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ABSTRACT—We study bison (*Bos bison*) herds that are managed year-long without protein or energy supplements in large mixed prairie pastures in Nebraska, South Dakota, and North Dakota. We also manage cattle (*B. taurus*) grazing during the growing season in separate, but adjacent pastures. Management reflects the divergent evolution of bison and cattle with their respective human cultures and landscapes. Bison exhibit a stronger preference for the perennial grasses that form the prairie matrix, and they are strongly attracted to open landscapes during the growing season. Cattle include more forbs in their diet, and they use wooded areas and riparian zones more intensively. At similar annual stocking rates, the amount of grass remaining at the start of the dormant season is higher under year-long bison grazing compared to growing season cattle grazing. There are inherent differences between bison and cattle, suggesting that they be managed differently. Under our respective management regimes, bison are less productive than cattle, but they require less processed feed and labor inputs. We recommend that the focus of mixed prairie conservation be on developing ecologically sound goals and practices for grazing management, rather than on whether bison or cattle are more appropriate grazers.

Introduction

Herds of bison (*Bos bison*) grazing across the prairie are fundamental to our image of the Great Plains (Stebbins 1981). With the settlement of the

West, bison numbers declined dramatically to a few hundred individuals (McHugh 1972). Through conservation efforts, bison numbers have rebounded to over 225,000; and, they offer an alternative to European cattle (*B. taurus*) for managing some grasslands in the Plains (Steuter et al. 1995; Knapp et al 1999).

The Nature Conservancy has managed and studied fire, bison, and cattle in mixed-grass prairie on its privately-owned preserves in Nebraska, South Dakota, and North Dakota since the late1970s. When coupled with ecological models, this management activity can be conceived as testing landscape-level hypotheses. The bison herds on Conservancy preserves are allowed to graze year-long in large pastures without protein or energy supplements. Our bison program began in 1978 on the S.H. Ordway Jr., Memorial Prairie in northcentral South Dakota. In 1984, we began using fire in combination with bison grazing on the S.H. Ordway and Cross Ranch (North Dakota) Preserves. By 1991, fire was being incorporated in a dynamic, landscape-scale pattern that is determined by the accumulation of fine fuel (Steuter et al. 1990b), and the Niobrara Valley Preserve (Nebraska) was included in our comparative regional study.

Cattle grazing is also an important management tool on Conservancy mixed prairie preserves. We use the accepted practice of deferring and rotating cattle grazing between pastures and years. Since bison are once again potential grazers of mixed prairie, an interest in comparing bison and cattle has grown (Plumb and Dodd 1993). In our research, we compare bison under mixed prairie conditions, similar to the conditions to which the species is adapted, and cattle under accepted management scenarios.

The evolutionary history of the two species contributes to an understanding of the use of bison and cattle in managing today's grasslands. Plains bison co-evolved with the grassland biome (Stebbins 1981; Axelrod 1985) and survive as a wild species. European cattle, on the other hand, are the domestic descendants of an extinct founder species (Aurochs, *B. primigenius*), a product of post-Pleistocene, woodland-grassland-farmland landscapes (Bailey et al. 1996; Bogucki 1996).

The cultural history of humans with bison and with cattle also contributes, and suggests different management scenarios. Cattle are one of 14 large (>45 kg) mammal species successfully domesticated during the mid-Holocene, out of the 148 species that existed then (Diamond 1997). European cattle in particular have undergone intensive selection over the last 4,500 years to fit the intensive management style favored by European agriculturalists. In contrast, bison have remained undomesticated, in spite of

providing much of the meat protein used by Plains Indian cultures during the last 10,000 years. Diamond (1997) suggested that bison, and most other large wild mammals, fail to meet minimum compatibility requirements for domestication in all six of the following critical traits: 1) broad diet; 2) relatively high growth rate; 3) minimal captive breeding restrictions; 4) reliable disposition; 5) low panic response; and, 6) well-developed social adaptations for living in herds, including well-developed dominance hierarchies and overlapping home ranges. Perhaps in response to the lack of such traits in bison, Native American cultures appear to have adopted an extensive land management system where bison were promoted and harvested without being domesticated.

Comparative Ecology within the Mixed-Grass Prairie

Comparisons of bison versus cattle impact on vegetation can be made at similar annual stocking rates, but under different management regimes, if done over a long time period. In our preserves, bison stocking rates are similar to moderately-stocked cattle pastures with similar soils and topography. Similar stocking rates result from similar proportions of the total annual forage production being consumed. However, bison consume that forage over 12 months, while cattle consume a similar proportion of the forage during the mid-May to mid-October growing season. Comparisons of bison and cattle—made by species, landscape and human management variables—show interesting differences in diet, habitat selection and plant community structure, as well as in herd productivity and animal ecophysiology (see below).

Physiology, Morphology and Stress Response

First, we can compare bison and cattle in terms of selected physiological and morphological traits. Bison can handle cold stress better than cattle, with lower metabolic rates, twice as much insulation and very low critical temperatures (Table 1; Christopherson et al. 1976, 1980; Christopherson and Hudson 1979). Both bison and cattle have cloven hooves and relatively short legs–poor adaptations for living in deep snow (Telfer and Kelsall 1979, 1984). However, bison are more effective than cattle since they use their well-insulated head and re-enforced neck muscles, associated with their shoulder hump, to clear deep snow away from forage (Meagher 1978). Such research emphasizes the relative hardiness of bison under extreme winter conditions.

TABLE 1
BISON AND CATTLE RESPONSE TO COLD STRESS
(SEE CHRISTOPHERSON ET AL. 1976, 1980)

	Response by:	
Parameter	Bison	Cattle
Metabolic Rate ($kcal/kg^{.75}/day$)	125	210
Insulation ($°C\ m^2\ 24hr/Mcal$)	59	24
Critical Temp (°C)	-46	13

Conservancy management data, in contrast, are obtained during fall round-ups, health monitoring and marketing, and emphasize response to handling as well. These data indicate that bison endure a higher level of stress than cattle during handling and shipping. Bison weight loss due to handling stress has ranged from 2% for bull calves to 12% for 2-year old bulls. Weight losses for adult bison bulls and cows have been measured in the range of 5% to 9%, respectively. Shipping and handling weight losses in cattle during the marketing process are generally considered to be in the 0 to 3% range (Western Video Auction, personal communication). An increased susceptibility to handling stress in bison suggests a need for management and pre-slaughter processing strategies to insure reasonable animal welfare and a high quality meat product from bison.

Diet and Habitat

Qualitative comparisons suggest bison and cattle differ in their diet (Table 2), and this likely reflects differences in habitat selection. Bison primarily feed on grasses and sedges, consuming more of these plants than expected, based on what is available (Peden et al. 1974; Van Vuren and Bray 1983; Steuter et al. 1995). In mixed prairie, bison also prefer more open habitats than cattle (A. Steuter, personal observation). Bison select fewer species of forage plants, and their diet quality is lower because of their

TABLE 2
QUALITATIVE COMPARISON OF FORAGING ECOLOGY OF BISON AND CATTLE (ADAPTED FROM HARTNETT ET AL. 1997)

Parameter	Bison	Cattle
Forage selectivity	lower	higher
Use of forbs and shrubs (% of diet)	lower (<10%)	higher (10-25%)
Use of graminoids	higher (>90%)	lower (75-90%)
Diet niche breadth (% available species consumed)	lower	higher
Time allocated to grazing (during growing season)	lower	higher
Time allocated to non-feed activity	higher	lower
General diet quality (crude protein, total digestible nutrients)	lower	higher
Digestibility of graminoids	higher	lower
Mean digesta retention time	higher	lower

preference for grasses (Table 2; Plumb and Dodd 1993). Cattle tend to select forbs and browse, in addition to grasses and sedges, during seasons when forage quality is high (Rice et al. 1974; Plumb and Dodd 1993). Forbs and woody species generally make up less than 10% of the bison diet, whereas they often make up more than 15% of cattle diets (Hartnett et al. 1997). By grazing predominantly on grasses and avoiding forbs, bison can increase plant species diversity by suppressing the dominant grasses and releasing limited resources to a diverse array of forbs (Collins et al. 1998).

Bison spend less time than cattle on grazing during the growing season, allocating more time to non-feeding activities, such as wallowing, horning

(i.e., rubbing on trees), and interacting socially (Plumb and Dodd 1993). The selection by bison of abundant and continuously distributed grasses (noted above) allows higher intake rates during shorter feeding bouts. We hypothesize that if bison received regular protein supplement similar to cattle, their foraging behavior and diet selection might be more similar to cattle.

Landscape Comparisons

A theoretical basis for the differences we observe between bison use of fire-managed mixed prairie and cattle grazing within deferred and rotated prairie pastures is provided by Sneft et al. (1987). During the growing season, bison strongly select for high quality regrowth on burn areas (Biondini et al. 1999) or for large, open grasslands (Steuter et al. 1995). In contrast, the spatial distribution of cattle "in time" is largely controlled by the manager's decisions, and in relation to pasture cross-fences and stock density.

Topography, soils, vegetation, and animal behavior influence cattle and bison distribution in unburned mixed prairie (Sneft et al. 1987; Steuter et al. 1995). However, when the same landscape is managed with a fire regime that mimics historic fire frequency and season, the effects of fire override topography and soil in determining bison distribution (Biondini et al. 1999). The interaction between bison and fire results in a coarse, dynamic vegetation pattern not present in cattle managed landscapes. Diversity in vegetation structure, resulting from either fire plus bison grazing or cattle management, can provide habitat opportunities for a variety of grassland birds (Griebel et al. 1998; Kantrud 1981), and invertebrate species (Fay 1998).

One of the most important differences between mixed prairie managed with bison plus fire versus with cattle is that much higher standing crop remains under the former regime at the on-set of the dormant season. This is the obvious result of allocating forage to bison over 12 months versus to cattle over the 5-month growing season (mid-May through mid-October). In addition, it is the result of concentrated grazing by bison on burned patches. Up to 80% of bison grazing during the growing season occurs on the 15-25% of the landscape that was most recently burned (Biondini et al. 1999). These two factors result in a landscape with distinct patches of uniformly short vegetation surrounded by a matrix of relatively high standing crop in bison pastures–the coarse pattern noted above. The burned plus intensively grazed patches tend to have more forb and less bunchgrass production in subsequent

Figure 1. Bison selecting for cool season grasses and sedges in the understory of a woody draw in mixed prairie during early spring, while upland warm season grasses are still dormant.

growing seasons, especially following summer fires (Pfeiffer and Steuter 1994). The shift in plant composition and the patches of short stature vegetation last from one to several years in the mixed prairie (Biondini et al. 1999). Grazing frequency and intensity are related to water distribution as well as to fire (Sneft et al. 1987). The naturally-occurring wetland and riparian areas that once influenced grazing distribution are now supplemented with stock wells and dams for both bison and cattle, including on the Conservancy preserves. Side-by-side comparisons suggest bison spend less time grazing and loafing next to water sources and, as a result, the animal impact zone is smaller and less severe (Van Vuren 1981; A. Steuter, personal observation). However, bison do select riparian zones in sandhills mixed prairie during the spring and fall forage transitions (Fig. 1; Steuter et al. 1995). During these transition periods, cool season grasses are still growing in the woodland understory, while the uplands are dominated by warm season grasses that are dormant.

Figure 2. Cattle on winter sandhills pasture coming to protein supplement being provided to maintain body condition and improve conception rates. Supplementing protein and energy in winter diets of cattle is a standard management practice in northern mixed-grass prairie.

Topography is also important. Bison prefer to use open, gently rolling uplands, especially when they are in large breeding herds during July and August (Steuter et al 1995). In contrast, cattle are attracted to the shade of woodlands and riparian zones, both during the heat of the summer and for protection from wind and cold during the winter (Smoliak and Peters 1955; Sneft et al. 1985; Van Vuren 1981). This contrast between bison and cattle does not persist in the mountainous west, where dense rhizomatous forages dominate riparian zones and relatively sparse bunch grass communities dominate the uplands (Mack and Thompson 1982). Bison appear to select riparian areas similarly to cattle in the intermountain West.

Many schemes of planned grazing on the landscape have been designed to sustain cattle production and grassland productivity (e.g., Heitschmidt and Stuth 1991). In general, a single herd of cattle is moved throughout the growing season among multiple, fenced pastures to harvest high-quality forage. This allows regrowth in temporarily-deferred pastures, to restore plant vigor following grazing. The season(s) of grazing for individual pastures can be shifted between years to maintain the preferred

composition of forage species, or they can be held constant to change the plant composition in favor of a particular group of plants. Plant community response to grazing, and the "manageable" nature of cattle, suggest that planned grazing with cattle can be used to meet specific conservation goals as well as production objectives (Fig. 2; Steuter 1995). The more specific the habitat objectives for a prairie fragment, the more likely that planned grazing with cattle will allow a manager to meet those objectives. Fire is rarely used today by cattlemen in mixed prairie, due to lost production in dry years. However, it may eventually become more common, as a tool to control woody plant encroachment and improve forage quality (Bragg and Steuter 1996).

Although some notable expanses of mixed-grass prairie remain, most have been fragmented by crop production, transportation corridors, and urban and residential development. Also, private ownership of land in the mixed prairie region results in management practices being applied in a fragmented pattern (Bragg and Steuter 1996). Woodlands developing in parts of the mixed prairie, due to fire suppression (Steuter et al. 1990a), also fragment the remaining prairie. These changes actually suggest a trend toward a landscape that is more compatible with the evolutionary history of cattle than of bison.

Animal Production

Bison are capable of maintaining productive populations on mixed prairie remnants on a year-round basis, doing so without supplemental energy or protein. However, without diet supplementation female bison mature more slowly and have their first calf when they are 3-years old. The average weaned calf crop (# calves surviving to 6-months / # 2- to 10-year old females exposed to bulls during the summer of the previous year * 100) for the bison herd on the Niobrara Valley Preserve has been 84% during 1987-1999 (Table 3). In comparison, the average weaned calf crop was 89% for a spring-calving, domestic cattle herd at the Gudmundsen Sandhills Laboratory during 1994-1997 (Table 3; University of Nebraska-Lincoln, Gudmundsen Sandhills Laboratory 1999). Calf crops below 80% for the Niobrara bison were associated with persistent deep snow during the winter before conception, while calf crops over 90% have been associated with mild winters with open forage conditions prior to conception. The somewhat higher weaned calf crops for domestic cattle may be explained partially by winter diet supplementation, and by human assistance provided to cows with birthing difficulty.

TABLE 3
WEANED CALF CROP COMPARISON BETWEEN BISON IN THE NIOBRARA VALLEY PRESERVE HERD AND DOMESTIC CATTLE IN A SPRING-CALVING CONTROL GROUP AT THE UNIVERSITY OF NEBRASKA-LINCOLN'S GUDMUNDSEN SANDHILLS LABORATORY ON SIMILAR MIXED PRAIRIE PASTURE.

	1/ Weaned Calves (%)	
Fall of Year	Bison	Cattle
1987	72%	—
1988	81%	—
1989	75%	—
1990	88%	—
1991	84%	—
1992	87%	—
1993	86%	—
1994	83%	90%
1995	78%	94%
1996	86%	84%
1997	93%	88%
1998	92%	—
1999	94%	—
Average	84%	89%

1/ # calves surviving until weaning / # females 2-to-10 years old exposed to bulls during the summer of the previous year.

Bison heifer calves at the Niobrara can be expected to weigh about 150 kg at approximately 6-months old, while bull calves weigh about 170 kg. In comparison, June-born heifer calves from the cattle herd at the Gudmundsen Lab weigh about 180 kg, and steer calves about 190 kg at a similar age (University of Nebraska-Lincoln, Gudmundsen Sandhills Laboratory 1999). Although yearling bison weight gains on summer pasture appear similar to cattle (Table 4), the potential for winter weight gain and for weight gain under feedlot conditions have been shown to be significantly less for bison than for cattle (Christopherson and Hudson 1979; Peters 1959). The results of these published studies suggest that intensive feeding of bison, especially

TABLE 4
AVERAGE INITIAL WEIGHT, END-OF-SUMMER WEIGHT, AND WEIGHT GAIN PER DAY OF YEARLING BISON AND CATTLE ON MIXED-GRASS PRAIRIE.

Animal	Date–Wt. (kg)	Date – Wt. (kg)	Rate of Gain (kg)/Day
Bison Bulls 1/ (n=10)	5/3/98 – 170	11/12/98 – 314	0.76
Cattle Steers 2/ (n=32)	5/1 – 245	11/1 – 395	0.82
3/ (n=15)	4/30/99 – 217	9/14/99 – 308	0.68

1/ Data from Niobrara Valley Preserve yearlings born about 1 May and weaned 1 November 1997; hay-fed to gain 0.23 kg/day during the winter /spring prior to the summer grazing trial.
2/ Data from Gudmundsen Sandhills Laboratory March-born yearlings during the summers of 1997 and 1998; fed to gain 0.23 kg/day during the winter/spring prior to the summer grazing trial.
3/ Data from Gudmundsen Sandhills Laboratory yearlings born in June 1998 and weaned in January 1999; fed to gain 0.18 kg/day during the winter/spring prior to the summer grazing trial.

during during the winter months, will produce lower feed conversion rates than it does in cattle. Conversely, bison are capable of producing nearly comparable calf crops and yearling gains exclusively on mixed prairie forages, without calving assistance or diet supplementation.

The Great Plains at the Millennium

The differences between the Great Plains at this millennium compared to the last appear as great, or greater, than the inherent differences between bison and cattle. Both bison and cattle are efficient at converting the abundant, but relatively low quality, native forage plants into useable food and leather products. We conclude that conserving the soil, water, and biological resources of the mixed-grass prairie will be accomplished with sound grazing management, rather than determined solely by the choice between bison

or cattle. Whether managing mixed prairie with bison or with cattle, the stocking rate and grazing management will determine the long-term health of both the prairie and grazing animal. Based on evolutionary history and domestication traits, cattle may be more appropriate in intensively managed agricultural systems. Bison may be more appropriate in extensively managed, larger grasslands. However, the human, land and financial resources available to managers, along with their goals and objectives, will also influence the choice between bison and cattle as grazers on mixed prairie in the next millennium. The option is still available, thanks to the far-sighted efforts of turn-of-the century conservationists who designed the first endangered species recovery plan for the American bison.

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