Great Plains Studies, Center for

Great Plains Research: A Journal of Natural and Social Sciences

University of Nebraska - Lincoln *Year* 2001

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Great Plains Research 11 (Spring 2001): 123-44

MANAGING BISON TO RESTORE BIODIVERSITY

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ABSTRACT—Prior to their demise in the late 1800s, bison coexisted with and helped sustain a diverse and spectacular assemblage of animals and plant communities on the Great Plains. Bison, in concert with fire, exerted strong control on the structure of the vegetation by grazing, trampling, and wallowing. The changes in the vegetation induced changes in many animal populations. These impacts, coupled with the bison's role as the major converter of grass to meat, so greatly affected other species that some have called bison a "keystone" species in the Great Plains ecosystem. The black-tailed prairie dog, dependent on bison grazing over a large part of the Great Plains, amplified the keystone influence of bison by its own grazing and burrowing activities and its utility as prey. Although modern bison-growing practices usually will preclude restoration of the large predators and scavengers that once were a part of the great faunal spectacle, other species can return, often even on small acreages. Maintenance of a habitat mosaic is the key to restoring some of the original biodiversity lost to the historic pursuit of single-species pastoralism.

KEY WORDS: biodiversity, bison, endangered species, grasslands, prairie

Introduction

On 30 December 1898, at the 31st annual meeting of the Kansas Academy of Science, Mr. J. R. Mead (1899) of Wichita read to the audience a set of natural history notes he had written about the Kansas prairies in 1859. Mead's observations, made in the heart of bison country a generation before that final slaughter by the hide hunters, attest to the diversity and abundance of wildlife on the Great Plains prior to extensive settlement:

> Lobo, the mountain wolf, locally known on the plains as "big gray," were congeners and associates of the buffalo, and lived almost exclusively upon them. . . . There were red foxes living on the plains with the wolves, called "swifts" from their remarkable speed. . . . A few black bear were found in Comanche County. . . . Beavers were very numerous . . . otter were common. . . . Black-tailed deer were numerous in the hills between the Saline and Solomon [Rivers], going in bunches of three or four to twenty or thirty. . . . Elk were quite numerous, especially along the Smoky Hill, Saline, and Solomon. . . . I saw a band of over 500 [elk] cross the Saline where the town of Lincoln [Kansas] now stands. . . . Prairie dogs were innumerable.

Mead also reported coyotes (*Canis latrans*), lynx (*Felis lynx*), "countless flocks" of ravens (*Corvus* sp.), "numerous" bald eagles (*Haliaeetus leucocephalus*), "common" prairie chickens (*Tympanuchus* sp.) and sharp-tailed grouse (*Pedioecetes phasianellus*), "abundant" turkeys (*Meleagris gallopavo*), and "common" bobwhite quail (*Colinus virginianus*). If he had looked in the right places nearby, he might also have found black-footed ferrets (*Mustela nigripes*), wolverines (*Gulo gulo*), mountain lions (*Felis concolor*), bighorn sheep (*Ovis canadensis*), and perhaps a remnant grizzly bear (*Ursus arctos*) (cf. Bogan 1997).

In his 1898 presentation, Mead estimated that "most of these birds and animals [that he saw in 1859] are practically extinct." A century later, Bogan (1997) noted that nine of the larger species—wolf (*Canis lupus*), black and grizzly bears (*Ursus americanus*, *U. arctos*), wolverine, mountain lion, lynx, elk (*Cervus elaphus*), bighorn sheep, and wild bison—and a small one, the black-footed ferret, had in fact been extirpated from nearby north central Nebraska.

The theme of biodiversity loss during the past 150 years resounds from one end of the Great Plains to the other. Diminishment of native biodiversity at the local level has resulted from Plains-wide extinctions, regional extinctions, and regional and local reductions in species abundances. Animals that have almost or completely disappeared from the Great Plains include grizzly bear, wolverine, wolf, lynx, elk, and black-footed ferret (Mech 1970:31; Hall 1981:952, 1009, 1050; Bryant and Maser 1982; Wilson 1982; Anderson et al. 1986; Bogan 1997). Species disappearing regionally or becoming scarce relative to former abundances include black-tailed prairie dog *(Cynomys ludovicianus)* (Mulhern and Knowles 1997), swift fox (*Vulpes velox*) (Hillman and Sharps 1978), sharp-tailed grouse (Miller and Graul 1980), and lesser prairie chicken (*Tympanuchus pallidicinctus)* (Crawford 1980). The list goes on (Licht 1997:29-51). Plains-wide, regional, and local extinctions in combination have left many local areas almost devoid of larger animals and impoverished of smaller animals and sometimes of plants (Bogan 1977; Licht 1997).

Bison played a significant role in maintaining the historic abundance and diversity of Plains biota. For example, as the principal large converters of grass to animal biomass, they supported large populations of predators and scavengers, such as aboriginal humans, wolves, bears, wolverines, bald eagles, ravens, coyotes, and swift foxes (Mead 1899; Roe 1970:155-58; Bogan 1997). They grazed heavily in some areas and lightly in others, thereby creating a mosaic of vegetation (Hartnett et al. 1996; Knapp et al. 1999), which influenced not only the plant community but a diverse suite of animals as well (Cody 1985; Clark et al. 1989). Our purpose here is to describe the influences of bison on prairie plants and animals and, on this basis, lay out some approaches to biodiversity conservation in the context of modern-day bison grazing.

We define the specialized terms that we use as follows. *Keystone species* are those having greater effects on ecosystem structure and function than most other species (Mills et al. 1993). *Biodiversity* is variety of species, habitat types, and ecological processes (Noss 1990). *Species diversity,* or *richness*, as used here refers to the number of species in a particular area (Scott et al. 1987). The *composition* of a biological community is the specific array of species it contains. *Habitat types* are landscape subdivisions that can be discriminated from each other by human observers and other species (Gysel and Lyon 1980). Several different habitat types in juxtaposition constitute a *mosaic* (Whittaker and Levin 1977). *Patchiness* is the degree to which different habitat types are interspersed (Forman and Godron 1981).

Influence of Bison on Great Plains Vegetation

Commonly quoted estimates of bison numbers on and adjacent to the Great Plains prior to appreciable mortality from Euro-Americans (e.g., Seton 1929; McHugh 1972 in Shaw 1998) range from 30 to 60 million. The early 19th-century carrying capacity of Great Plains grasslands for bison, as estimated by Flores (1991), approached 30 million, very close to McHugh's (1972) estimate of numbers. Bison numbers undoubtedly fluctuated over time because of the temporally variable effects of aboriginal hunting (Flores 1991; Martin and Szuter 1999), drought (Shaw 1998), and other factors.

Observations made prior to the late 1800s suggest bison grazing had major effects on Great Plains landscapes. Roe (1970:361, 362, 448) cited early observations that bison had grazed the forage so intensively that domestic stock could find little food. Larson (1940) referenced primary historical accounts to posit that bison grazing prior to the mid-19th century was sufficiently intense to maintain shortgrass plains over large areas, in both northern and southern parts of the Great Plains, that otherwise would have supported mid-grasses. Brown (1993) provided historical evidence that supported Larson's contention—he showed that the boundary between shortgrass and tallgrass dominance in the mid-continental Great Plains (Oklahoma to South Dakota) may have moved up to 150 miles westward since the early 19th century, that is, during and following the demise of bison.

Historical accounts also show that the intensity of grazing and other impacts by bison varied spatially. Roe (1970:101-20) presented evidence that bison altered the landscape especially severely along traditional trails, near water, at favorite wallowing places, and near salt deposits. Snow cover induced distributional shifts in grazing, both seasonally and annually (Roe 1970:184-86). Differential hunting pressures by aboriginal peoples induced spatially patchy distribution of bison (Martin and Szuter 1999).

Do modern studies suggest that bison are capable of inducing such dramatic changes in Great Plains landscapes, and that the changes would be spatially patchy? Below, we review some of the presently understood consequences of bison grazing, relying in some cases on studies of grazing by domestic cattle, a close (Hartnett et al. 1996; Knapp et al. 1999) though not perfect analog of bison in terms of impacts on grasslands. Bison digest roughage better than cattle do and can subsist on forage of lower protein content, for example (Peden et al. 1974; Plumb and Dodd 1993).

A wide array of ungulate (hoofed mammal) grazers maintain grasses in many grasslands around the world at a substantially lower stature than would exist without grazing (McNaughton 1984; Hobbs 1996). The same has been found to be true of bison and cattle on the Great Plains. For example in tallgrass prairie in Kansas, bison grazing induced increases in mid-grasses, such as sideoats grama (*Bouteloua curtipendula*) and western wheatgrass (*Agropyron smithii*), by selectively grazing big bluestem (*Andropogon gerardii*), indiangrass (*Sorghastrum nutans*), and other tall grasses (Hartnett et al. 1996; Knapp et al. 1999). Grazing by cattle, bison, and prairie dogs in mixed-grass prairie sites reduced the height of grasses both by selectively removing mid-grasses, to the advantage of shortgrass species (Heitschmidt et al. 1989), and by selecting for genetically dwarfed forms of some species (Brizuela et al. 1986). In shortgrass prairie the dominant grasses, having evolved presumably in part in response to intensive grazing (Larson 1940; Jaramillo and Detling 1988), have naturally low growth forms, and average grass height differs by only a few inches between grazed and ungrazed areas (Milchunas et al. 1988). The more intensive and persistent the grazing pressure, the greater the tendency for the dominant grass species and growth forms, especially in mixed- and tallgrass regions, to be shorter than those in ungrazed sites (Hobbs 1996).

Spatially different levels of grazing across landscapes result from several factors, not the least of which is spatial variation in physical features. Where water sources are far apart and slopes sometimes steep, sites nearer water and on gentler slopes receive the most use by cattle (Bailey et al. 1996). Although less well studied in this respect, bison apparently also preferentially use gentler slopes (Phillips 2000) and sites nearer water (Roe 1970:105-8).

Grazing itself induces long-term effects on grazing distribution, partly by elevating the nutritional quality of grasses. Numerous investigations (e.g., Heitschmidt et al. 1989; Cid et al. 1991; Coughenour 1991a; Detling 1998) confirm that grazing increases the quality of forage by enhancing both the protein (N) content and digestibility of the forage (McNaughton 1984; Milchunas et al. 1995; Bailey et al. 1996; Detling 1998). The improved nitrogen content of grazed forage results from the elevated rate of nitrogen recycling in the ecosystem via conversion of grass to urine and feces (Hobbs 1996), the higher nitrogen content of regrowth (Detling 1998), and also from other factors such as reduced plant biomass and concomitant lower competition for the available soil nutrients by individual plants (Vinton et al. 1993). Bison (Knapp et al. 1999), like cattle and other grazers (Bailey et al. 1996; Hobbs 1996), are attracted to the relatively high-quality forage in previously grazed areas. Over time this creates a patchwork of heavily grazed sites, to which the animals repeatedly return, and lightly grazed and ungrazed sites (Hobbs et al. 1991; Hartnett et al. 1996; Knapp et al. 1999). The visible signature of this mosaic is appreciable in tallgrass prairie (Knapp et al. 1999) but less so in shorter grasses (Milchunas et al. 1995), as would be expected given the relative heights of the ungrazed grasses.

Grazing enhances not only diversity of vegetative type and form but also richness of plant species. Part of the increase in richness results from the mosaic effect, for example, replacement of a single plant assemblage without grazing by a combination of grazed and ungrazed types. But richness also increases because both opening of the vegetative canopy and disturbance of the soil by grazing and trampling encourage the invasion of early successional forbs and, in some places, cool season grasses (Hartnett et al. 1996; Knapp et al. 1999). Enhancement of vegetation diversity by moderate grazing is not unexpected. It conforms to the well-known "intermediate disturbance" hypothesis (Petraitis et al. 1989).

Fire interacts with physical features and grazing to intensify the patchwork effect on the vegetation. Prior to settlement, fire in tallgrass prairie occurred as often as once every one to five years (Collins and Gibson 1990). Fire frequency generally declined with distance westward, as tall grasses were replaced by mid- and shortgrasses (Sieg 1997). Fire reduces the height of vegetation and attracts foraging bison for at least the first few years postburn (Shaw and Carter 1990; Vinton et al. 1993; Hartnett et al. 1996; Knapp et al. 1999). Grazing in turn reduces natural fire frequency (Hobbs 1996), causing ungrazed sites to burn selectively thereafter. Burning tends to favor grass dominance over that of woody species, which in fire-prone prairies may be restricted to riparian zones, draws, north-facing slopes, and other topographic refuges where fires seldom burn (Sieg 1997).

Burning in the absence of grazing tends to reduce vegetative diversity. Burning tallgrass prairie selects for the dominant warm-season grasses and against cool-season grasses, forbs, and woody species (Vinton et al. 1993; Hartnett et al. 1996). This reduces the structural diversity of the vegetation as well as the species richness (Gibson and Hulbert 1987). The encroachment of woody species into grasslands since European settlers instituted fire suppression suggests the dramatic effects that fire previously had induced in Great Plains grasslands (Wright and Bailey 1980).

Bison can enhance vegetative diversity by mechanisms other than grazing and trampling. Most notably, they kill vegetation and generate depressions in the ground by repeatedly wallowing at the same sites (Polley and Collins 1984). This stimulates broadleafed herbs (forbs) to invade, which creates anomalous patches in a grassy landscape (Knapp et al. 1999). When large wallows are abandoned, they may seasonally hold water and support mesic and even aquatic vegetation (Polley and Collins 1983; Knapp et al. 1999).

It is normal for bison to graze, trample, and wallow at different intensities across landscapes. This creates a mosaic of vegetative types and elevates plant species diversity. The nature of this mosaic may be altered by availability of water, topography, previous grazing patterns, and fire. The visual distinctiveness of patches within the mosaic increases from shortgrass to tallgrass communities. Next, we assess how these changes in vegetation induce changes in the wildlife communities of Great Plains grasslands.

Influence of Bison Grazing on Wildlife

Bison grazing affects other Plains animals by altering the structure, species composition, and nutritional quality of the vegetation. The overriding effect on most small birds (Wiens 1973, 1985; Davis et al. 1974; Cody 1985) and mammals (Grant et al. 1982; Clark et al. 1989) comes through changes in vegetation structural attributes, such as grass height, ground cover, and shrub abundance. Large herbivorous mammals tend to respond primarily to changes in forage quality (Coughenour 1991b; Detling 1998).

Prairie grouse show marked responses to vegetation structure, benefiting from mosaics that give them access to complex structural habitat within their home ranges. In the northern Great Plains, sharp-tailed grouse flourish best in tall- and mid-grass areas where they have access to stands of woody vegetation; large tracts where rangelands have been uniformly overgrazed or converted to intensive agriculture have few or no grouse (Miller and Graul 1980). Greater prairie chickens (*Tympanuchus cupido*) inhabit primarily tallgrass but also mid-grass prairies; like sharp-tailed grouse, they thrive best where tall and thick grassland is interspersed with other vegetation types (Robel et al. 1970; Christisen and Krohn 1980), and they diminish where large tracts are uniformly overgrazed or farmed. Lesser prairie chickens live in mid- and shortgrass prairies, generally requiring a brush component within their home ranges for cover and food (Crawford 1980;

Doerr and Guthery 1980) and declining with large-scale farming or overgrazing. Sage grouse (*Centrocercus urophasianus*) inhabit western margins of the northern Great Plains where sagebrush (*Artemisia* spp.) is interspersed with grass; such interspersion on a small scale benefits them, but conversion of large tracts of sagebrush to grassland is a major cause of their decline (Braun et al. 1977). All of these species flourish where different habitat types create a mosaic, with the different types occupying a few to a few hundred acres each. Even grain farming in small patches can be beneficial to these prairie grouse. Shrubs are critical to some. The conversion of mosaics to large, unbroken tracts, whether of farmland, overgrazed range, or ungrazed prairie commonly diminishes the value of the range for these birds.

Both scaled (*Callipepla squamata*) and bobwhite quails require habitat mosaics and typically flourish under disturbance by grazing animals. In the southern Great Plains, moderately to heavily grazed grasslands with clumps or patches of woody vegetation as cover provide these birds the best habitat (Schemnitz 1961; Guthery 1986; Saiwana et al. 1998). Woody vegetation has invaded some parts of the southern Great Plains often as a consequence of past cattle grazing combined with lack of fire (Licht 1997:70). Because the home ranges of these birds may be smaller than those of prairie grouse, ideal mosaics may have smaller spatial scales than those best for grouse.

Passerine birds likewise select among grassland habitats on the basis of structure (Wiens 1973; Cody 1985), and each species prefers a somewhat different combination of structural attributes (Wiens 1985). Thus a structurally heterogeneous grassland supports a greater diversity and total abundance of birds than a homogenous one (Patterson and Best 1996). Like the grouses and quails, some of these birds are "edge" species, benefiting from access to two or more habitat types, but others largely use a single type (Patterson and Best 1996). In tallgrass areas, bison and cattle grazing (and other disturbances) create more obvious patchiness than in shortgrass areas, thus grazing in and of itself has a greater ability to enhance bird diversity in tallgrass than in shortgrass areas (Cody 1985). The addition of a shrub or tree component to grasslands, in some places a long-term consequence of fire suppression and heavy grazing (Wright and Bailey 1980; Schlesinger et al. 1990), provides a structural feature that often sharply enhances diversity of passerine birds (Davis et al. 1974; Wiens 1985; Vinton and Collins 1997).

Pronghorn antelope (*Antilocapra americana*) and mule deer (*Odocoileus hemionus*) are among the few large mammals that have persisted in any abundance in Great Plains grasslands. Their persistence is a consequence in part of their ability to coexist with and benefit from cattle. Large grazers such as cattle and bison benefit these species primarily because grazing promotes the abundance of forbs and shrubs that constitute the dietary mainstays of both species (Wallmo 1978; Yoakum 1978).

Small mammals, like birds, respond strongly to habitat structure and, thus, to grazing that influences the structure. Grant et al. (1982) found grazing to influence small mammals more in tallgrass than in shortgrass or bunchgrass grasslands, apparently because grazing created more dramatic structural changes in the former. Grazing in tallgrass prairie influenced the mammal species composition but not the species richness or numbers (Clark et al. 1989). The superimposition of grazed and ungrazed sites in a mosaic enhanced species richness.

As illustrated by this review, the effects of bison grazing on biodiversity do not stop with the plants but also affect the wildlife community. In the following section we further track the ecological ramifications of bison grazing through a small mammal that is markedly affected by grazing—the black-tailed prairie dog.

The Prairie Dog Ecosystem

In his 1898 address to the Kansas Academy of Science, Mead (1899) made an interesting assessment of the welfare of central Kansas prairie dogs during the late 19th century. In 1859, he had found them "innumerable. The divide between Saline and Solomon [Rivers] in Ellsworth County [Kansas] and west was a continuous dog town for miles." But during the interim between 1859 and 1898, which saw the extermination of bison, he observed that "Prairie dogs, except for a few remnants, disappeared. The foot of the buffalo was necessary for their existence. As soon as the ground ceased to be tramped hard and the grass and weeds grew they perished."

Did later scientific inquiry support Mead's belief that prairie dogs needed bison? More than a century after Mead's observations, Smith (1967:35) studied black-tailed prairie dogs in an overgrazed pasture three counties to the south in Kansas: "[O]ne of the most successful methods of controlling prairie dogs is to remove the cattle from the range until it has had a chance to recover. Prairie dogs are the 'result' of range depletion by overgrazing by cattle." Others have drawn similar conclusions about the relationship between large grazers and black-tailed prairie dogs in southwestern Oklahoma (Osborn and Allan 1949), several Great Plains sites

(Koford 1958), northeastern Montana (Knowles 1986), western Nebraska (Cable and Timm 1988), and southwestern South Dakota and southeastern Montana (Licht and Sanchez 1993).

The pattern that emerges from these and other studies is that black-tailed prairie dogs require very short grass in their surroundings to thrive and expand, apparently because they need good horizontal visibility at the height of a sitting prairie dog to detect predators (Hoogland 1981). Thus, where the grass consistently grows thick and tall, prairie dogs require grazing by a larger herbivore or some other force, such as fire, to shorten the grass (Truett and Savage 1998). The prairie dogs help to maintain visibility within colonies by their own foraging and clipping activities (Hoogland 1995). As would be expected, the dependence of prairie dogs on bison or cattle grazing declines from tallgrass to shortgrass situations (Hansen and Gold 1977); colonies dominated by blue grama and buffalograss may need little or no help from bison or cattle to persist or expand. Given that black-tailed prairie dogs occurred in the time of the buffalo not only in shortgrass prairies but also throughout the mixed-grass prairies and into tallgrass grasslands from Canada to Mexico (cf. Hall 1981:412; Licht 1997:3), bison probably "enabled" their existence over thousands of square miles.

Some studies suggest that grazing by prairie dogs reciprocally benefits large herbivores. Grazing by prairie dogs, like that by bison and cattle, elevates the protein (N) content of forage (Coppock et al. 1983; Krueger 1986; Whicker and Detling 1988; Detling 1998). Prairie dog colonies in mixed-grass prairie in the northern Great Plains attracted bison and pronghorn during most of the growing season (Coppock et al. 1983; Krueger 1986; Detling 1998). Bison fed preferentially at dogtown edges, where grasses predominated, and pronghorn antelope preferred town centers, where forbs and small shrubs predominated (Krueger 1986). Effects of these preferences on the annual energy budgets of the bison and pronghorn are unknown, but they probably depend at least partly on the proportion of the total foraging area that is occupied by prairie dog colonies, by colony edges, and by colony centers. Simple geometry, coupled with the tendency for forage production to be reduced in town centers (Hansen and Gold 1977; Weltzin et al. 1997), suggests that numerous small towns would provide more edge and greater vegetation production than a few large ones, and thus provide the better option for at least bison.

Plant species diversity may be higher or lower on prairie dog colonies than off, depending on original vegetation type, precipitation prior to time of measurement, location within colony (center or edge), age of colony, and other variables (cf. Osborn and Allan 1949; Bonham and Lerwick 1976; Hansen and Gold 1977; Coppock et al. 1983; Agnew et al. 1986; Weltzin et al. 1997). These studies suggest that diversity inside colonies tends to be greater in shortgrass prairie, near colony edges, and following high rainfall periods that stimulate germination of annuals. Prairie dog colonies as landscape patches enhance diversity partly because plant species inside colonies differ in composition from those outside (Coppock et al. 1983).

Numerous Great Plains wildlife species benefit from black-tailed prairie dogs as food, as excavators of burrows, or as intensive grazers. Birds known to selectively use black-tailed prairie dog colonies include mountain plovers (*Charadrius montanus*) (Knowles et al. 1982), ferruginous hawks (*Buteo regalis*) (Roth and Marzluff 1989), burrowing owls (*Speotyto cunicularis*) (Desmond and Savidge 1996; Truett and Savage 1998), mourning doves (*Zenaida macroura*), and horned larks (*Eremophila alpestris*) (Agnew et al. 1986). The first three of these have attracted recent attention as priority species for conservation; the mountain plover has been proposed for listing as threatened (Roth and Peterson 1997; US Fish and Wildlife Service 1999). Small mammals known to favor black-tailed prairie dog colonies include the endangered black-footed ferret (Hillman 1979) (which requires prairie dogs to survive in the wild), the spotted ground squirrel (*Spermophilus spilosoma*) (Hoffmeister 1986:191), the desert cottontail (*Sylvilagus audubonii*) (Hansen and Gold 1977), and insectivorous rodents, such as the northern grasshopper mouse (*Onychomys leucogaster*) (Agnew et al. 1986).

The existence of prairie dog colonies often enhances wildlife diversity. Bird diversity was greater inside than outside prairie dog colonies in South Dakota (Agnew et al. 1986). Mammal diversity was greater inside than outside colonies in Chihuahua (Ceballos et al. 1999). Prairie dog burrows offer refuge to numerous species--small mammals, reptiles, amphibians, and insects (Campbell and Clark 1981; Sharps and Uresk 1990; Stapp 1998)--but the full effects on biodiversity have not been measured. Because the species composition of the wildlife community tends to be somewhat different inside than outside prairie dog colonies (Knowles et al. 1982; Agnew et al. 1986; Ceballos et al. 1999), juxtaposition of colonized and uncolonized habitats commonly supports greater wildlife diversity than either type alone (Manzano-Fischer et al. 1999).

In summary, where mid- and tallgrasses prevail, prairie dogs thrive mainly where bison or cattle shorten the grasses by their grazing and trampling. Prairie dogs, like bison, function as keystone animals strongly influencing ecosystem structure and function. Prairie dogs may reciprocally benefit bison or cattle under some circumstances. Their utility as prey for small predators, their provision of burrows useful as refugia, and their intensive grazing activities in combination attract birds and mammals that fare poorly in uncolonized prairie. The presence of their colonies commonly enhances species diversity not only because more plant and vertebrate species often occur inside prairie dog towns than outside, but also because their colonies typically create a patchwork within a larger matrix of uncolonized prairie. The two habitat types together support a richer diversity than either alone. Several birds of particular concern because of their rarity or declining abundance benefit from the presence of the black-tailed prairie dog, and the endangered black-footed ferret cannot survive in the wild without prairie dogs.

Managing Bison to Enhance Biodiversity

Can bison today be managed as keystone species on both small and large acreages to help restore some of the early Great Plains biodiversity? Can the information reviewed here be applied in the real world of bison production? We believe that some, though not all, plants and animals can be successfully restored to grasslands they originally occupied. Establishment and management of habitat mosaics may enable managers in some cases to attract even more species on small areas area than historically existed. Management tools available include bison grazing, fire, manipulation of woody vegetation, and prairie dogs. Note that cattle, horses, or other nonnative large grazers can be similarly managed to enhance diversity, as implied below, although the details of management to best achieve that diversity may vary among these large grazers.

Livestock management, which has provided the general model from which modern bison management evolved, was designed to produce maximum sustained yields of a single species, usually the domestic cow, for human consumption. This management model is counterintuitive to biodiversity conservation. The following four tenets of conventional range and livestock management illustrate why restoration of all Great Plains species probably is impossible but, on the other hand, that some level of biodiversity restoration is feasible.

First, the purpose of livestock production is to feed people, and continued population growth will increase the demand for that production. In effect, people are competing with the historic predators and scavengers—

wolves, grizzly and black bears, wolverines, and some smaller scavengers—for the same food resource. Given the slim margins in traditional livestock economics and the cultural predisposition to efficiency, the singular pursuit of livestock production to feed humans will tend to triumph over the restoration of historic diversity. Change will require more profitability in livestock production, perhaps through alternatives like bison, and a redefinition of efficiency that considers long-term sustainability.

Second, managers commonly attempt to remove species that reduce forage available to livestock. Removal of woody plants has been an ongoing focus of range managers in and near the Great Plains for several decades (e.g., Stoddart and Smith 1955; Vallentine 1989) because under some circumstances woody vegetation drastically reduces forage production. Prairie dogs have been controlled because they have been viewed as competitors for forage (Stoddart and Smith 1955:201). Alternative ways of managing woody vegetation (Guthery 1986; Cable 1991) and prairie dogs (Coppock et al. 1983; Detling 1998) offer fertile areas for biodiversity restoration.

Third, managers usually try to avoid heavy grazing and severe soil disturbance. Because these phenomena occurring historically over large areas reduced the long-term ability of many landscapes to support cattle, their prevention ranks among the most sacred tenets of good range management. However, some rare native plants (e.g., blowout penstemon, *Penstemon haydenii*) (Stubbendieck et al. 1997) and animals (e.g., black-footed ferret, mountain plover, and other prairie-dog-ecosystem species) (Koford 1959; Knowles et al. 1982; Knowles 1986) are associated with sites considered overgrazed by conventional standards. Management for these and some other "disturbance" species will require balancing their needs against potentially undesirable side effects of heavy grazing and disturbance, such as encroachment of invasive exotics.

Fourth, managers strive for uniform cropping of the forage base. Grazing management on western ranges is based on the use of water and salt distribution, fencing, and sometimes herding to achieve spatially uniform utilization of forage (Stoddart and Smith 1955:324; Coughenour 1991b). As this review suggests, the concept of uniform utilization contradicts that of biodiversity conservation. Because spatially patchy grazing is normal behavior for grazing animals, capitalizing on this tendency can be a prime management tool for enhancing biodiversity.

In sum, development of habitat mosaics, perhaps on a smaller scale than occurred historically, is the key to present-day conservation of biodiversity. Historical accounts suggest that patch size in the Great Plains grassland mosaic in the early 1800s often may have been rather large. As noted earlier, prairie dog colonies sometimes extended unbroken for miles and forage sometimes had been depleted by bison over similarly large areas. Prairie fires probably created a larger-scale mosaic than would have occurred with grazing alone (Vinton et al. 1993), and recurring fires left vast areas devoid of woody plants (Wells 1965).

To "pack" more species into smaller acreages than was the historical norm, patch size can be reduced by applying the same historical patch makers but on a smaller scale. Strategic placement of water (which may itself attract many species) and fences in mid- and tallgrass areas can induce bison to create a mosaic by grazing heavily in some areas and lightly in others. In such situations relatively small prairie dog colonies can be maintained in heavily grazed sites without fear of their spreading rapidly into areas where the grass is denser and taller (Snell and Hlavachick 1980; Licht and Sanchez 1993). Controlled application of range fires on a small scale can help manipulate grazing distribution and at the same time preserve windbreaks, shrub thickets, and other patches of woody plants critical to the persistence of many animals. Fire can be used to maintain shrub savannas (McPherson 1995), which may attract a variety of wildlife species (Nelson et al. 1999) not found in shrubless grasslands.

To conclude, although some components of the original biodiversity of the Great Plains cannot reasonably be restored, a large proportion of the plants and the smaller animal species lost from specific areas can be restored within the context of present-day bison management. A focus on the creation of landscape mosaics can lead in many areas to biodiversity enhancement, with relatively little loss in livestock production. Diversity can be packed into rather small acreages by creating a finer-scale habitat mosaic than existed 200 years ago. One major challenge for resource managers will be overcoming traditional mindsets that equate value only with a quantifiable economic return. Even though no dollar value can be easily assigned to its restoration, biodiversity is invaluable to the long-term sustainability of the grasslands.

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