

Restoring Heterogeneity on Rangelands: Ecosystem Management Based on Evolutionary Grazing Patterns

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Rangelands are the most common form of terrain in both the United States (where it accounts for 61% of all land surface) and the world (70% of all land surface). Rangelands consist primarily of native plant communities managed, typically, for livestock production (Holechek et al. 1998). Because they can embrace extensive native plant communities, rangelands can serve as biodiversity repositories. However, in the Great Plains of the United States, where decisions about land use are made largely at the discretion of the private landowner, many plant and animal species dependent on rangelands are imperiled.

For example, according to data from the North American Breeding Bird Survey, 70% of the 29 bird species characteristic of North American prairies experienced a decline in population between 1966 and 1993. Indeed, these grassland species are declining at a faster rate than any other guild of terrestrial birds in North America (Knopf 1994). Excessive herbivory by domestic livestock may have contributed to the decline in some of these species, but many species endemic to North American prairies evolved with large grazing animals. The Mountain Plover (*Charadrius montanus*), Baird's Sparrow (*Ammodramus bairdii*), and Chestnut-collared Longspur (*Calcarius ornatus*) are examples of birds that occur in highest densities in grazed landscapes (Kantrud 1981, Renken and Dinsmore 1987, Knopf 1996).

There are many potential causes for this decline in grassland bird populations, but the fact that it occurred when the condition of rangelands had improved, according to traditional means of evaluation (Holechek et al. 1998), suggests that techniques currently used to manage rangelands may be insufficient to maintain biological diversity.

Most techniques of rangeland management were developed under the paradigm of increasing and sustaining livestock production by decreasing the inherent variability associated with

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rangelands and grazing. This rangeland management approach is incapable of providing an ecological framework for alternative management objectives that have become more important over the past quarter-century. For example, the maintenance of biodiversity, as well as the preservation of habitat for many individual species, depends on the interspersion of diverse habitat types throughout a heterogeneous landscape.

We contend that traditional rangeland management techniques reduce rangeland heterogeneity by favoring the most productive, most palatable forage species for domestic cattle. In this article, we propose a paradigm that promotes the potential heterogeneity of landscapes through an alternative approach to managing those rangelands with a long evolutionary history of large-ungulate grazing (Milchunas et al. 1988). Hence, for these rangelands we attempt to link the goals

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of conservation biologists, ecologists, and rangeland managers by presenting an approach to land management that simultaneously considers biological diversity and agricultural productivity.

Maintaining heterogeneity on rangelands is important

Divergent views of the influence of livestock grazing on rangeland ecosystems are largely the result of a narrow focus that compares grazed landscapes to grazing exclosures. Our study systems are the rangelands of the Great Plains, where the evolutionary history of grazing is long and grazing is accepted by grassland ecologists as a keystone process of the grassland ecosystem (Milchunas et al. 1988, Knapp et al. 1999). The long evolutionary history of grazing in these prairie ecosystems suggests that biodiversity can be enhanced by mimicking temporal and spatial grazing patterns that occurred before European settlement. To accomplish this, one must first understand the structural heterogeneity of rangelands and the effects of different spatial and temporal grazing patterns on landscape patterns and ecosystem processes.

The term *heterogeneity* can have many meanings (Kolasa and Pickett 1991), but the relevant parameters in the present context derive from variability in vegetation stature, composition, density, and biomass. This type of heterogeneity influences species diversity, variety of wildlife habitats, and ecosystem function (Christensen 1997, Wiens 1997, Bailey et al. 1998). Heterogeneity is therefore the precursor to biological diversity at most levels of ecological organization and should serve as the foundation for conservation and ecosystem management (Christensen 1997, Ostfeld et al. 1997, Wiens 1997). Rangelands have been described as inherently heterogeneous because composition, productivity, and diversity are highly variable across multiple scales (Ludwig and Tongway 1995, Patten and Ellis 1995, Fuhlendorf and Smeins 1999). A heterogeneous patchwork on rangelands can result from differential timing of disturbances and corresponding out-of-phase succession among patches, spatial variability of resources associated with topographic and edaphic patterns, or competitive interactions among plant species (Fuhlendorf and Smeins 1998).

Ecologists understand that many rangeland ecosystems evolved with disturbances, including fire and grazing, but until recently the importance of the spatial patterns and heterogeneity evidenced by these disturbances was not widely recognized. Recent descriptions indicate that disturbance patterns on the Great Plains led to a shifting mosaic in which, at any point in time, the landscape included areas that had been recently burned or grazed (or both), as well as areas that had not been disturbed for years or even decades (Kay 1998). Many of the species that are declining on grasslands today most likely evolved on rangelands best described as heterogeneous across many spatiotemporal scales.

The evolutionary importance of heterogeneity on rangelands is evident from the variability in habitat requirements of grassland birds. The structure of grassland avian

communities is influenced strongly by the degree of structural heterogeneity in associated plant communities (Wiens 1974), with some bird species having affinities for grassland habitats with specific structural characteristics (Cody 1985). For example, the Dickcissel (*Spiza americana*) is more abundant in those grasslands that have more vertical cover and forb cover. Alternatively, the Grasshopper Sparrow (*Ammodramus saviannarum*) is more abundant in grasslands with less vertical cover (Zimmerman 1971, Patterson and Best 1996). Abundance of the Western Meadowlark (*Sturnella neglecta*) has been correlated negatively with vertical cover but positively with vertical patchiness (Patterson and Best 1996). The variability in habitat selection of these coexisting species indicates that heterogeneous grasslands are necessary for maintaining diverse communities of this avian guild.

Another illustration of the importance of heterogeneity is provided by the lesser prairie-chicken (*Tympanuchus pallidicinctus*), which has suffered a decrease in range of 92% and a decline in overall population of 97% over the past century (Taylor and Guthery 1980). The lesser prairie-chicken requires diverse habitat types to support different behavioral activities. For example, nesting cover and brood-rearing habitat are best provided by relatively undisturbed prairie vegetation with native grasses that average 30–50 cm in height, whereas booming activity (courtship displays) and feeding on certain preferred foods both require a vegetation height less than 10 cm. This diversity in structural requirements suggests that habitat management for this species and other grassland species of concern requires a multiscale perspective that focuses on restoring heterogeneity across local areas and landscapes similar to those that may have existed on grasslands before European settlement (Kay 1998).

Traditional homogeneity-based rangeland management

Most rangeland management practices were developed to increase livestock production and promote dominance of a few key forage species by reducing inherent landscape heterogeneity caused by topo-edaphic features and herbivore behavior. Traditional management of rangelands has focused largely on two primary elements of grazing management: distribution of grazing in space and time and grazing intensity (stocking rate).

Distribution of grazing across rangelands. Grazing animals react to their environment through a hierarchy of instinctive responses and behavioral actions that result in variable distributions at the landscape, community, patch, and feeding station levels (Senft et al. 1987, Stuth 1991). Under continuous moderate grazing, livestock tends to select local areas that lack accumulations of biomass from previous years. This behavior produces small, heavily grazed patches interspersed within ungrazed or lightly grazed patches—a pattern of small-scale structural heterogeneity (Bailey et al. 1998). At a larger scale, livestock concentrate near water, thus increasing grazing pressure on vegetation near water and reducing

grazing pressure on vegetation distant from water. The result is larger-scale heterogeneity. This gradient of grazing pressure associated with distance to water masks the small-scale heterogeneity both close to and distant from watering points. In ecosystems with a short evolutionary history of grazing, repeatedly grazed patches represent the initial stages of rangeland deterioration and desertification as a result of decreased water infiltration and increased runoff (Fuls 1992, NRC 1994).

Grazing systems, defined as the specialization of grazing management with recurring periods of grazing and deferment for two or more pastures or management units (SRM 1989), have been designed primarily to maximize livestock distribution in space and time so that forage is harvested uniformly across the landscape (Hart 1978). Many rangeland managers believe that specialized grazing systems requiring livestock rotation among pastures will improve the rangeland condition and livestock production better than continuous grazing, in which livestock remain in the same pasture throughout the grazing season. However, numerous studies on rangelands throughout the world have demonstrated that continuous grazing of moderate intensity does not degrade rangeland productivity and composition (Holechek et al. 1998).

Some specialized grazing systems employ extreme measures to override livestock behavior (Figure 1). Rapid rotational grazing systems rotate livestock across the landscape

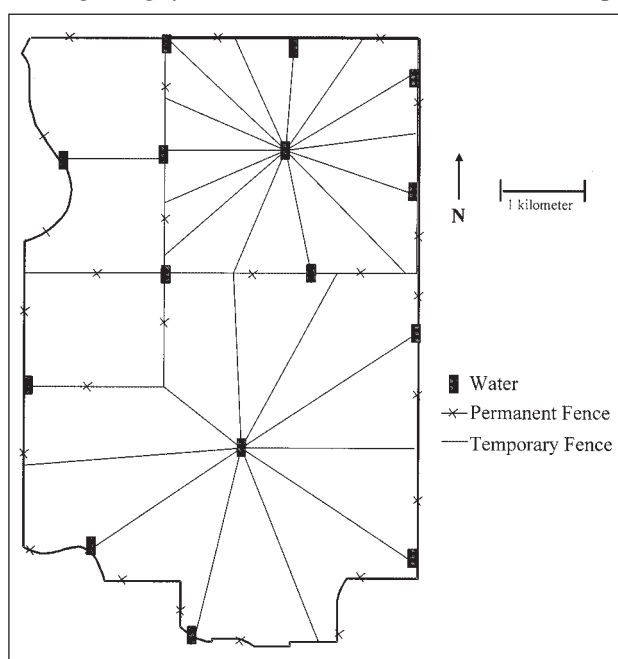


Figure 1. Landscape plan for rotational grazing. A cross-fencing scheme for a traditional grazing management plan implements a rapid rotational grazing system; the objective is to achieve a more uniform distribution of grazing across the landscape. This and similar traditional grazing management practices promote uniform forage utilization, in contrast to the patch burn (heterogeneity-based) plan on the Tallgrass Prairie Preserve (Figure 6).

through relatively small pastures. This approach is used to minimize differential distribution of livestock, obtain uniform utilization of forage, reduce inherent landscape heterogeneity, and, ultimately, achieve greater livestock production (Figure 2). The objective is to rotate livestock through all pastures within about a 3-month period to assure uniform utilization of forage. More uniform forage utilization can be achieved, but livestock production and sustainability may actually decrease (Holechek et al. 1998, McCollum et al. 1999).

Under all grazing regimes, heterogeneity within management units increases as the scale grows (Figure 3; see also Fuhlendorf and Smeins 1996, 1999). Rapid rotational grazing systems are designed to reduce spatial heterogeneity through more even spatial utilization of forage, with relatively low levels of structural and compositional heterogeneity resulting across most scales. Under continuous grazing, repeated selection of the same local areas results in higher levels of heterogeneity at small scales. Yet because lightly foraged and heavily foraged areas both exist more or less permanently under continuous grazing in the absence of fire, and because moderate, continuous grazing does not allow for sufficient formation of severely used and unused areas—which are necessary if spatial heterogeneity is to increase—an alternative grazing strategy is needed to maximize larger-scale heterogeneity and plant species diversity.

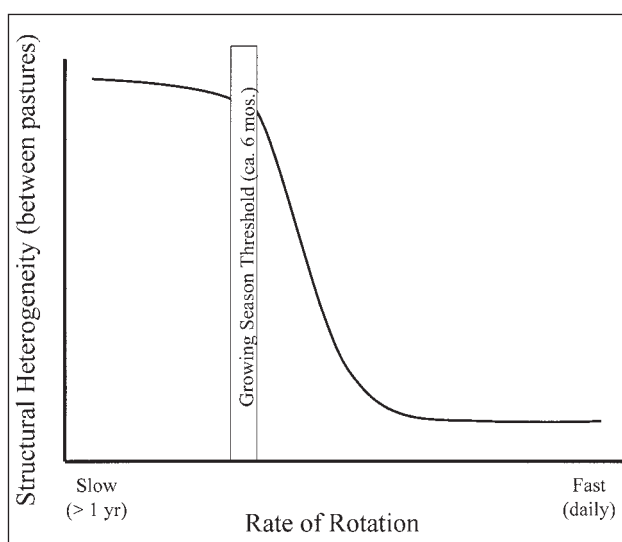


Figure 2. A conceptual model demonstrating the relationship between rate of grazing rotation and structural heterogeneity within rangeland landscapes. Rapid rotation of livestock through multiple pastures results in uniform utilization of forage and low levels of structural heterogeneity within the landscape. Slow rotation and long rest periods (more than one growing season) result in standing biomass that is several years old and dominated by taller, more palatable grass species in rested areas, and shorter, less palatable early successional plants in local areas that have experienced relatively heavy short-term grazing pressure.

Grazing intensity. Grazing intensity, the demand placed upon forage by animals, largely dictates the influences of livestock grazing on rangeland vegetation (Vallentine 1990, Fuhlendorf and Smeins 1997). Moderate, continuous grazing, which has been identified as the most ecologically and economically sustainable grazing management practice for domestic livestock on rangelands (Vallentine 1990, Heitschmidt and Walker 1996), can amplify the inherent heterogeneity of rangelands at some scales. Long-term data from one of the few studies of the effects of grazing intensity on heterogeneity indicate that the impact of grazing—whether positive, negative, or negligible—depends on the level of intensity and the scale of observation (Fuhlendorf and Smeins 1999). On productive rangelands with a long evolutionary history of grazing, heterogeneity is greatest under moderate grazing at most scales. When the natural spatial heterogeneity and topographic variation within rangelands is superimposed on the variation in selective grazing pressure, even low levels of grazing pressure can lead to increased heterogeneity relative to ungrazed conditions (Earl and Jones 1996). In the tallgrass prairie of North America, ungrazed communities are typically more homogeneous than moderately grazed communities because tall competitive dominants, such as *Andropogon gerardii*, form dense stands that limit species richness and structural

heterogeneity. Heavy grazing, on the other hand, reduces most biomass, which overrides variable selection pressure by livestock and inherent landscape heterogeneity, with the result being a homogenous structure in which most plants have been defoliated.

An alternative paradigm for increasing heterogeneity

The interaction of grazing and fire is an important influence on diversity and spatial patterns of vegetation in mesic Great Plains grasslands (Biondini et al. 1989, Vinton et al. 1993, Steuter et al. 1995, Hartnett et al. 1996). Fire influences bison grazing patterns, and bison grazing determines the extent and intensity of fires. Bison prefer recently burned areas because of the high-quality regrowth after a fire (Coppedge and Shaw 1998). When only a portion of the area available to bison is burned, intense grazing of burned patches postpones grazing on unburned patches (Figure 4), which results in an accumulation of fuel and an increased probability of fire in unburned patches (Steuter 1986, Hobbs et al. 1991). This interactive model is complicated by the season in which a burn occurs, which influences the effects of fire (Ewing and Engle 1988, Biondini et al. 1989, Howe 1994a) and bison preferences for certain patches (Shaw and Carter 1990, Coppedge and Shaw 1998). Thus, the interaction of these two disturbances—fire and bison grazing patterns—is capable of producing a dynamic patch mosaic of plant communities within grazed grasslands (Steuter et al. 1995, Hamilton 1996).

In 1989, the Nature Conservancy purchased the 14,000-ha Barnard Ranch in north-central Osage County, Oklahoma, and designated this area the Tallgrass Prairie Preserve. A spatially and seasonally variable prescribed burning program was initiated in September 1993, and bison were introduced to a 1,973-ha portion of the preserve in October 1993.



Figure 4. Bison graze palatable new growth of grasses in a recently burned patch. The decadent standing biomass of previous years' growth that accumulates in surrounding unburned areas provides structural heterogeneity and reduces bison preference for unburned patches because the accumulations of old growth are less palatable to bison than forage produced on recently burned patches. Photo: Courtesy of Bob Hamilton, The Nature Conservancy.

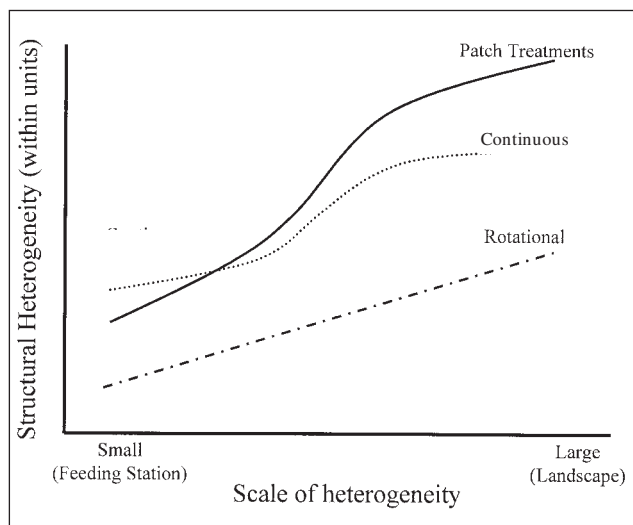


Figure 3. Structural heterogeneity within units in response to different grazing systems across several spatial scales (i.e., feeding station, patch, landscape) of herbivore site selection. Rotational grazing results in a relatively low level of structural heterogeneity across all of these spatial scales because of uniform forage utilization. Continuous grazing promotes heterogeneity at small scales (e.g., feeding stations). Patch treatments focus livestock grazing on patches that can be rotated across the landscape over several years, which increases heterogeneity within large-scale units and among patches. Rotating these focal grazing points across the landscape over several years results in a shifting mosaic, with patches within the landscape varying in time elapsed since heavy grazing.

Prescribed burning consists of 80% dormant-season burns (40% in the fall and 40% in late spring) and 20% growing-season burns conducted randomly in a regime designed to mimic the seasonal pattern and frequency rate of tallgrass fires in the time before European settlement (Figures 5 and 6). Burns have been conducted on patches of varying size under a variety of fuel and weather conditions with a fire return interval of about 5 years (Hamilton 1996). In keeping with the grazing–fire interaction model, bison movement and selective grazing have been unrestricted.

The randomly located burn patches within the bison enclosure at the Tallgrass Prairie Preserve (Figure 6) have created a shifting patchwork of areas grazed with varying intensity and frequency by the free-ranging bison herd. The result is a corresponding out-of-phase succession among patches, just as the bison grazing–fire interaction model predicts (Coppedge et al. 1998a, Coppedge and Shaw 1998). Even though grazing intensity for the entire bison enclosure is moderate (6–7 ha per female bison) (Coppedge et al. 1998a), forage use of recently burned patches by bison is heavy, while forage use of unburned areas is light (Coppedge and Shaw 1998). Bison are strongly grammivorous (Coppedge et al. 1998b), so forbs, the primary contributors to plant diversity in tallgrass prairie (Howe 1994b, Collins and Glenn 1995), increase dramatically within the recently burned patches. Thus species richness and heterogeneity in the landscape increase. Without patch grazing, frequent burning as practiced on cattle ranches in the region reduces plant diversity and increases the homogeneity of tallgrass prairie (Collins 1992, Collins et al. 1995).

The objective of the Tallgrass Prairie Preserve management approach is to increase biodiversity, but the approach may have other advantages over traditional rangeland management. Management for heterogeneity through patch burning, followed by grazing by free-roaming bison, has not hurt bison production. In fact, bison have maintained high reproductive rates without nutritional supplementation (Robert Hamilton [The Nature Conservancy], personal communication, 1999), in contrast to cattle, whose reproductive rates in the absence of protein supplementation decline considerably when dominant forage grasses mature under traditional rangeland management (Hughes et al. 1978, McCollum and Horn 1990). It is unclear whether this difference between bison and cattle is a result of physiological differences between the two species or the result of differences in management, including patch burning. Compared to unburned areas, recently burned patches contain more cool-season plants that are preferentially selected by animals during the primary nutritional stress period of the winter dormant season (Coppedge et al. 1998b). Under traditional rangeland management, cattle expected to reproduce require protein supplements in winter, when the primary forage plants are dormant. This supplementation is the single greatest nonland cost to both cow–calf and stocker cattle enterprises on tallgrass prairie rangelands.

Patch burning followed by heavy forage grazing by bison has not degraded resources but rather has promoted short-



Figure 5. Aerial view, Tallgrass Prairie Preserve, Oklahoma, where management for biodiversity has been accomplished using the patch-burn approach. The green areas are recently burned patches within a matrix of unburned grassland. Bison concentrate their grazing activities on the most recently burned patches, creating disturbance patches that are rotated across the landscape in a random pattern. Photo: Courtesy of Bob Hamilton, The Nature Conservancy.

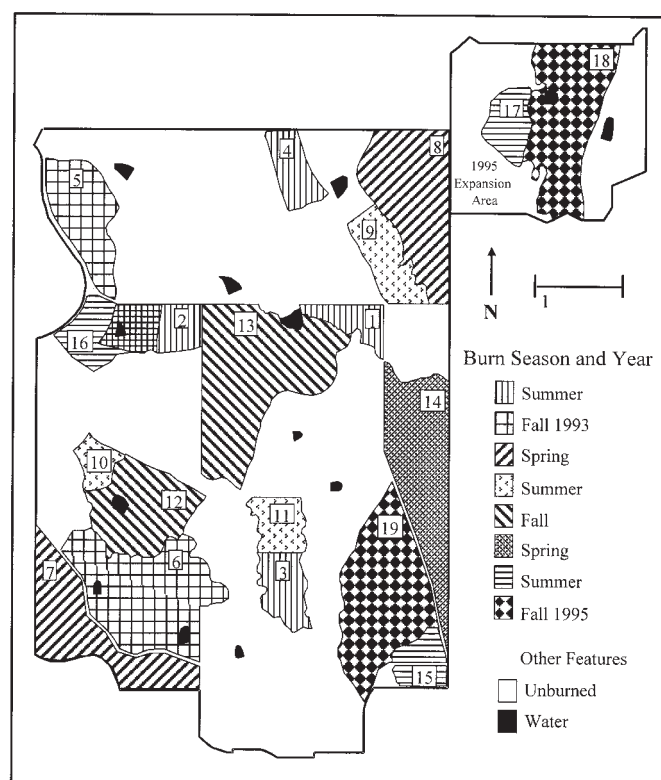


Figure 6. Chronology of patch burning within the bison enclosure on the Tallgrass Prairie Preserve, Oklahoma, 1993–1995. Numbers refer to the order in which burns were conducted. Bison within this area were allowed unrestricted selection of patches within the landscape. Figure from Coppedge and Shaw (1998).

lived pulses of early seral vegetation across the landscape coinciding with burned patches. Following heavy forage grazing of burned patches by bison, ruderal plant species not preferred by bison increase in the patches, but within 2 to 3 years the matrix tallgrass species regain dominance and patches not recently burned are indistinguishable from unburned areas (Coppedge et al. 1998a). This process differs from patch degradation associated with recurrent patch grazing by livestock under continuous grazing in more arid regions (Fuls 1992), in that burned and heavily utilized patches are rotated across the landscape. The result is a shifting mosaic that includes long-term ungrazed patches and patches that have been heavily grazed following burning, interspersed in a matrix of patches in various stages of successional recovery, with the stage of recovery dependent on the length of time since burning (Coppedge and Shaw 1998). This approach is counter to traditional methods in that grazing distribution is maximized over several years but minimized within individual years, thus promoting structural and compositional heterogeneity.

Converting homogeneity-based rangeland management to heterogeneity-based rangeland management

Grassland ecologists recognize that grazing is a keystone process in maintaining the diversity of grasslands in the North American Great Plains (Collins 1992, Knapp et al. 1999). However, before European settlement, the grazing distribution of ungulates was extremely patchy; the result was a shifting mosaic across the landscape (Kay 1998). Some researchers have suggested that although bison are a keystone herbivore promoting grassland biodiversity, grazing by domestic cattle and bison would influence grasslands in distinctly different ways. However, recent studies demonstrate only minor differences in biodiversity when cattle and bison are grazed similarly; these studies also show that the greatest difference is caused by differences in management practices (Hartnett et al. 1997, Knapp et al. 1999). Regardless of the differences, the two species are sufficiently similar that management of cattle grazing can benefit from consideration of the evolutionary patterns of bison grazing before European settlement.

We believe that an ecosystem approach to rangeland management should focus more on restoring the heterogeneity inherent within the landscape than on restoring the late successional composition of grasslands, which is the approach used in traditional rangeland management. On rangelands with a long evolutionary history of grazing, specifically the tall-

grass and mixed-grass prairies of the Great Plains, heterogeneity can be partially achieved by restoring spatially dependent disturbances, such as the grazing–fire interactions that occurred before European settlement. Once the spatial and temporal disturbance pattern is restored to the landscape, increased heterogeneity at several spatiotemporal scales will be a primary structural feature of these landscapes, potentially increasing critical wildlife habitat and plant species diversity. This increased heterogeneity also has the potential to improve livestock production—as has occurred among the bison at the Tallgrass Prairie Preserve—by increasing the diversity of forage species that contribute to enhanced diet quality throughout the year.

Managing for heterogeneity by using cattle to impose the spatially and temporally variable disturbance patterns requires alternatives to traditional homogeneity-based rangeland management practices (Table 1). To facilitate heterogeneity, we propose altering several traditional management practices by applying them to patches within the landscape. Each practice is recommended in the rangeland management literature for attracting livestock to lightly grazed or ungrazed areas, with the objective of reducing spatial heterogeneity and increasing harvest efficiency (Hooper et al. 1969, Samuel et al. 1980, Vallentine 1990, Holechek et al. 1998). Regarding the application of these practices, our interest is not in achieving more uniform distribution of livestock grazing for more efficient forage harvest but in creating focal points for intense herbivory that can be rotated across the landscape over several years. The response to local grazing disturbances followed by successional change over subsequent years will produce a shifting mosaic of community types and increased structural heterogeneity (Figure 3). Patches will differ in composition and structure depending on the length of time since a patch served as a grazing focal point.

Any of the alternative practices we propose could be used to attract cattle to treated patches. However, these grasslands evolved under a grazing–fire interaction, which suggests that fire is a preferred patch treatment on Great Plains grasslands. Localized patches are burned within moderately and

Table 1. Spatial variability of management units (pastures) under traditional rangeland management practices and alternative management practices.

Spatial variability of management units	Homogeneous	Heterogeneous	Shifting mosaic
Traditional rangeland practices			
Continuous grazing		X	
Rotational grazing	X		
Herbicide application	X		
Multispecies grazing	X		
Area burns	X		
Improved water distribution	X		
Alternative practices			
Patch burning			X
Patch herbicide application			X
Patch fertilization			X
Focused grazing disturbances			X
Shifting attractants			X

continuously grazed pastures of any size to promote patch grazing and severe local disturbance. Burned focal patches can be randomly or strategically rotated around a pasture over many years to produce a shifting mosaic of composition and structure in response to grazing and fire. Moreover, burned patches positioned at random across a pasture or landscape will provide a shifting mosaic of heterogeneity in time and space. Optimal patch size and fire return intervals are dependent on rangeland management objectives and the amount of time required for focal patches to recover. For North American tallgrass prairies, an example would be burning one-third of a pasture each year (half of the third in the summer and half in the spring), which allows an interval between burns (called the *fire-return interval*) of 3 years.

Unlike rotational grazing systems with their fixed pastures, patch-burning systems can vary the size and location of grazing areas. Also, the rotation of burns over a period of years results in a pattern of severe disturbance followed by several years of recovery, which is more typical of the uneven distribution of grazing and fire reported to occur before European settlement. Implementation of rapid-rotation grazing systems results in recovery periods typically less than 3 months, an interval that does not promote structural differences between grazed and ungrazed pastures. Application of patch burns can vary by season, length of fire-return interval, and severity (e.g., by altering burning conditions), which can further promote heterogeneity across time and space. This heterogeneity can range from a fine-grained to coarse-grained mosaic, and, depending on management goals, the spatiotemporal pattern can be either fixed or random. In practice, the patch-burn mosaic can be applied to pastures of any size, but pastures could be consolidated by removing fences, which are a necessary feature of traditional homogeneity-based approaches.

The heterogeneity-based approach to rangeland management that we propose is an attempt to mimic the historical grazing–fire interactions on mesic North American prairies, which have a long evolutionary history of ungulate grazing. Because of large-scale land-use changes and ownership boundaries, the exact disturbance patterns can never be fully restored. More research is needed to determine the effects of this approach on critical conservation issues such as invasive species, as well as sustainability issues associated with long-term agricultural production and economics. It is likely that the grazing–fire interaction model is not universally applicable. Even within North America, many rangelands did not evolve with the same grazing, climate, and fire patterns that characterized the Great Plains prairies, so one should be cautious in applying this approach on those rangelands. However, it is important to recognize that most rangeland management practices have focused on simplifying ecosystem structure and achieving uniform disturbances across the landscape. Although the grazing–fire interaction may not be universally appropriate, traditional homogeneity-based approaches are rarely capable of managing rangelands for many alternative objectives such as enhanced biological diversity and wildlife

habitat. We therefore conclude that a new paradigm is necessary for the management of these native landscapes—a paradigm that considers heterogeneity fundamental to the healthy functioning of these ecosystems.

Conclusion

Three points encapsulate our observations on the restoration of rangeland heterogeneity:

1. Rangelands are inherently heterogeneous where composition, productivity, and diversity are highly variable across multiple scales. A heterogeneous patchwork can result from differential timing of disturbances and corresponding out-of-phase succession among patches, spatial heterogeneity of resources associated with topographic patterns, or competitive interactions among plant species.
2. Traditional rangeland management promotes homogeneity through uniform distribution of livestock grazing across the landscape. The results of traditional management are uniform utilization among plants and areas and a reduction of inherent landscape heterogeneity, which may have a critical impact on biodiversity and wildlife habitat.
3. Alternative management approaches can facilitate patch heterogeneity. In the Great Plains of North America, heterogeneity can be promoted through fire and grazing disturbances of focal points within landscapes in which focal patches shift through time, producing a shifting mosaic that can enhance biodiversity and enrich wildlife habitat in grasslands with a long evolutionary history of grazing.

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References cited

- Bailey DW, Dumont B, Wallis DeVries MF. 1998. Utilization of heterogeneous grasslands by domestic herbivores: Theory to management. *Annals of Zootechnology* 47: 321–333.
- Biondini ME, Steuter AA, Grygiel CE. 1989. Seasonal fire effects on the diversity patterns, spatial distribution, and community structure of forbs in the northern mixed prairie, USA. *Vegetatio* 85: 21–31.
- Christensen NL. 1997. Managing for heterogeneity and complexity on dynamic landscapes. Pages 167–186 in Pickett STA, Ostfeld RS, Shachak M, Likens GE, eds. *The Ecological Basis for Conservation: Heterogeneity, Ecosystems, and Biodiversity*. New York: Chapman and Hall.
- Cody ML. 1985. Habitat selection in grassland and open-country birds. Pages 191–226 in Cody ML, ed. *Habitat Selection in Birds*. Orlando (FL): Academic Press.
- Collins SL. 1992. Fire frequency and community heterogeneity in tallgrass prairie: A field experiment. *Ecology* 73: 2001–2006.
- Collins SL, Glenn SM. 1995. Grassland ecosystems and landscape dynamics. Pages 128–156 in Anthony J, Keeler KH, eds. *The Changing Prairie: North American Grasslands*. New York: Oxford University Press.
- Collins SL, Glenn SM, Gibson DJ. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: Decoupling cause and effect. *Ecology* 76: 486–492.

- Coppedge BR, Shaw JH. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. *Journal of Range Management* 51: 258–264.
- Coppedge BR, Engle DM, Toepfer CS, Shaw JH. 1998a. Effects of seasonal fire, bison grazing, and climatic variation on tallgrass prairie vegetation. *Plant Ecology* 139: 235–246.
- Coppedge BR, Leslie DM Jr, Shaw JH. 1998b. Botanical composition of bison diets on tallgrass prairie in Oklahoma. *Journal of Range Management* 51: 379–382.
- Earl JM, Jones CE. 1996. The need for a new approach to grazing management: Is cell grazing the answer? *Rangeland Journal* 18: 327–350.
- Ewing AL, Engle DM. 1988. Effect of late summer fire on tallgrass prairie microclimate and community composition. *American Midland Naturalist* 120: 212–223.
- Fuhlendorf SD, Smeins FE. 1996. Spatial scale influence on long-term temporal patterns of a semi-arid grassland. *Landscape Ecology* 11: 107–113.
- . 1997. Long-term vegetation dynamics mediated by herbivores, weather and fire in a *Juniperus-Quercus* savanna. *Journal of Vegetation Science* 8: 819–828.
- . 1998. Soil heterogeneity influence on plant species response to grazing within a semi-arid savanna. *Plant Ecology* 138: 89–96.
- . 1999. Scaling effects of grazing in a semi-arid grassland. *Journal of Vegetation Science* 10: 731–738.
- Fuls ER. 1992. Semi-arid and arid rangelands: A resource under siege due to patch-selective grazing. *Journal of Arid Environments* 22: 191–193.
- Hamilton RG. 1996. Using fire and bison to restore a functional tallgrass prairie landscape. *Transactions of the North American Wildland and Natural Resource Conference* 61: 208–214.
- Hart RH. 1978. Stocking rate theory and its application to grazing on rangelands. Pages 547–550 in Hyder DN, ed. *Proceedings of the First International Rangeland Congress*. Denver (CO): Society for Range Management.
- Hartnett DC, Hickman KR, Fischer Walter LE. 1996. Effects of bison grazing, fire, and topography on floristic diversity in tallgrass prairie. *Journal of Range Management* 49: 413–420.
- Hartnett DC, Steuter AA, Hickman KR. 1997. Comparative ecology of native and introduced ungulates. Pages 72–101 in Knopf FL, Samson FB, eds. *Ecology and Conservation of Great Plains Vertebrates*. New York: Springer.
- Heitschmidt RK, Walker JW. 1996. Grazing management: Technology for sustaining rangeland ecosystems. *Rangeland Journal* 18: 194–215.
- Hobbs RJ, Schimel DS, Owensby CE, Ojima DS. 1991. Fire and grazing in the tallgrass prairie: Contingent effects on nitrogen budgets. *Ecology* 72: 1374–1382.
- Holechek JL, RD Pieper, Herbel CH. 1998. Range management principles and practices. Upper Saddle River (NJ): Prentice Hall.
- Hooper JF, Workman JP, Grumbles JB, Cook CW. 1969. Improved livestock distribution with fertilizer: A preliminary economic evaluation. *Journal of Range Management* 22: 108–110.
- Howe HF. 1994a. Response of early- and late-flowering plants to fire season in experimental prairies. *Ecological Applications* 4: 121–133.
- . 1994b. Managing species diversity in tallgrass prairie: Assumptions and implications. *Conservation Biology* 8: 691–704.
- Hughes JH, Stephens DF, Lusby KS, Pope LS, Whiteman JV, Smithson LJ, Totusek R. 1978. Long-term effects of winter supplement on the productivity of range cows. *Journal of Animal Science* 47: 816–827.
- Kantrud HA. 1981. Grazing intensity effects on the breeding avifauna of North Dakota native grasslands. *Canadian Field Naturalist* 95: 404–417.
- Kay CE. 1998. Are ecosystems structured from the top-down or bottom-up? A new look at an old debate. *Wildlife Society Bulletin* 26: 484–498.
- Knapp AK, Blair JM, Briggs JM, Collins SL, Hartnett DC, Johnson LC, Towne EG. 1999. The keystone role of bison in North American tallgrass prairie. *BioScience* 49: 39–50.
- Knopf FL. 1994. Avian assemblages on altered grasslands. *Studies in Avian Biology* 15: 247–257.
- . 1996. Perspectives on grazing nongame bird habitats. Pages 51–58 in Krausman PR, ed. *Rangeland Wildlife*. Denver (CO): Society for Range Management.
- Kolasa J, Pickett STA. 1991. *Ecological Heterogeneity*. New York: Springer-Verlag.
- Ludwig JA, Tongway DJ. 1995. Spatial organisation of landscapes and its function in semi-arid woodlands, Australia. *Landscape Ecology* 10: 51–63.
- McCullum FT, Horn GW. 1990. Protein supplementation of grazing livestock: A review. *Professional Animal Scientist* 6: 1–16.
- McCullum FT III, Gillen RL, Karges BR, Hodges ME. 1999. Stocker cattle response to grazing management in tallgrass prairie. *Journal of Range Management* 52: 120–126.
- Milchunas DG, Sala OE, Lauenroth WK. 1988. A generalized model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132: 87–106.
- [NRC] National Research Council. 1994. *Rangeland Health: New Methods to Classify, Inventory, and Monitor Rangelands*. Washington (DC): National Academy Press.
- Ostfeld RS, Pickett STA, Shachak M, Likens GE. 1997. Defining scientific issues. Pages 3–10 in Pickett STA, Ostfeld RS, Shachak M, Likens GE, eds. *The Ecological Basis for Conservation: Heterogeneity, Ecosystems, and Biodiversity*. New York: Chapman and Hall.
- Patten RS, Ellis JE. 1995. Patterns of species and community distributions related to environmental gradients in an arid tropical ecosystem. *Vegetatio* 117: 69–79.
- Patterson MP, Best LB. 1996. Bird abundance and nesting success in Iowa CRP fields: The importance of vegetation structure and composition. *American Midland Naturalist* 135: 153–167.
- Renken RB, Dinsmore JJ. 1987. Nongame bird communities on managed grasslands in North Dakota. *Canadian Field Naturalist* 101: 551–557.
- Samuel MJ, Rauzi F, Hart RH. 1980. Nitrogen fertilization of range: Yield, protein content, and cattle behavior. *Journal of Range Management* 33: 119–121.
- Senft RL, Coughenour MB, Bailey DW, Rittenhouse LB, Sala OE, Swift DM. 1987. Large herbivores' foraging and ecological hierarchies. *BioScience* 37: 789–799.
- Shaw JH, Carter TS. 1990. Bison movements in relation to fire and seasonality. *Wildlife Society Bulletin* 18: 426–430.
- [SRM] Society for Range Management. 1989. *A Glossary of Terms Used in Range Management*. 3rd ed. Denver (CO): Society for Range Management.
- Steuter AA. 1986. Fire behavior and standing crop characteristics on repeated seasonal burns: Northern mixed prairie. Pages 54–59 in Koonce AL, ed. *Prescribed Burning in the Midwest: State of the Art*. Stevens Point (WI): University of Wisconsin, College of Natural Resources, Fire Science Center.
- Steuter AA, Steinauer EM, Hill GL, Bowers PA, Tieszen LL. 1995. Distribution and diet of bison and pocket gophers in a sandhill prairie. *Ecological Application* 5: 756–766.
- Stuth JW. 1991. Foraging behavior. Pages 65–83 in Stuth JW, Heitschmidt RK, eds. *Grazing Management: An Ecological Perspective*. Portland (OR): Timber Press.
- Taylor MA, Guthery FS. 1980. Status, Ecology, and Management of the Lesser Prairie Chicken. Fort Collins (CO): US Forest Service. General Technical Report no. RM-77.
- Vallentine JF. 1990. *Grazing management*. San Diego: Academic Press.
- Vinton MA, Hartnett DC, Finck EJ, Briggs JM. 1993. Interactive effects of fire, bison (*Bison bison*) grazing, and plant community composition in tallgrass prairie. *American Midland Naturalist* 129: 10–18.
- Wiens JA. 1974. Habitat heterogeneity and avian community structure in North American grassland birds. *American Midland Naturalist* 91: 195–213.
- . 1997. The emerging role of patchiness in conservation biology. Pages 93–107 in Pickett STA, Ostfeld RS, Shachak M, Likens GE, eds. *The Ecological Basis for Conservation: Heterogeneity, Ecosystems, and Biodiversity*. New York: Chapman and Hall.
- Zimmerman JL. 1971. The territory and its density-dependent effect in *Spiza americana*. *Auk* 88: 591–612.