Spatial relations of American bison (*Bison bison*) and domestic cattle in a montane environment

D. H. Van Vuren

Van Vuren, D. H., 2001. Spatial relations of American bison *Bison bison* and domestic cattle in a montane environment. *Animal Biodiversity and Conservation*, 24.1: 117–124.

Abstract

Spatial relations of American bison Bison bison *and domestic cattle in a montane environment.*— Restoration of American bison (*Bison bison*) to montane environments where they once occurred requires information on ecological relationships with domestic cattle (*Bos taurus*) that now live there. Comparisons of the foraging distributions of sympatric bison and cattle in a 375–ha basin revealed that cattle were constrained by slope and distance from water, especially vertical distance, whereas bison responded mostly to forage availability. Cattle appeared to be central place foragers oriented around water and followed a strategy of meeting their energetic needs with the least cost. Bison, in contrast, appeared to be energy maximizers that moved often in response to forage availability. The result was relatively little overlap (29%) in spatial distributions. If bison replace cattle in montane environments, managers can expect a more even distribution of grazing pressure. Bison and cattle might be managed sympatrically; their spatial distributions may be sufficiently different to minimize competition for food, and the risk of interspecific disease transmission as well.

Key words: Bison, Cattle, Foraging Ecology, Montane environments, Spatial relations.

Resumen

Relaciones espaciales entre el bisonte americano Bison bison *y el ganado vacuno en un medio de montaña.*— La reintroducción del bisonte americano (*Bison bison*) en un ambiente de montaña donde ya había vivido antes requiere información acerca de las relaciones ecológicas con el ganado vacuno (*Bos taurus*) que ahora habita en ese lugar. La comparación de las distribuciones de forrajeo del bisonte con las de la vaca en una cuenca de 375 ha demostraron que la vaca estaba limitada por la inclinación del terreno y la distancia al agua, especialmente la distancia vertical, mientras que el bisonte lo estaba principalmente por la disponibilidad de pasto. La vaca mostró clara orientación a pacer principalmente alrededor del agua y siguió una estrategia de obtención de sus necesidades energéticas con el mínimo coste. En contraste, el bisonte se mostró maximizador de energía, efectuando frecuentes desplazamientos en función de la disponibilidad de pastos. El resultado dio una coincidencia relativamente reducida (29%) en las distribuciones espaciales. Si el bisonte sustituye al ganado en medios de montaña, puede esperarse una mejor distribución de la presión sobre los pastos. Los bisontes y el ganado vacuno pueden convivir en la misma área geográfica, puesto que sus distribuciones espaciales son suficientemente diferentes para minimizar la competencia por el alimento, así como el riesgo de transmisión interespecífica de enfermedades.

Palabras clave: Bisonte, Ganado, Ecología de forrajeo, Medios de montaña, Relaciones espaciales.

(Received: 29 VI 01; Final acceptance: 18 VII 01)

D. H. Van Vuren, Dept. of Wildlife, Fish, and Conservation Biology, Univ. of California, Davis, CA 95616, USA.

ISSN: 1578–665X

Introduction

Most grasslands around the world once supported vast herds of migratory ungulates (Fryxell et al., 1988; Frank, et al., 1998). Over the past 150 years, however, these herds have been drastically reduced by overhunting, and much of their grassland habitat has been cultivated for crops or converted to pasture for domestic livestock (Fryxell & Sinclair, 1988; Frank et al., 1998). Conservation of remaining herds is threatened by continued encroachment by an increasing human population and conflicts with domestic livestock (Reynolds & Hawley, 1987; Norton–Griffiths, 1995; Frank et al., 1998).

The American bison, a large migratory ungulate that was once distributed throughout much of North America, is no exception. Densities were greatest in the grasslands of the Great Plains, which supported numbers in the tens of millions (Roe, 1970), but bison also lived at lower densities in meadows and shrub–steppe communities to the west, in the Rocky Mountains and in the mountains and valleys beyond (Roe, 1970; Van Vuren, 1987; Meaney & Van Vuren, 1993). Indiscriminate slaughter during the 1800s led to near–extinction; by 1900, only a few hundred bison remained, almost all of them in captivity. Intensive conservation efforts narrowly averted extinction, and numbers have recovered to about 200,000. Most bison today, however, are intensively managed on private lands for commercial purposes or are confined by fences on wildlife refuges (Dary, 1989; Manning, 1996). The extensive range formerly inhabited by bison has been plowed and converted to crops or is grazed by domestic cattle. Consequently, bison have recovered from near–extinction, but the ecological role they once played has not been restored.

Recent research has demonstrated the ecological importance of bison in a variety of the biotic communities that they once inhabited (Krueger, 1986; Frank & McNaughton, 1993; Campbell et al., 1994; Knapp et al., 1999; Steinauer & Collins, 2001). Consequently, there has been increasing interest in restoring bison to a functional role in natural areas, both in the grasslands of the Great Plains and in montane environments to the west (Plumb & Dodd, 1993; Wuerthner, 1993; Callenbach, 1996; Hamilton, 1996; Stephenson & Fleener, 1998; Knapp et al., 1999). However, domestic cattle, often considered the ecological equivalent of bison (Noss & Cooperrider, 1994; Hartnett et al., 1997; Wuerthner, 1998), now occupy many of these areas, raising concerns about the consequences of restoring bison. If bison and cattle have similar niches and occur in the same area, then competition for food may result in management conflicts (Wagner, 1978). Further, the possibility of disease transmission between sympatric bison and cattle has caused controversy at several localities (Van Vuren & Scott, 1995).

Comparisons of bison and cattle in the Great Plains have revealed interspecific differences in foraging ecology (Peden et al., 1974; Plumb & Dodd, 1993; Hartnett et al., 1997), but corresponding studies have not been done in montane environments, where abiotic factors may be particularly important in influencing foraging distribution. Cattle distribution is strongly constrained by slope and distance from water (Mueggler, 1955; Roath & Krueger, 1982; Gillen et al., 1984; Ganskopp & Vavra, 1987; Pinchak et al., 1991; Telfer, 1994), and elevation may have an effect as well (Senft et al., 1983). In contrast, several authors have claimed that bison are relatively unaffected by these factors (Warren, 1927; Fryxell, 1928; Cahalane, 1947; Callenbach, 1996), suggesting the potential for niche differentiation between bison and cattle. These claims, however, remain unsubstantiated.

The Henry Mountains, a semi–arid range west of the Rocky Mountains, support free–ranging bison and cattle that co–exist in an area characterized by rugged topography and limited water. Although located about 100 km outside of the former range of bison (Van Vuren, unpublished data), the Henry Mountains are typical of montane environments where bison are known to have occurred (Meaney & Van Vuren, 1993). Foraging distributions of bison and cattle were studied in relation to slope, distance from water, and elevation. A preliminary analysis suggested that bison and cattle responded differently to these factors (Van Vuren, 1982). In the present report those preliminary findings are confirmed and extended by showing that differential responses to environmental factors, perhaps stemming from differing evolutionary histories, result in spatial segregation of bison and cattle, with implications for conservation.

Study area

Located in southeastern Utah, USA, the Henry Mountains (38° 5′ N, 110° 50′ W) rise abruptly above the Colorado Plateau (ca. 1,500 m elevation) to 3,540 m elevation at the summit of Mount Ellen, the highest peak. Precipitation increases with elevation, ranging from 15 cm in the surrounding deserts of the plateau to > 50 cm on the higher slopes. The lower slopes of the range (ca. 1,800–2,400 m elevation) support extensive pinyon pine (*Pinus edulis*) and juniper (*Juniperus* spp.) woodlands. Slopes above 2,400 m are an interspersion of Douglas fir (*Pseudotsuga menziesii*), spruce (*Picea engelmannnii*), and fir (*Abies* spp.) forests, groves of quaking aspen (*Populus tremuloides*), and shrub–steppe openings dominated by shrubs (*Artemisia* spp., *Symphoricarpos alba*), forbs (*Penstemon* spp., *Oxytropis* spp., *Astragalus* spp.) and perennial grasses (*Poa* spp., *Festuca* spp., *Nassella* spp.).

The highest elevations support subalpine grasslands dominated by *Festuca thurberi* and *Carex* spp.

Bison were introduced to the area in 1941 as part of early efforts to restore bison and numbered about 200 at the time of this study (Van Vuren & Bray, 1986). The bison were free-ranging and migrated seasonally, spending summers on the upper slopes of the mountains and moving to lower elevations, mostly to the west and southwest, during winter. Domestic cattle have grazed the Henry Mountains since the late 1800s; the two species were sympatric during summer but allopatric during winter, when cattle were herded to ranges apart from bison.

The study area comprised the 375–ha basin that formed the headwaters of South Creek, which drained the west side of Mount Ellen. Elevation ranged from 2,800 m on the west side of the basin to 3,400 m at the head. Slopes were gentle in much of the central and western portion of the basin but increased steadily toward the east, reaching 40° at the head of the basin. Vegetation in the lower portion of the basin consisted of conifer or aspen groves interspersed with shrub-steppe openings, the middle portion was mostly shrub–steppe, and the upper portion supported subalpine grassland. Both bison and cattle frequently grazed the basin during the study; about 30 cattle lived there all summer, and groups of up to 60 bison were often present. Drinking water was available all summer at seven springs and catchment basins. There were no fences, and cattle were not herded after being moved into the basin during late spring; thus, the entire basin was physically accessible to both species.

Methods

The study was conducted July and August 1977 and June through September 1978. Spatial distributions were determined visually; bison and cattle were observed and classified as foraging or not, and their locations were plotted at 30–minute intervals on a 1:24,000 topographic map of the basin. The map was overlaid with a grid scaled at 100–m intervals (thus, 1 ha per grid cell), and each observation was assigned to the grid cell that it fell within. Bison and cattle were observed from several vantage points, none of which allowed a view of the entire basin, so vantage points were rotated among to ensure that all parts of the basin were surveyed. Observations were distributed throughout daylight hours.

The numbers of observations of foraging bison and cattle were summed for each grid cell. Environmental factors were measured at the center of each grid cell. A clinometer was used to measure slope and a topographic map was used to determine elevation and distance from the nearest source of drinking water; horizontal and vertical distance from water were recorded as separate factors. Frequency distributions were used to compare the spatial distributions of bison and cattle in relation to each environmental factor. The range of each factor was divided into intervals and all observations of bison or cattle that fell within each interval for slope (4° intervals), horizontal (100–m intervals) and vertical (30–m intervals) distance from water, and elevation (50–m intervals) were totaled. Frequency distributions of bison and cattle were compared using a G–test of independence. Observations were not independent, but this is a concern only if analyses yield marginally significant results, which did not happen. To compare the spatial distributions of bison and cattle graphically a three–dimensional mesh plot was used, in which *x*– and *y*–coordinates corresponded to the axes of the grid that overlay the basin, and the *z*–coordinate represented the frequency of use of each grid cell. To compare spatial distributions numerically, Kulczynski's similarity index was calculated (Oosting, 1956), which compares frequencies in each grid square, then sums for all grid squares. The index ranges from 0 (completely different use of space) to 1 (identical use of space).

The foraging distribution of cattle often declines exponentially with increasing distance from water (Mueggler, 1955; Roath & Krueger, 1982; Nash et al., 1999), creating a "piosphere", a zone of attenuating impact away from each watering point (Andrew, 1988). A similar exponential decline may exist with increasing slope (Ganskopp & Vavra, 1987). This relationship was evaluated for bison and for cattle by regressing the square root of proportion of observations on each of three variables, horizontal distance from water, vertical distance from water, and slope. Because only a negative relationship was expected, one–tailed tests were used.

Results

Among > 22,000 observations of bison and >3,000 of cattle recorded in the study area, 9745 were of foraging bison and 1,196 were of foraging cattle. The species differed markedly in the slopes they grazed ($G = 1,264.0$, $P < 0.001$); cattle occurrence declined rapidly as slope increased beyond 4°, whereas bison exhibited a bimodal pattern with the highest peak in occurrence at 28–32° (fig. 1). Cattle observations fit a negative exponential relationship with slope ($r^2 = 0.86$, $P < 0.001$), but bison observations did not ($r^2 = 0.03$, $P > 0.50$).

The species were less differentiated according to horizontal distance from water, yet differences were evident ($G = 492.0$, $P < 0.001$). Cattle occurrence declined with increasing distance, while bison occurrence was unrelated to distance until beyond 700 m. Cattle observations fit a negative exponential relationship with horizontal distance from water ($r^2 = 0.88$, $P < 0.001$); so did bison observations, but the fit was poor ($r^2 = 0.33$, $P = 0.04$) and the slope was less negative than that of cattle ($t = 2.53$, $P < 0.05$).

The species differed strikingly according to vertical distance from water ($G = 1,260.7$, $P < 0.001$). Cattle occurrence declined steeply with increasing distance, whereas bison occurrence decreased only slightly. Cattle observations fit a negative exponential relationship with vertical distance from water ($r^2 = 0.78$, $P < 0.001$); the decline was so steep, however, that examination of the residuals indicated a fourth–root transformation was a better representation of the relationship ($r^2 = 0.83$, $P < 0.001$). Bison observations also fit a negative exponential relationship ($r^2 = 0.72$, $P < 0.001$), but the slope was less negative than that of cattle ($t = 2.75$, $P < 0.02$).

Bison and cattle differed in the elevations they grazed ($G = 1,354.0$, $P < 0.001$), with bison grazing more often at higher elevations.

The spatial distributions of bison and cattle in the basin were not uniform, in part because both species grazed almost entirely in shrub-steppe or subalpine grassland communities and used conifer or aspen groves mostly for resting. However, within shrub–steppe and grassland communities, differential response of bison and cattle to slope, distance from water, and elevation translated into differential use of space. Bison and cattle were recorded in similar numbers of grid squares (163 and 16, respectively), but only 66 grid squares were grazed by both species. Intensity of use differed as well. Two pronounced peaks in cattle distribution, in the north and northwest portions of the basin, occurred at large "flats" with level or gentle slopes and drinking water nearby (fig. 2). Most of the lesser peaks in cattle occurrence were located at smaller flats with adjacent water. Some bison also grazed these areas, but most bison observations were distributed in an arc that extended across the highest (and steepest) slopes at the head of the basin and along the north slope of the ridge that formed the southern boundary of the basin (fig. 2). Graphical differences in distribution were supported numerically; the similarity index was only 0.286, indicating that spatial distributions of foraging bison and cattle were largely dissimilar.

Discussion

Distribution of cattle was strongly constrained by slope, although not as severely as in other studies, which reported that cattle seldom used slopes greater than 11° (Gillen et al., 1984; Ganskopp & Vavra, 1987; Pinchak et al., 1991; Telfer, 1994). Bison, in contrast, frequented much steeper slopes than did cattle, both in the Henry Mountains and elsewhere, exhibiting a peak in distribution at about 30° and confirming earlier assertions (Fryxell, 1928). Horizontal distance from water seemed less important to cattle distribution than did slope, probably because all parts of the basin were relatively close to water (< 1000 m) and because response of cattle to proximity of water is influenced by other factors, especially topography (Holechek et al., 1989). Nonetheless, bison were relatively unaffected by availability of water compared with cattle and in particular were less likely to graze close to water, again confirming previous claims (Cahalane, 1947; Callenbach, 1996). In contrast to horizontal distance from water, vertical distance from water sharply constrained cattle distribution. These findings parallel those of Roath & Krueger (1982), who found that cattle rarely grazed sites more than 80 m above water. Bison were much less affected than cattle by vertical distance from water.

Bison grazed at higher elevations than cattle; however, they probably were responding to forage availability rather than elevation. Precipitation in the Henry Mountains increases linearly with elevation (Van Vuren & Bray, 1986), and so does forage availability; production of graminoids, the primary food of both bison and cattle (Van Vuren, 1984), ranged 31–179 kg/ha (dry basis) in the study area and increased with elevation ($r = 0.85$, $P < 0.05$; Van Vuren, unpublished data). This gradient may have been exacerbated by depletion of forage at lower elevations by cattle concentrated on gentle slopes near water (Andrew, 1988; Holechek et al., 1989). These findings agree with those from the Great Plains, where availability of graminoids was a more important factor for bison than cattle in determining foraging distribution (Plumb & Dodd, 1993).

Thus, these results suggest that slope and distance from water, especially vertical distance, are most important in influencing cattle distribution, whereas availability of forage is more important for bison. The result was little spatial overlap between the species. An alternative explanation, that spatial segregation resulted from behavioral avoidance, is unlikely; the species sometimes grazed close to each other, and neither species altered its behavior in response to the other until about 4 m apart, whereupon cattle always avoided bison (Van Vuren, 1980).

Bison and cattle are closely related and are generally similar in size, appearance, and food preference (Wuerthner, 1998), consequently their differing spatial distributions are somewhat surprising. Perhaps the explanation lies in their differing evolutionary histories. Cattle originated in mesic environments of Eurasia whereas bison evolved in the semi–arid Great Plains, consequently cattle may have a greater requirement for water (Noss & Cooperrider, 1994; Wuerthner,

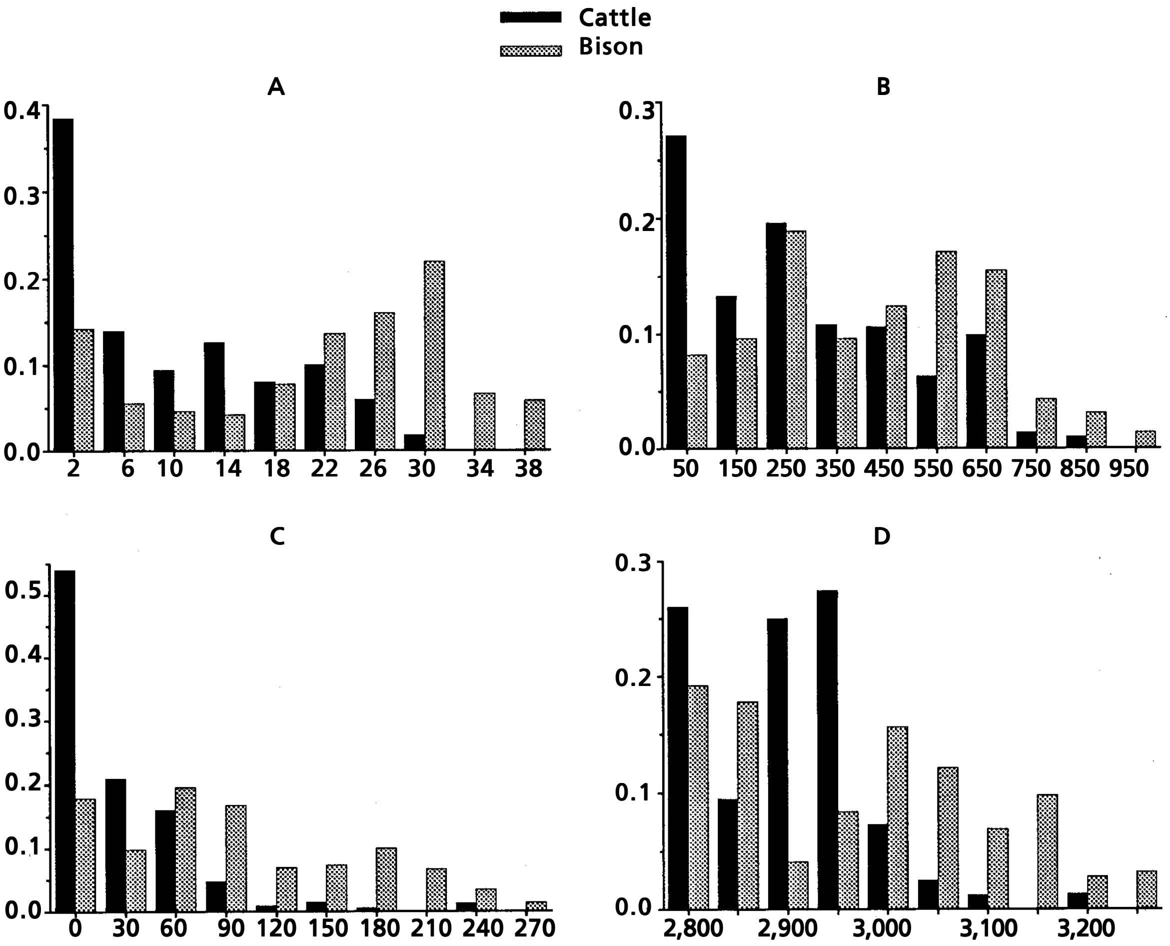

Fig. 1. Proportion of observations of foraging bison and cattle in relation to: A. Slope, in degrees; B. Horizontal distance from water, in m; C. Vertical distance from water, in m; D. Elevation, in m, at the headwaters of South Creek, Henry Mountains, Utah.

Fig. 1. Proporción de observaciones de forrajeo del bisonte y del ganado vacuno en relación con: A. Inclinación del terreno, en grados; B. Distancia horizontal al agua, en m; C. Distancia vertical al agua, en m; D. Altura, en m, de la cabecera del río South Creek, Henry Mountains, Utah.

1998). Moreover, cattle have undergone intense artificial selection for traits that maximize productivity. Maximizing fat storage for overwinter survival probably is less important because cattle are herded to pastures known to provide sufficient forage, or they are supplementally provisioned. Bison, in contrast, face the risk of starvation during harsh winters (MEAGHER, 1986), thus they exhibit adaptations for overwinter survival superior to those of cattle (HAWLEY, 1987; PLUMB & DODD, 1993).

Cattle distribution was most constrained by slope and vertical distance from water. Both involve movement in a vertical plane, which is roughly 10 times more expensive energetically than horizontal movement (CLAPPERTON, 1964; BROCKWAY & GESSAMAN, 1977; PARKER et al., 1984), suggesting that cattle were minimizing their foraging costs. Increased travel costs result in reduced productivity (HOLECHEK et al., 1989). Consequently, cattle appeared to be following a strategy of meeting their energetic needs with least overall cost, a strategy reported for kudu (*Tragelaphus strepsiceros*; OWEN–SMITH, 1994). The result was that cattle behaved as central place foragers, with grazing activity centered on a water source or perhaps on thermal cover, but not on the feeding site (ROATH & KRUEGER, 1982; STUTH, 1991; GUTHERY, 1996). Forage is depleted on gentle slopes near water, but cattle foraging there evidently can meet their energetic needs with minimal energy expenditure. Bison, in

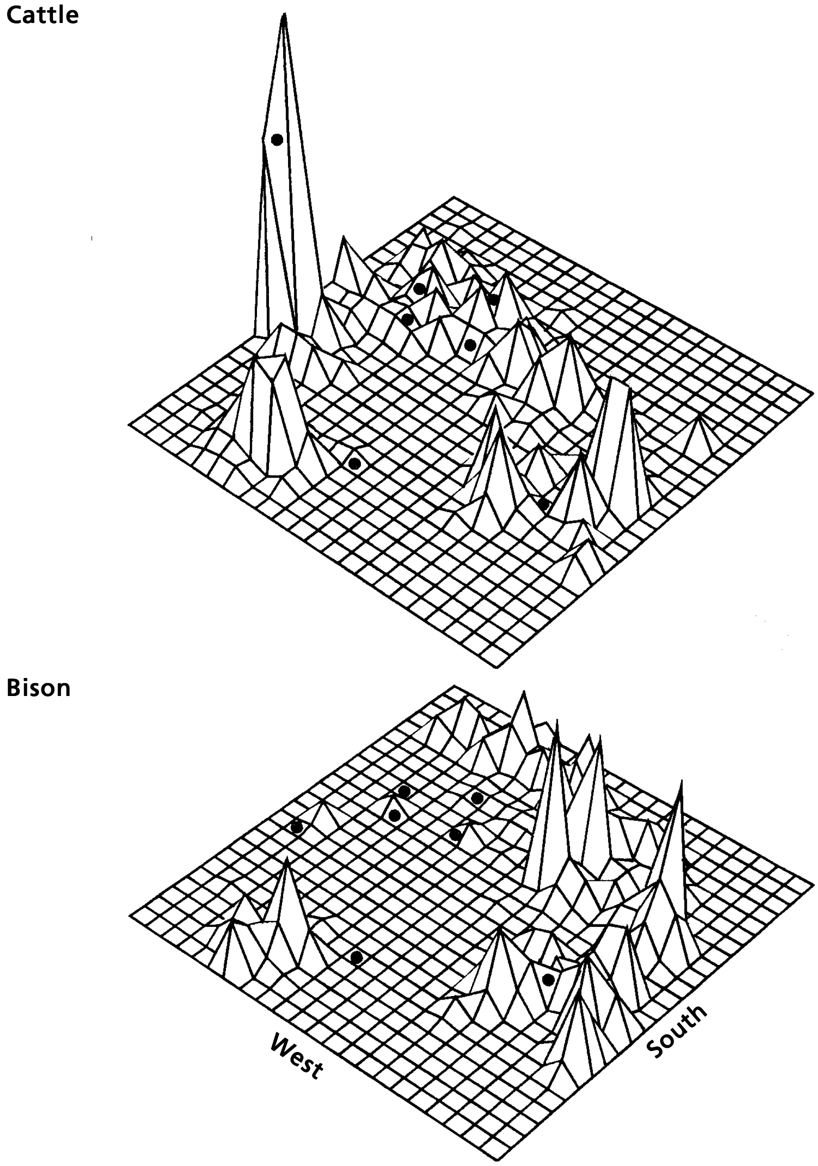

Fig. 2. Three–dimensional mesh plots of the foraging distributions of bison and cattle at the headwaters of South Creek, Henry Mountains, Utah. The *z*–coordinate indicates frequency of occurrence in each grid square. Slope and elevation increase from west to east, and water sources are denoted by black circles.

Fig. 2. Gráfico en malla tridimensional de la distribución de pasto del bisonte y del ganado vacuno en las cabeceras del río South Creek, Henry Mountains, Utah. La coordenada z indica la frecuencia de forrajeo en cada cuadrícula. La inclinación y la altura aumentan de oeste a este, las fuentes de agua se indican con círculos negros.

contrast, behaved as energy maximizers, willing to expend energy to obtain richer rewards, with grazing activity oriented on the feeding site rather than on a water source. Bison typically rested within or adjacent to the feeding site, traveled once per day to water and drank briefly ($\bar{x}$ = 21 minutes), then returned to the feeding site or moved to a new one (Van Vuren, 1980). Bison moved much more than cattle; most cattle remained within the 375–ha basin throughout the summer, whereas bison roamed about home ranges that averaged 5,220 ha (Van Vuren, 1983), rarely remaining in the same area longer than 3 days (Van Vuren, 1980).

Spatial segregation of sympatric bison and cattle on montane ranges during summer, resulting from differential response to environmental factors, has important implications for conservation. If bison replace cattle, managers can expect a more even distribution of grazing pressure in response to forage availability, with little evidence of a piosphere, instead of a clumped distribution in response to slope and distance from water.

Bison and cattle might even be managed sympatrically; although their diets are generally similar, their spatial distributions may be sufficiently different not only to minimize competition for food, but also to reduce the risk of transmission of diseases requiring close spatial proximity.

Acknowledgments

I thank the U. S. Bureau of Land Management, Utah Division of Wildlife Resources, Mzuri Safari Foundation, and Sigma Xi for financial and logistical support; Marty Bray, Bruce Coblentz, and Golden and Keith Durfey for assistance throughout the study; and Vickie Bakker, Chris Floyd and Rob Klinger for helpful comments on the manuscript.

References

Andrew, M. H., 1988. Grazing impact in relation to livestock watering points. *Trends Ecol. & Evol.*, 3: 336–339.

Brockway, J. M. & Gessaman, J. A., 1977. The energy cost of locomotion on the level and on gradients for the red deer (*Cervus elaphus*). *Quart. J. Exp. Physiol.*, 62: 333–339.

Cahalane, V. H., 1947. *Mammals of North America*. MacMillan Company, New York.

Callenbach, E., 1996. *Bring back the buffalo!* Island Press, Washington, DC.

Campbell, C., Blyth, C. B. & McAndrews, J. H., 1994. Bison extirpation may have caused aspen expansion in western Canada. *Ecography*, 17: 360–362.

Clapperton, J. L., 1964. The energy metabolism of sheep walking on the level and on gradients. *Brit. J. Nutr.*, 18: 47–54.

Dary, D. A., 1989. *The buffalo book*. Swallow Press/Ohio University Press, Athens, Ohio.

Frank, D. A. & McNaughton, S. J., 1993. Evidence for the promotion of aboveground grassland production by native large herbivores in Yellowstone National Park. *Oecologia*, 96: 157–161.

Frank, D. A., McNaughton, S. J. & Tracy, B. F., 1998. The ecology of the Earth's grazing ecosystems. *Bioscience*, 48: 513–521.

Fryxell, F. M., 1928. The former range of the bison in the Rocky Mountains. *J. Mammal.*, 9: 129–139.

Fryxell, J. M., Greever, J. & Sinclair, A. R. E., 1988. Why are migratory ungulates so abundant? *Am. Nat.*, 131: 781–798.

Fryxell, J. M. & Sinclair, A. R. E., 1988. Causes and consequences of migration by large herbivores. *Trends Ecol. & Evol.*, 3: 237–241.

Ganskopp, D. & Vavra, M., 1987. Slope use by cattle, feral horses, deer, and bighorn sheep. *Northwest Sci.*, 61: 74–81.

Gillen, R. L., Krueger, W. C. & Miller, R. F., 1984. Cattle distribution on mountain rangeland in northwestern Oregon. *J. Range Manage.*, 37: 549–553.

Guthery, F. S., 1996. Upland gamebirds. In: *Rangeland wildlife:* 59–69 (P. R. Krausman, Ed.). Society for Range Management, Denver.

Hamilton, R. G., 1996. Using fire and bison to restore a functional tallgrass prairie landscape. *Trans. N. Am. Wildl. & Nat. Resour. Conf.*, 61: 208–214.

Hartnett, D. C., Steuter, A. A. & Hickman, K. R., 1997. Comparative ecology of native and introduced ungulates. In: *Ecology and conservation of Great Plains vertebrates:* 72–101 (F. L. Knopf & F. B. Samson, Eds.). Springer–Verlag, New York.

Hawley, A. W. L., 1987. Bison and cattle use of forages. In: *Bison ecology in relation to agricultural development in the Slave River lowlands, NWT.* Occasional Paper 63,: 49–52 (H. W. Reynolds & A. W. L. Hawley, Eds.). Canadian Wildlife Service, Edmonton.

Holechek, J. L., Pieper, R. D. & Herbel, C. H., 1989. *Range management*. Prentice Hall, Englewood Cliffs.

Knapp, A. K., Blair, J. M., Briggs, J. M., Collins, S. L., Hartnett, D. C., Johnson, L. C. & Towne, E. G., 1999. The keystone role of bison in North American tallgrass prairie. *Bioscience*, 49: 39–50.

Krueger, K., 1986. Feeding relationships among bison, pronghorn, and prairie dogs: an experimental analysis. *Ecology*, 67: 760–770.

Manning, R., 1996. The buffalo is coming back. *Defenders*, 71(1): 6–15.

Meagher, M. M., 1986. *Bison bison. Mammal. Spec.*, 266: 1–8.

Meaney, C. A. & Van Vuren, D., 1993. Recent distribution of bison in Colorado west of the Great Plains. *Proc. Denver Mus. Nat. Hist.*, 3(4): 1–10.

Mueggler, W. F., 1955. Cattle distribution on steep slopes. *J. Range Manage.*, 18: 255–257.

Nash, M. S, Whitford, W. G., De Soyza, A. G., Van Zee, J. W. & Havstad, K. M., 1999. Livestock activity and Chihuahuan Desert annual–plant communities: boundary analysis of disturbance gradients. *Ecol. Applic.*, 9: 814–823.

Noss, R. F. & Cooperrider, A. Y., 1994. *Saving nature's legacy*. Island Press, Washington, DC.

Norton–Griffiths, M., 1995. Economic incentives to develop the rangelands of the Serengeti:

implications for wildlife conservation. In: *Serengeti II: dynamics, management and conservation of an ecosystem:* 588–604 (A. R. E. Sinclair & P. Arcese, Eds.). University of Chicago Press, Chicago.

OOSTING, H. J., 1956. *The study of plant communities*, 2nd ed. W. H. Freeman, San Francisco.

OWEN–SMITH, O., 1994. Foraging responses of kudus to seasonal changes in food resources: elasticity in constraints. *Ecology*, 75: 1,050–1,062.

PARKER, K. L., ROBBINS, C. T. & HANLEY, T. A., 1984. Energy expenditures for locomotion by mule deer and elk. *J. Wildl. Manage.*, 48: 474–488.

PEDEN, D. G., VAN DYNE, G. M., RICE, R. W. & HANSEN, R. M., 1974. The trophic ecology of *Bison bison* L. on shortgrass plains. *J. Appl. Ecol.*, 11: 489–497.

PINCHAK, W. E., SMITH, M. A., HART, R. H. & WAGGONER, J. W. JR., 1991. Beef cattle distribution patterns on foothill range. *J. Range Manage.*, 44: 267–275.

PLUMB, G. E. & DODD, J. L., 1993. Foraging ecology of bison and cattle on a mixed prairie: implications for natural area management. *Ecol. Applic.*, 3: 631–643.

REYNOLDS, H. W. & HAWLEY, A. W. L., 1987. Introduction. In: *Bison ecology in relation to agricultural development in the Slave River lowlands, NWT,* Occasional Paper 63*:* 10–12 (H. W. Reynolds & A. W. L. Hawley, Eds.). Canadian Wildlife Service, Edmonton.

ROATH, L. R. & KRUEGER, W. C., 1982. Cattle grazing and behavior on a forested range. *J. Range Manage.*, 35: 332–338.

ROE, F. G., 1970. *The North American buffalo*, 2nd ed. University of Toronto Press, Toronto.

SENFT, R. L., RITTENHOUSE, L. R. & WOODMANSEE, R. G., 1983. The use of regression models to predict spatial patterns of cattle behavior. *J. Range Manage.*, 36: 553–557.

STEINAUER, E. M. & COLLINS, S. L., 2001. Feedback loops in ecological hierarchies following urine deposition in tallgrass prairie. *Ecology*, 82: 1,319–1,329.

STEPHENSON, R. O. & FLEENER, C. L., 1998. Biopolitical perspectives on a proposed wood bison reintroduction to Alaska. In: *International symposium on bison ecology and management in North America:* 251–257 (L. Irby & J. Knight, Eds.). Montana State University, Bozeman.

STUTH, J. W., 1991. Foraging behavior. In: *Grazing management:* 65–83 (R. K. Heitschmidt & J. W. Stuth, Eds.). Timber Press, Portland.

TELFER, E. S., 1994. Cattle and cervid interactions on a foothills watershed in southwestern Alberta. *Can. Field–Nat.*, 108: 186–194.

VAN VUREN, D., 1980. Ecology and behavior of bison in the Henry Mountains, Utah. M. S. Thesis, Oregon State University.

– 1982. Comparative ecology of bison and cattle in the Henry Mountains, Utah. In: *Proceedings of the wildlife–livestock relationships symposium:* 449–457 (J. M. Peek & P. D. Dalke, Eds.). University of Idaho Forestry, Wildlife & Range Experiment Station, Moscow, Idaho.

– 1983. Group dynamics and summer home range of bison in southern Utah. *J. Mammal.*, 64: 329–332.

– 1984. Summer diets of bison and cattle in southern Utah. *J. Range Manage.*, 37: 260–261.

– 1987. Bison west of the Rocky Mountains: an alternative explanation. *Northwest Sci.*, 61: 65–69.

VAN VUREN, D. & BRAY, M. P., 1986. Population dynamics of bison in the Henry Mountains, Utah. *J. Mammal.*, 67: 503–511.

VAN VUREN, D. & SCOTT, C. A., 1995. Internal parasites of sympatric bison, *Bison bison*, and cattle, *Bos taurus*. *Can. Field–Nat.*, 109: 467–469.

WAGNER, F. H., 1978. Livestock grazing and the livestock industry. In: *Wildlife and America:* 121–145 (H. P. Brokaw, Ed.). Council on Environmental Quality, Washington, DC.

WARREN, E. R., 1927. Altitude limit of bison. *J. Mammal.*, 8: 60–61.

WUERTHNER, G., 1993. Envisioning wildland restoration. *Wild Earth*, 3(3): 70–74.

– 1998. Are cows just domestic bison? Behavioral and habitat use differences between cattle and bison. In: *International symposium on bison ecology and management in North America:* 374–383 (L. Irby & J. Knight, Eds.). Montana State University, Bozeman.