 1987).

Topography affects social grouping and home range formation. Distinct cattle groups used different parts of a mountainous rangeland (Roath and Krueger 1982). This was suggested to have been due to the influence of visual and topographic barriers which increased social links between individual animals in a group.

The distribution of physical vegetation structure is another habitat variable having widely recognized effects. Habitats containing adequate quantities of vegetation cover are often preferentially utilized. Shrub cover is important for elk (McCarquondale 1987) and deer (Wambolt and McNeal 1987). Dorcas gazelle in Africa require streambeds lined by shade-providing *Acacia* trees (Baharav 1982). Kangaroos prefer areas with protective cover (Terpstra and Wilson 1989). Gregarious ungulates avoid wooded cover. Cattle are seldom seen in small grassland openings, possibly because the openings are too small to support a complete herd (Pratt et al. 1986).

The effects of water distribution are well known (e.g., Ares 1936b, Western 1975), but they are infrequently quantified. Water availability can be more limiting than forage for African ungulates (Western 1975, Williamson et al. 1988). Recent studies have demonstrated: the extent to which water affects cattle land use on Oregon mountain rangeland (Roath and Krueger 1982); that summer horse ranges tend to be within 4.8 km of water (Miller 1983); and that water determines dry season kangaroo distributions (Low et al. 1981).

Mineral licks have well-known effects on ungulate distributions (Ares 1936a, Jones and Hanson 1985, Kruelen 1985). The spatial distributions of forage mineral contents are seldom considered, however. Ungulate foraging habitat preferences in the Serengeti are highly related to the mineral contents of plants, which in turn, are related to mineral contents of soils (McNaughton 1988, 1990). Soil nutrient levels significantly affect the distribution of ungulate carrying capacities at regional scales (Bell 1982, East 1984).

Models of Herbivore Movements and Distributions

An early quantification of the relationship between ungulate spatial distribution and landscape factors was Cook's (1966) use of multiple regressions to explain livestock spatial utilization patterns. Regression equations were later used to model ungulate distributions over an entire landscape (Senft et al. 1983, 1985a, 1985b). Topographic factors at each position on the landscape were used as input to the regression model. A regression approach was used to analyze winter elk foraging sites (Grover and Thompson 1986). Relationships with single variables such as distance to cover, distance to road, and forage density were noisy. However, a significant portion of the variance was explained by combinations of variables. Favorable combinations were in short supply on the landscape. Average distribution of sheep in an Australian pasture was modeled with a multiple regression equation that included

terms such as inverse squared distance to water, linear distance to shade, linear vegetation preference, and presence/absence of fence (Smith 1988). Continental scale distributions of kangaroos in Australia were modeled from a number of climatic variables (Walker 1990).

Multiple regression analyses have some limitations. They usually do not consider interactions among variables. They are usually static; otherwise separate models must be constructed for different seasons (e.g., Senft et al. 1983, 1985b).

These limitations have been overcome in the technique of habitat suitability index modeling (Schamberger and Krohn 1982, Cook and Irwin 1985). Habitat suitability index modeling is part of the general Habitat Evaluation Procedures (HEP) developed and used within the U.S. Fish and Wildlife Service. A first step in this procedure is to use simple correlation and multiple regression to identify habitat variables that are correlated with ungulate densities and measures of reproductive success (Irwin and Cook 1985). Sampling is conducted over a wide range of conditions. Individual suitability index functions are then constructed for the most explanatory variables and these functions are combined together into an equation for the habitat suitability index. Ideally, animals would be distributed in proportion to habitat suitability.

The ideal free distribution described by Fretwell (1972) assumes an equilibrium wherein additional movements cannot improve resource availability to any animal. Ideal free assumptions are implicit in regression models as well as habitat matching rules (Herrnstein 1974, Pulliam and Caracao 1984, Fagan 1987) and optimal foraging models, in which the relative numbers of individuals using different habitats perfectly match resource availabilities. Matching models are based on the assumption that competition among individuals brings about an efficient spacing of individuals in relation to biotic and abiotic resources. Optimal foraging theory assumes ungulates have perfect knowledge of forage distribution.

The assumption of a static equilibrium can be partially surmounted by recalculating the distribution as the landscape changes. A dynamic model of sheep distribution was formulated based upon a water balance equation, which was affected by seasonally and spatially varying evaporative demand and vegetation condition (Smith 1989). In another dynamic application (Coughenour 1991a, 1991b), a habitat suitability index was calculated on a weekly to monthly interval for each spatial grid cell of a simulated regional pastoral ecosystem. The index incorporated functional responses to temporal variations in forage abundance due to rainfall variation, prior grazing, and loss of forage to litter and abiotic weathering as well as functions for static effects of water, topography, and cover.

As competitive interactions among individuals are weak or nonexistent in variable and harsh habitats, density distributions are more prone to be random (Weins 1984, 1985). Imprecision is inevitable when attempting to explain individual animal locations at fine spatial and temporal scales. However, the random noise at fine scales can be averaged out over longer time periods so that the mean distribution does approximate the distribution of resources on the landscape, irrespective of competition.

Mismatching between dynamic animal and resource distributions arises when movements are slow in comparison to rates of environmental change. Animal movements must be explicitly treated to address this type of problem. One approach is to consider the movements of animals in space as a diffusion process (e.g., Taylor and Taylor 1977, Okubo 1980). The migration model of Taylor and Taylor (1977) included immigration and emigration rates as functions of density. The model was applied to a time varying random mosaic of cells having 1 of 3 habitat qualities. Movements became a game of hide and seek, with net distribution reflecting "the balance between rates of environmental change and

the movement and reproductive rates of the organism, which fails to use some resources because they are not discovered in time" (Taylor and Taylor 1977).

Time required for population growth also poses problems for the equilibrial assumptions of an ideal free distribution. Hobbs and Hanley (1990) used simulation modeling to show that distribution among habitats also depends on the relative positions of local populations along their growth trajectories, and random disturbances in those trajectories. A mismatch of density and resource abundance can arise, for example, from a dramatic reduction in population density due to locally catastrophic weather. Slow immigration and population growth would cause the mismatch to persist for a significant period of time. Empirical "snapshot" distributions cannot be assumed, therefore, to reflect relative carrying capacities.

Individual habitat selection is not likely to be optimal (Weins 1984, 1985). In reality, individuals lack perfect knowledge of the distribution of resources in the environment, particularly when the distributions are changing stochastically. At any given point in time, populations are unlikely to be spaced in perfect proportion to resource abundance. Movements are sometimes made impossible or they are significantly impeded by barriers (Weins et al. 1985).

Limitations of aggregate population models are a consequence of the simplifying assumptions about the mean behavior of the population. Individual organisms interact with their immediate local environments; and these local environments are heterogeneous in space and time. An individual based modeling approach (Huston et al. 1988) avoids many of the simplifying assumptions that are required when these heterogeneities are ignored. Predictions of individual based models will be different than predictions of aggregate models if heterogeneity at small spatial scales promotes unique processes—and especially if those processes involve positive feedback (Huston et al. 1988).

The actual mechanisms of animal foraging are considered in an individual based approach. Individual based movement models that have been constructed (eg. Siniff and Jessen 1969, Owen-Smith and Novellie 1982, Saarenmaa et al. 1988, Folse et al. 1989) have proven very useful for explaining foraging patterns and efficiencies. For example, one group (Senft et al. 1987) constructed a rule-based model of individual ungulate foraging. The model has proven useful in classroom exercises to demonstrate net effects of fine scale foraging behavior within and among feeding stations on total intake over one or more foraging bouts (L. Rittenhouse and D. Swift, pers. comm.).

Unfortunately, the behavioral rules that govern individual foraging behavior are poorly known. To elucidate these rules, individual animals must be subjected to carefully controlled environments such as the mazes used in animal psychological research. Using such an approach, Bailey et al. (1988) have found that cattle tended to follow a win-switch strategy, as individuals moved after discovering productive patches. Cattle tended to return to productive areas more often, which suggested spatial memory (Bailey et al. 1987).

A serious limitation of individual based models is the computational demand required to represent large numbers of animals over large areas. For example, it would be highly impractical to apply an individual-based approach to model 10,000 pastoral herdsmen and their livestock in over a 10,000-km^2 area in southern Turkana, Kenya. Consider that the interactions of each herdsman with many neighboring herdsmen would have to be simulated to repesent population distribution.

Both individual based and aggregate models have advantages and disadvantages. To a large extent the appropriate model depends on the spatial and temporal scale of the questions that are to be answered. However, a two-way flow of information among

both approaches would be optimal, to understand ungulate use of space over a wide range of scales.

Modeling Plant Growth Response to Spatial Herbivory Pattern

The salient question here is how plants respond to different spatio-temporal patterns of herbivory. Given herbivore movement responses to landscape variables, including forage quantity and quality, grazing regimes imposed upon stationary plants can be deduced—ie. the frequency, intensity, and seasonality of defoliation. Knowledge of plant responses to various defoliation regimes can then be used to predict responses to the pattern of herbivore movement.

As an example, a detailed model was formulated to explain graminoid responses to herbivory in the Serengeti ecosystem, Tanzania (Coughenour et al. 1984a, Coughenour 1984). The model was subjected to factorial combinations of grazing height and frequency (Coughenour et al. 1984b) and results were portrayed as response surfaces of plant production. Short grasses yielded most when grazed at low heights every 24 days while tall grasses responded more favorably to a longer grazing interval of about 55 days. Tallgrass was relatively insensitive to grazing heights below 16 cm. In actuality, migratory Serengeti wildebeest graze short grasslands to a minimal height, moving about the plains in 2-week (Vesey-Fitzgerald 1973) to 4-week (Sinclair 1977) rotations. The herds spend less time in any given area of the tallgrass region (Maddock 1979). According to the model response surfaces, short-grass yields would be near maximal under the observed regime. Tallgrass yields would be high, but less than maximal.

Consequences of spatial plant-herbivore interactions in rotation systems were modeled by Noy-Meir (1976). At moderate stocking rates short cycle rotation grazing had little effect on productivity compared with continuous grazing, while intensive (long cycle or many paddock) rotation depressed production. Intensive rotation substantially increased productivity at high stocking rates. When initial range condition was poor, intensive rotation increased production relative to continuous grazing. When initial range condition was good, continuous grazing was more productive. Intensive rotation at low stocking rate caused herbivory to deplete vegetation below the critical level where plant growth rate and consumption rates are equal. Rotation was more favorable on the poor condition range because of the low initial plant biomass. Rest periods were provided for vegetation to escape above the critical point where growth and consumption rates were equal.

Senft (1988) simulated spatially interactive short duration and continuous grazing systems. Herds were moved among 10–16 paddocks. SDG decreased forage production, but increased the fraction of available forage that was utilized.

A spatial model of ungulate movements and plant growth was formulated and parameterized for the Serengeti, Tanzania, migratory and Turkana, Kenya, nomadic pastoral ecosystems (Coughenour 1986). In this model shoot and root growth rates and death rates responded to stochastic rainfall patterns. Grid cell size was scaled to ungulate density to simulate a single herd at observed densities.

There proved to be little difference in Serengeti short-grass root mass between continuous and rotation grazing at moderate animal densities ($\leq$300 km^{-2}). At higher densities, shortgrass could only persist under a long (60 day) rotation system, but forage intake rates were too low to support the population. The Serengeti midgrass could not withstand densities above 200 km^{-2} without a larger ungrazable reserve or a rotation cycle. A herbivore density of 400 km^{-2} was sustained with a 240-day rotation among six cells. The standard Turkana movement pattern was a concentration onto about one fourth of the total area during the wet season, followed by increasing dispersal among cells as the dry season progressed. This movement pattern was compared to an even, stationary livestock distribution, a regular rotation scheme, dispersion during the wet season, and a pattern where the entire population was moved to the adjacent most resource rich cell at 2-week intervals. Dry season dispersal allowed more plants to persist after 10 years because livestock were densely concentrated only during periods of high plant growth rate. Regular rotation and wet season dispersion reduced perennial plant tissue by one third. Movements to the best adjacent foraging area reduced plant density the most. Other movement patterns reduced perennial plants to very low levels in areas where initial plant density was low. Fixed rotation forced overly high densities into single cells during critical plant growth periods.

Spatial Plant-Herbivore Systems and Spatial Predator-Prey Systems

Theoretical studies of spatially distributed predator-prey systems are relevant here because they explain how spatial heterogeneity can affect system stability. A hypothesis that excited much theoretical work in the 1970's was that spatial heterogeneity can stabilize predator-prey systems and promote their persistence. Specifically, heterogeneity could prevent predators or (herbivores) from overexploiting their prey or (forage).

Both ecosystem spatial heterogeneity and size can increase stability. Thus, orange mites and their predators were more likely to coexist in environments comprised of larger numbers of oranges (Huffaker 1958). As the sizes of flasks containing microbial predator-prey system were increased, prey became more difficult to find at low densities (Luckenbill 1974). Predators were unable to search out low numbers of prey in a large volume in a short period of time; thus prey could recover while predators searched. Host trees were camouflaged from spruce budworm attack when they were intermixed with nonhost trees (Morris 1963), due to physical barriers to predator dispersal (Murdoch and Oaten 1975). Patchiness in a predator-prey system draws predators away from areas of low prey abundance, effectively forming a prey refuge (Hassel and May 1973). The stability of the system is thus enhanced. Several other modeling studies have supported this hypothesis (Hilborne 1975, Myers 1976, Ziegler 1977).

The positive effects of spatial heterogeneity on predator-prey stability can be quite important for plant-herbivore ecosystems (May and Beddington 1981). Presumably, the stability promoting mechanism would be patchy aggregations of herbivores rotating amongst a shifting mosaic of vegetation patches in various stages of recovery from herbivory damage. If so, problems of herbivore overabundance are especially likely in wildlife reserves which are too small to support a stable patch dynamic system.

Conclusions

It becomes ever more important to understand the spatial components of plant-herbivore interactions as human and ungulate uses of space intensify. Conflicts between human and ungulate land use increase as the human population grows and expands. Space becomes more limiting, wildlands are fenced off, and open rangelands are parceled out or converted to settled, irrigated agriculture. Wild ungulates are forced into smaller spaces and livestock numbers continue to increase.

Spatial components of plant-ungulate interactions underly domestic livestock grazing systems, pastoral land use practices, and native ungulate ecosystems. The sustainability and persistence of these ecosystems over the long term are strongly affected by links between spatial pattern and process. However, the linkages are unclear in all 3 types of ecosystem.

Early rotation grazing systems were patterned in design and in concept, after movements of free roaming native ungulates. Such an analogy would be much easier to support scientifically if the spatial components of herbivory were better understood. In actuality, natural movement patterns of wild ungulates in relation to plant growth are not well known and many tests of rotation grazing systems have failed to show any clear advantages.

The degree to which overgrazing in traditional pastoral ecosystems is prevented by landscape limitations on forage use is potentially high, but little understood. Pastoral development efforts must consider the ramifications of patchy rainfall over large areas and traditional movement responses to these spatio-temporal patterns. The extent to which such movements might limit population size, prevent localized overgrazing, prevent local extinctions, thus stabilizing the plant-herbivore interactions as well as the pastoral population, is not well understood. Yet much evidence suggests that spatial heterogeneity is important for pastoral ecosystem persistence.

Ecologically sound management of spatially extensive wild ungulate ecosystems demands a particularly high level of understanding of natural spatial plant-herbivore interactions. It is often difficult to provide irrefutable support for hypotheses that disruptions of natural dispersal movements cause overgrazing. Total support requires knowing the manner in which dispersal rates and patterns vary in relation to population density and forage abundance.

Carrying capacity can be variable or unpredictable in space just as it can in time (Weins 1977, Ellis and Swift 1989, Westoby et al. 1989). Density-independent periods of resource "bottlenecks" clearly exert significant limitations on populations in variable environments (Weins 1977). Spatial distributions of multiple resources also limit the spatial component of population abundance, thus creating resource bottlenecks in space.

These limitations of nonforage resources on ungulate distributions and their impacts on plants are poorly documented. Water, topography, minerals, and other resource distributions influence carrying capacity as well as plant-animal interactions. Areas of the landscape which are avoided because of inadequate nonforage resources can provide important refugia for plants. Landscape constraints then determine the minimum ungulate density which can persist through drought. The joint distribution of water and forage on the landscape during drought determines the area and thus the quantity of forage that is available. A limited, predictable number of ungulates would be supported by this area. This would suggest a form of density dependence that has been little investigated. The ability of spatio-temporal bottlenecks to support limited populations would have an important effect on the long-term carrying capacity of the landscape.

While wild ungulates cannot usually fully utilize landscapes, production-oriented systems attempt to sustainably extract as much from an ecosystem as possible. Wildlife distributions are often limited by localized deficiencies of water, minerals, and navigable terrain. Production livestock systems attempt to remove these landscape constraints by manipulating resources or animal behavior. In both cases, nonforage constraints significantly alter the plant-herbivore balance.

Experiments and models of predator-prey interactions in spatially diverse environments suggest that movements might also stabilize plant-herbivore systems. However, there are few, if any demonstrations of this concept for large herbivore populations. Herbivores should tend to move away from areas of low forage abundance, thus providing forage refugia. Patchy and unpredictable rainfall cause localized forage depletions which stimulate movement. The large scale disturbance mosaic could be stable in the aggregate. The time required for ungulate movement and search provides opportunities for plant escape from herbivory. Ironically, stability should arise from unpredictability.

Spatial interactions and processes in ungulate ecosystems must be better known. The problems of spatial plant-herbivore interactions of today are more critical, and often more complex than those confronted by humans decades, hundreds or thousands of years ago. Failure to consider the spatial components of herbivory in carrying capacity calculations and assessments of ecosystem persistence can contribute to overgrazing, failed economic development efforts, and declines of wildlife populations. Technologies such as spatial simulation modeling and geographic information systems now exist which make analyses of spatial plant-ungulate ecosystems more feasible. It is likely that these approaches will be increasingly utilized to incorporate the spatial dimension into analyses of plant-herbivore interactions.

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