

The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle

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Abstract. The Great Plains of North America evolved with significant influence from bison (*Bison bison*), but is presently dominated by cattle (*Bos taurus*). While there are a variety of opinions concerning differences between these two species, there is a lack of scientific comparisons, including those that incorporate important ecological variation. We developed a framework to study and compare the grazing behavior and effects of bison and cattle within grassland ecosystems. Environmental (e.g., resource distribution, disturbance) and animal (e.g., number, social organization) factors play a critical role in determining grazing effects and should be incorporated into discussions that compare the effects of bison and cattle. Using this framework we specifically compare the grazing behavior of both species in tallgrass prairie and discuss the implications of these differences in the context of conservation. We collared bison and cattle with global positioning systems and used resource selection functions to estimate the importance of various environmental factors on site selection. Both species preferred recently burned areas and avoided steeper slopes. Cattle selected areas that were closer to water, while bison were not limited by distance to water; cattle also preferred areas with woody vegetation, while bison avoided them. Incorporating broad scale environmental complexity allows for an effective comparison of ecological differences between bison and cattle. While there are similarities and differences in these species, a comprehensive analysis of all conditions and scenarios is not possible. It is clear, however, that the greatest differences between these species will likely be evident from broad scale studies across complex landscapes. In addition to species, conservation and land managers need to consider other environmental factors that are critical to grazing effects and overall conservation.

Key words: fire; grassland; grazing; herbivory; restoration; species comparisons; tallgrass prairie.

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INTRODUCTION

The role of herbivores in grassland ecosystems has been an important topic debated by ecologists and ecosystem managers for more than a century. The Great Plains of North America are central to this discussion as most flora and fauna evolved with significant impact from large herbivores and other disturbances (Axelrod 1985, Anderson 2006). Until their near extirpa-

tion in the late 1800s, American Bison (*Bison bison*) were keystone herbivores within the Great Plains, sharing complex landscapes with other herbivores and predators for nearly 10,000 years (Knapp et al. 1999, Anderson 2006). Since their near extinction, the vast and complex landscapes that contained the roaming herds have been replaced by fragmented agricultural lands where domestic cattle are the dominant grazers. Restoration and conservation of bison has been

pursued by private citizens, conservation organizations, and government agencies with a primary goal of conserving the species and restoring critical ecosystem processes and functions.

Grazing by large herbivores can affect a system in many different ways (Milchunas et al. 1988, Augustine and McNaughton 1998, Anderson et al. 2006). The effects of grazing are often viewed in isolation of each other, removing all complexity and variation besides that of grazing. Such work has enhanced the understanding and management of grasslands. The evolutionary effects of grazing, however, are much more complex than traditional, small scale experimental designs can replicate (Levin 1992, Fuhlendorf et al. 2009). Grazing is a dynamic process that interacts with complex landscapes to form disturbance patterns that are critical to many ecosystem functions, including biodiversity (Collins et al. 1998, Tews et al. 2004). Because of this, the effects of grazing are influenced by many factors, including those associated with animals and the environment.

The species of animal alone is not the only determinant of grazing effects. Age, sex, number, and social organization of animals contribute to altering behavior and ecological influences. In addition to the structure of the grazer community, environmental factors (e.g., disturbances, climate, predation, resources) will also contribute to grazing effects. When discussing grazing or grazing behavior, a traditional reductionist approach is to focus on one factor without considering the complexity of other factors. In the Great Plains of North America, ecologists, conservation biologists, and land managers have studied and debated the effects of grazing by bison and domestic cattle (*Bos taurus*), often without including other interacting factors (Hartnett et al. 1997, Steuter and Hidingier 1999). Common managerial differences associated with bison and cattle also confound differences in effects between the two species (Towne et al. 2005). Cattle herds are often associated with ranches that are based on commodity production, where animals are commonly separated for most of the year based on sex or age (e.g., cows and calves, bulls). In the Great Plains of North America, cattle are rarely, if ever, managed as wildlife or with a conservation focus. Bison, on

the other hand, may be managed as either production or conservation herds.

While similarities and differences between cattle and bison are widely discussed and debated, the peer reviewed literature comparing the two is largely inconclusive. For example, in popular press, government reports, and scientific literature, it is often stated that bison spend less time near water or riparian areas than cattle (Manning 1995, Hartnett et al. 1997, Fritz et al. 1999, Reynolds et al. 2003, National Park Service 2009). Indeed, van Vuren (1982) found a greater percentage of observations of cattle closer to water than bison. Unfortunately, it is apparent that the confounding management strategies of the two species were not taken into account, specifically with regard to stocking rate or animal density: “a herd of about 300 wild bison ... shares its summer range with several hundred range cattle” (van Vuren 1982). With no clear definition of how many animals were present or specific management plans for each species, a reliable conclusion cannot be made. Direct comparisons of foraging ecology or behavior between bison and cattle have also been minimal. Plumb and Dodd (1993) found that in general, bison spent less time feeding with shorter grazing bouts than cattle, but had greater number of bouts per day.

We argue that recognizing ecological differences between bison and cattle would be best studied on large, complex landscapes that do not limit behavior to finer scales (Holland et al. 2004, Boyce 2006, Bowyer and Kie 2006). Incorporating landscape variability will allow for a more effective comparison of grazing behavior and effects between bison and cattle, as animals can interact with environmental factors that contribute to grazing effects. We describe the design, results, and limitations of a current study comparing bison and cattle behavior on complex landscapes that include other disturbances (e.g., fire). We then develop a conceptual model to facilitate the discussion of the conservation value of reintroducing bison within human dominated landscapes of the Great Plains.

METHODS

The Tallgrass Prairie Preserve: a model for experimental design

The Nature Conservancy Tallgrass Prairie Preserve, located in northeast Oklahoma, USA, is a 16,000 ha natural area that is managed for biodiversity and heterogeneity (Hamilton 2007). The preserve lies at the southern end of the Flint Hills of the Great Plains. Vegetation is classified as tallgrass prairie, with small patches of cross timbers forest. Dominant grasses include *Andropogon gerardii* Vitman, *Schizachyrium scoparium* (Michx.) Nash, *Panicum virgatum* L., and *Sorghastrum nutans* (L.) Nash. Crosstimbers vegetation is dominated by *Quercus stellata* Wang. and *Q. marilandica* Münchh. Precipitation and various climate measurements are measured on site by an Oklahoma Mesonet station (Brock et al. 1995). Total precipitation for April through September for 2009 and 2010 (time period of study) was 64.7 and 72.5 cm, respectively. Long term mean total for April through September is 62.2 cm (14.94 standard deviation).

Within the site, there is one large bison unit (9532 ha) and seven smaller cattle units (430–980 ha) (Fig. 1). Only perimeter fences are present and animals are free to roam within their respective units. There is minimal handling of both bison and cattle with no supplemental feeding. Bison are maintained in their respective unit all year; herd size is approximately 2,300 animals. Sex ratio of the bison herd is approximately seven females per male; ages of females range from 0–10 years, while males are 0–6 years. Cattle units are stocked with stocker steers approximately one year old (mixed European breeds); cattle are only present April through September. Cattle herds vary with each unit, ranging from 169 to 463 animals. Bison and cattle units are stocked with similar moderate stocking rates (bison: 2.1 AUM/ha; cattle: 2.4 AUM/ha). The entire preserve is managed extensively with fire and in such way that fire and grazing are allowed to interact (Hamilton 2007, Fuhlendorf et al. 2009). Bison and cattle units are shifting mosaics with fire occurring in discrete portions of the landscape (Fig. 1). Fire-grazing interactions become present as animals select between recently burned areas and those with greater time since fire (Archibald et al. 2005, Fuhlendorf et al. 2009).

To specifically examine herbivore site selection, we deployed global positioning system (GPS) collars on seven female bison (four to six years in age) from November 2008 through November 2010 and seven cattle (steers, one year in age; one per unit) from April through September of 2009 and 2010. For bison, GPS batteries were replaced and new animals chosen in November 2009; for cattle, new animals were chosen and new batteries used in April 2010. We recorded location information of animals at two different frequencies, alternately weekly from 12 minutes to one hour. Schedule of GPS fixes was equal for bison and cattle. We imported all GPS location data into a spatially enabled database (PostgreSQL/PostGIS) and reduced bison data to match that of cattle (April–September). We mapped treatment unit perimeters, fire histories, and water sources (ponds and streams) with handheld GPS units, aerial photographs, and United States Geological Survey 7.5 minute topographic maps. Slope and aspect were calculated from digital elevation models for the area (United States Geological Survey; 10 m resolution). We transformed aspect data by simple trigonometric functions; two variables were created, northing = cosine(aspect) and easting = sin(aspect). Herbaceous and woody vegetation was determined for the site using a GeoEye-1 satellite image acquired September 20, 2009.

We compared similarity of units by randomly placing 1,000 sampling points within each unit. At each sampling point, distance to water, distance to patch edge, distance to woody vegetation, slope, northing, and easting were calculated. Measured characteristics among animal units were compared individually using analysis of variance and did not differ between units ($P > 0.05$). We used Ivlev electivity indices (Ivlev 1961, Jacobs 1974) to evaluate the use of riparian areas by bison and cattle. Riparian areas were defined by putting a 20 and 40 m buffer around all mapped water sources. We calculated electivity indices using the formula $E_i = (r_i - p_i) / (r_i + p_i)$ where r_i is the fraction of GPS locations recorded in a riparian area by animal i and p_i is the fraction of area enclosed by the sum of buffers available to animal i . A value of +1 indicates complete preference to riparian areas, while a value of -1 indicates complete avoidance. Indices were calculated for each collared bison

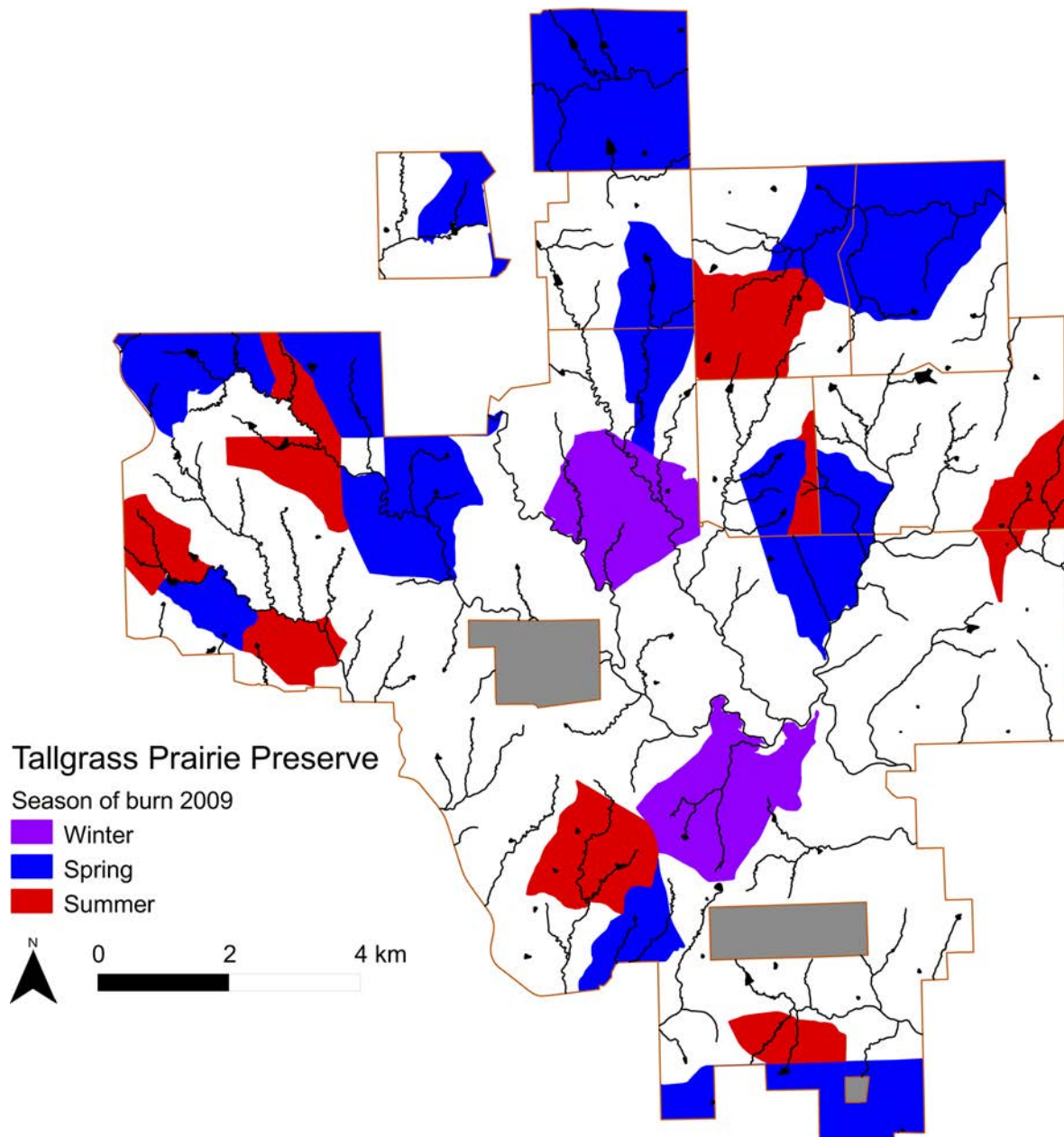


Fig. 1. Map of prescribed fire and water distribution within bison and cattle units at The Nature Conservancy Tallgrass Prairie Preserve, OK, USA, September 2009. Solid orange lines represent perimeter fences and delineate units. Black interior lines and areas represent water sources. Gray areas inside bison unit represent inholdings which bison cannot access. The large southern unit is 9532 ha in size and contains bison year round. The northern units are 430–980 ha in size and contains mixed European breeds of cattle April–September. Differing colors represent season of burn for 2009 and illustrate the patchiness of fire. Patches from previous years are not shown, but vary from one to five years since fire. Grazing animals have free access to all burns within their respective units (no internal fences present).

and cattle individual, separating water sources into ponds, streams, and pond/stream combination. Indices between bison and cattle were compared for each size riparian area (i.e., 20 and 40 m) using a *t*-test. We also used Ivlev electivity indices to compare bison and cattle preferences for recently burned areas (six months or less since fire). We calculated indices for each collared animal based upon recently burned area available; we compared indices using a *t*-test.

To examine the influence of environmental factors on the grazing behavior of bison and cattle, we estimated resource selection functions using mixed-effect logistic regression models (used/available design; Boyce et al. 2002, Manly et al. 2002). To depict available habitat, we created five random locations for each observed location. We calculated the amount of time since fire, distance to water, distance to fire patch edge, slope, northing, and easting for all locations. We also classified each location as herbaceous or woody vegetation. To determine if the presence of woody vegetation is confounded with water sources (i.e., the presence of woody vegetation is primarily near water sources), we quantified the distribution of woody vegetation around water sources. The percentage of woody vegetation within 20 and 40 m of water sources across the site was 3% and 7%, respectively. Furthermore, we examined variables for collinearity and found none ($r^2 < 0.27$ for all variable combinations), indicating that variables are not confounding with one another (i.e., woody vegetation is not limited near water sources). To account for variation among individual animals within resource selection functions, individuals were included as a random intercept within logistic regressions. To account for fire availability among units and potential response variation to fire, time since fire and its interaction with other variables (e.g., time since fire $\times$ distance to water; see below) were included as random slopes within logistic regressions (Gillies et al. 2006).

We created models using various combinations of environmental factors; as the influence of time since fire is likely to be highly influential (Vinton et al. 1993, Fuhlendorf and Engle 2004, Archibald et al. 2005), we included interaction terms for this variable with all others individually (i.e., time since fire $\times$ distance to water, time since fire $\times$ slope, etc.). In all models with interaction terms,

main effects of both variables were included. To allow for comparison of environmental factors and to more easily interpret interaction terms, we standardized variables by subtracting the mean and dividing by the standard deviation (Gelman and Hill 2007). We compared and ranked models using Akaike information criterion (AIC; Burnham and Anderson 2002). We used bootstrapping procedures to further estimate the precision of resource selection coefficients of the top ranked model. We calculated 95% confidence intervals of coefficients after 1,000 iterations of randomly sampled datasets. To further examine variation among individual animal behavior, we calculated resource selection functions for each animal per year (28 animals total) using top ranked models. We performed all analyses in R (R Development Core Team 2009) with additional use of the *lme4* (Bates and Maechler 2010), *doMPI* (Weston 2009), *foreach* (Revolution Computing 2009) and *Rmpi* (Yu 2010) packages.

RESULTS

Of bison locations, 9 and 15% fell within riparian areas of size 20 and 40 m, respectively (ponds and streams combined). Of cattle locations, 13 and 20% fell within riparian areas of size 20 and 40 m, respectively. Mean Ivlev electivity indices of riparian areas varied significantly between bison and cattle with all water sources and riparian area sizes ($P < 0.01$; Fig. 2). Cattle had a greater preference for ponds (Fig. 2A), while bison avoided streams (Fig. 2B). When ponds and streams were combined, bison had a small avoidance of water, while cattle had a greater preference for it (Fig. 2C). These data show the difference between bison and cattle in their use of water and riparian areas, in similar fire-managed landscapes with abundant water.

Bison and cattle strongly preferred recently burned patches (Table 1). Mean percentages of GPS locations in areas with six months or less since fire did not vary between bison and cattle ($P = 0.11$). With bison, 68% of locations were found in recently burned areas (less than six months), while cattle were 58%. The amount of area burned within six months was approximately 25% of the landscape in both bison and cattle units. Bison and cattle were nearly three times likely to be in a burned area than by random

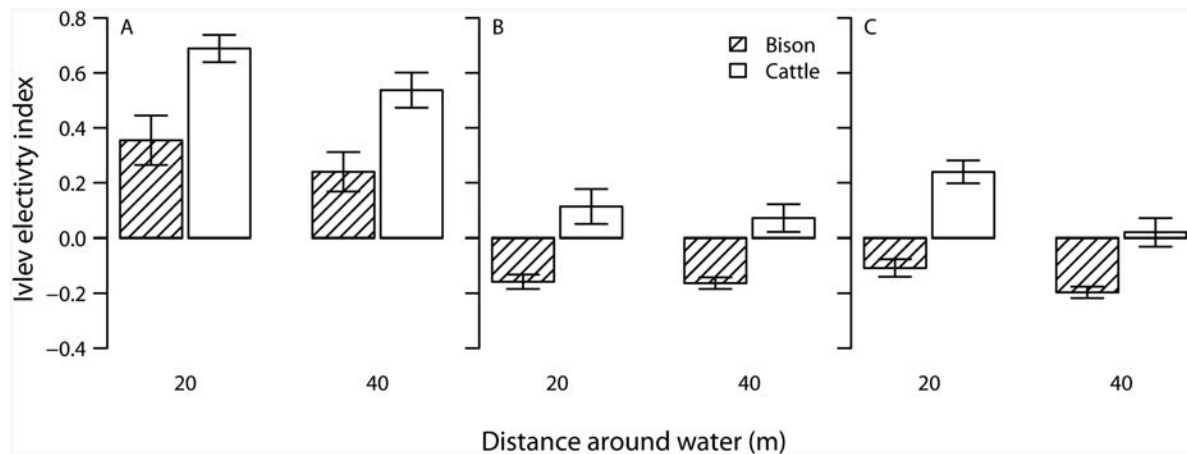


Fig. 2. Ivlev electivity indices for riparian areas, separated by bison and cattle at the Tallgrass Prairie Preserve, OK, USA. Bars are means ($n = 14$; animals), error bars are one standard deviation. Potential values range from -1 (complete avoidance) to $+1$ (complete preference). Distance around water indicates the size of buffer placed around water sources. A) Ivlev electivity indices for ponds only, separated by bison and cattle. Cattle preferred riparian pond areas more than bison. B) Ivlev electivity indices for streams only, separated by bison and cattle. Cattle preferred riparian stream areas more than bison; bison demonstrated a small avoidance to riparian stream areas. C) Ivlev electivity indices for ponds and streams combined, separated by bison and cattle. Cattle preferred all riparian areas more than bison; bison demonstrated a small avoidance to all riparian areas. Mean electivity indices of riparian areas varied significantly between bison and cattle for all water sources and buffer sizes ($P < 0.01$).

Table 1. Percentage of individual bison and cattle locations and annual means and confidence intervals (95%; bottom row) in recently burned areas (six months or less) at the Tallgrass Prairie Preserve, OK, USA, April through September 2009 and 2010.

Bison 2009	Bison 2010	Cattle 2009	Cattle 2010
68.3	64.1	78.6	42.4
71.5	59.1	55.7	88.7
69.1	66.9	77.5	100.0 [†]
68.8	67.8	60.8	73.2
75.3	69.0	25.0	55.0
66.2	65.2	100.0 [†]	37.4
75.1	75.1	67.6	40.6
70.6 (2.6)	66.7 (3.6)	60.9 (15.8)	56.2 (16.5)

[†]Due to fire patch design; not included in mean or confidence interval calculation.

chance alone. Mean Ivlev electivity indices of recently burned areas were 0.57 (0.01) and 0.43 (0.15) for bison and cattle, respectively (standard deviations in parentheses); indices did not differ between species ($P = 0.12$).

Estimation of resource selection functions permitted a detailed examination of environmental factors that influence selection behavior. Of models examined, the combination of interaction terms of time since fire with all variables (less northing and easting) appeared to have the best

fit for both bison and cattle (Table 2). Resource selection functions for bison revealed that time since fire had the strongest influence in determining site selection. Furthermore, bison tended to avoid steeper slopes and wooded areas. Distance to water did not influence selection (Table 3). Interactions of time since fire with other environmental factors indicates the connectedness of fire with grazing behavior. The influence of time since fire increased as slope and distance to patch edge increased; conversely, the influence

Table 2. The difference in Akaike information criterion (Δ AIC) and the number of parameters (K) for varying models of resource selection for bison and cattle at the Tallgrass Prairie Preserve, OK, USA; model parameters include distance to water (*water*; m), distance to patch edge (*edge*; m), slope (*slope*; degrees), northing (*north*; degrees), easting (*east*; degrees), wooded area (*wood*), and time since fire (*tsf*; days).

Model	K	Δ AIC
Bison		
<i>tsf</i> $\times$ <i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i> + <i>tsf</i> $\times$ <i>north</i> + <i>tsf</i> $\times$ <i>east</i>	15	1.8
<i>tsf</i> $\times$ <i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i> + <i>north</i> + <i>east</i>	13	0.00
<i>tsf</i> $\times$ <i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i>	10	2.7
<i>tsf</i> $\times$ <i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>wood</i>	11	3.8
<i>tsf</i> $\times$ <i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i>	10	4006.4
<i>tsf</i> $\times$ <i>water</i> + <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i>	10	882.4
<i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i>	10	505.7
<i>tsf</i> + <i>water</i> + <i>slope</i> + <i>edge</i> + <i>wood</i>	7	6328.7
Cattle		
<i>tsf</i> $\times$ <i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i> + <i>tsf</i> $\times$ <i>north</i> + <i>tsf</i> $\times$ <i>east</i>	15	3.26
<i>tsf</i> $\times$ <i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i> + <i>north</i> + <i>east</i>	13	0.00
<i>tsf</i> $\times$ <i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i>	10	2.71
<i>tsf</i> $\times$ <i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>wood</i>	11	15.89
<i>tsf</i> $\times$ <i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i>	10	126.34
<i>tsf</i> $\times$ <i>water</i> + <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i>	10	42.78
<i>water</i> + <i>tsf</i> $\times$ <i>slope</i> + <i>tsf</i> $\times$ <i>edge</i> + <i>tsf</i> $\times$ <i>wood</i>	10	329.18
<i>tsf</i> + <i>water</i> + <i>slope</i> + <i>edge</i> + <i>wood</i>	7	451.37

Notes: We included main effects in all models with interaction terms. Interaction terms represented with $\times$.

Table 3. Estimated resource selection function coefficients of the top ranked model for bison and cattle at the Tallgrass Prairie Preserve, OK, USA; model parameters include distance to water (*water*; m), distance to patch edge (*edge*; m), slope (*slope*; degrees), northing (*north*; degrees), easting (*east*; degrees), wooded area (*wood*), and time since fire (*tsf*; days).

Parameter	Estimate†	SE	Z value	P	CI‡
Bison					
intercept	-1.8460	0.120	-15.34	<0.01	(-1.8513, -1.8384)
time since fire	-1.5521	0.353	-4.40	<0.01	(-1.5538, -1.5509)
distance to water	0.0324	0.007	4.51	<0.01	(0.0316, 0.0328)
slope	-0.5785	0.011	-49.59	<0.01	(-0.5793, -0.5778)
distance to patch edge	-0.3351	0.009	-35.87	<0.01	(-0.3360, -0.3344)
woody vegetation	-1.9116	0.077	-24.53	<0.01	(-1.9164, -1.9092)
northing	-0.0117	0.005	-2.33	0.02	(-0.0120, -0.0115)
easting	0.0246	0.005	4.87	<0.01	(0.0242, 0.0251)
time since fire $\times$ distance to water	0.1548	0.007	19.48	<0.01	(0.1543, 0.1550)
time since fire $\times$ slope	-0.3814	0.013	-28.23	<0.01	(-0.3818, -0.3809)
time since fire $\times$ distance to patch edge	-0.5412	0.011	-48.86	<0.01	(-0.5420, -0.5408)
time since fire $\times$ woody vegetation	0.0509	0.041	1.24	0.21	(0.0478, 0.0549)
Cattle					
intercept	-0.8892	0.644	-1.38	0.16	(-0.8963, -0.8824)
time since fire	-1.2611	0.313	-4.03	<0.01	(-1.2621, -1.2602)
distance to water	-0.0768	0.006	-11.11	<0.01	(-0.0785, -0.0755)
slope	-0.1696	0.007	-21.50	<0.01	(-0.1699, -0.1691)
distance to patch edge	-0.5019	0.011	-42.44	<0.01	(-0.5025, -0.5015)
woody vegetation	1.4398	0.053	27.16	<0.01	(1.4390, 1.4404)
northing	-0.0044	0.005	-0.84	0.40	(-0.0048, -0.0040)
easting	-0.0109	0.005	-2.08	0.03	(-0.0112, -0.0107)
time since fire $\times$ distance to water	-0.0514	0.059	-2.08	0.03	(-0.0520, -0.0511)
time since fire $\times$ slope	0.0199	0.049	0.40	0.68	(-0.0210, -0.0190)
time since fire $\times$ distance to patch edge	-0.2667	0.219	1.22	0.22	(-0.2692, -0.2648)
time since fire $\times$ woody vegetation	0.4213	0.382	1.10	0.27	(0.4201, 0.4219)

†Standardized variables are shown for coefficient comparison and interaction term interpretation.

‡Confidence interval (95%) calculated from bootstrapping procedures (1,000 iterations).

of time since fire decreased as woody vegetation and distance to water increased. This decrease is minimal due to the initial strong influence of fire. The probability of selection for bison, based upon time since fire, distance to water, and the interaction of those two factors, is displayed in Fig. 3. In recently burned areas, bison avoid water slightly; in areas with greater time since fire, bison are not influenced by water.

Similar to bison, cattle also selected recently burned areas and avoided steeper slopes. Unlike bison, however, the most influential environmental factor was the preference of woody vegetation. Moreover, cattle appeared to minimize distance to water, opposite that of bison (Table 3). Interactions of time since fire with other variables further shows the importance of fire to understanding grazing within these ecosystems. As distance to water and patch edge increase, so does the influence of time since fire; the presence of woody vegetation, however, decreases the influence of time since fire. The probability of selection for cattle, based upon time since fire, distance to water, and the interaction of the two, is displayed in Fig. 4. Cattle minimize their distance to water in both recently burned areas and areas with greater time since fire.

Resource selection functions for individual animals revealed variation in site selection (Table 4). Though individual animals generally followed trends indicated by the population model, cattle tended to be more variable in their response to environmental factors. Individual bison and cattle still strongly preferred recently burned areas (minimizing the amount of time since fire), but the response of cattle varied considerably among individuals. All individual cattle minimized their distance to water, while only three bison did so. Other factors, including interactions with time since fire, varied among animals. Because different animals were chosen each year, we cannot separate the variation among animals and the variation between years.

DISCUSSION

The design of this study more effectively permits comparisons between bison and cattle, both in examining grazing behavior differences between the species (results presented here) and their ecological effects (e.g., plant response, water

quality, etc.; data not collected). Our design incorporates more of the variability found in complex landscapes than previous studies, allowing animals to interact and respond to variation and complexity across the landscape. Bison and cattle had similarities in some aspects of their behavior. Both species had a strong preference for recently burned areas, similar to separate studies of the individual species (Coppedge et al. 1998, Fuhlendorf and Engle 2004). Along with similarities we also identified two key differences. Cattle preferred areas with woody vegetation, while bison avoided them. This likely plays a critical role in thermal regulation, with woody canopy cover providing shade from solar radiation. Detailed mapping of the thermal environment is required to determine the influence of heat on the grazing behavior of bison and cattle. Additionally, because location information obtained by the GPS does not differentiate between grazing or resting, it is unclear if the preference for woody vegetation is a result of grazing or resting behavior. It does show, however, behavioral preferences and differences that are likely to influence both selection and grazing decisions, especially when studying behavior at broad spatial scales.

Selection for sites closer to water was also greater in cattle than bison; bison appeared to maximize their distance to water while cattle minimized it. These differences occurred in a well watered landscape and may be even more important in lands with greater distance between water sources. Though water included ponds and streams, ephemeral water sources were not included due to difficulty in measuring them at this spatial scale. Differences in use of ephemeral water between bison and cattle may explain measured differences. Additionally, both bison and cattle distribution and behavior may be influenced by precipitation patterns (Lott 2002, McAllister et al. 2006). At broader scales such as the Tallgrass Prairie Preserve, variability in spatial precipitation patterns may exist (Augustine 2010). Though not quantified, spatial variability in precipitation would likely influence animal distribution indirectly through vegetation responses and ephemeral water sources.

Although we did not collect data on ecological implications of grazing, it is likely that distribution differences between bison and cattle would

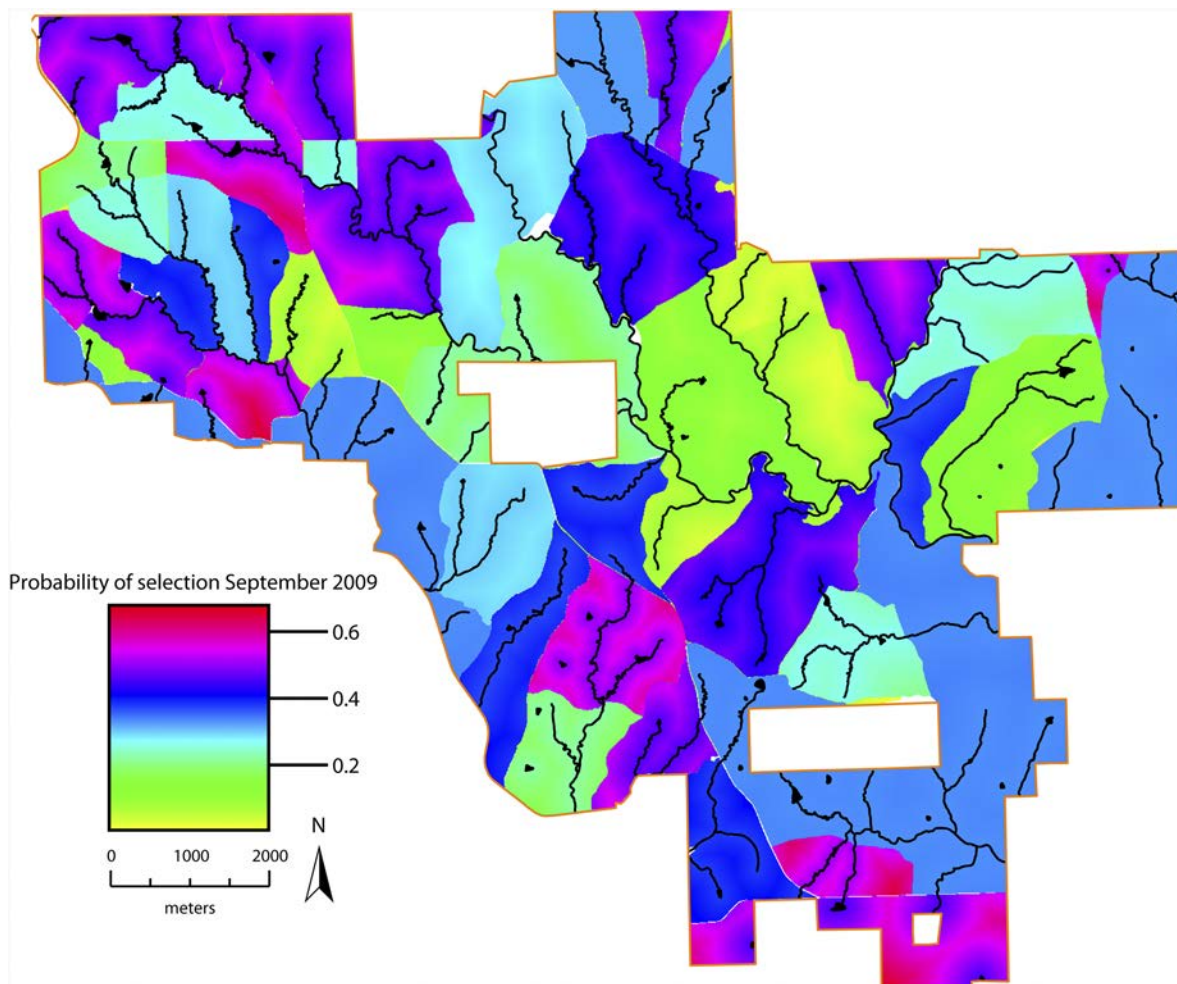


Fig. 3. Probability of selection for bison at the Tallgrass Prairie Preserve, OK, USA September 2009. Probabilities presented as a function of time since fire, distance to water, and their interaction. Black interior lines and areas represent water sources. Solid orange lines represent perimeter fences. Refer to Fig. 1 for recently burned areas. Bison prefer recently burned areas and do not minimize their distance to water. Due to the preference of recently burned areas, probabilities will change as fire is applied and moved around the landscape.

result in contrasting effects. The preference or focusing of grazing in a particular area (large or small) will influence vegetation community and characteristics. The continued attraction of both bison and cattle to recently burned areas alters vegetation structure which affects biodiversity (Fuhlendorf et al. 2006), fire behavior (Leonard et al. 2010), invasive species populations (Cummins et al. 2007), invertebrate populations and communities (Engle et al. 2008), and nutrient cycling and distribution (Anderson et al. 2006). The preference of riparian and woody vegetation areas by cattle will also likely result in vegetation

and system changes. Reduced herbaceous cover, biomass, and productivity generally result from cattle grazing within riparian areas (Kauffman et al. 1983, Clary 1995, Belsky et al. 1999). Preference for water sources may also affect stream bank morphology, hydrology, and water quality (Kauffman and Krueger 1984, Trimble and Mendel 1995, Belsky and Blumenthal 1997). Concentration of livestock around ponds and streams may also likely increase nutrient concentrations (Schepers and Francis 1982, Belsky et al. 1999). We note, however, that direct comparisons of bison and cattle grazing effects on riparian

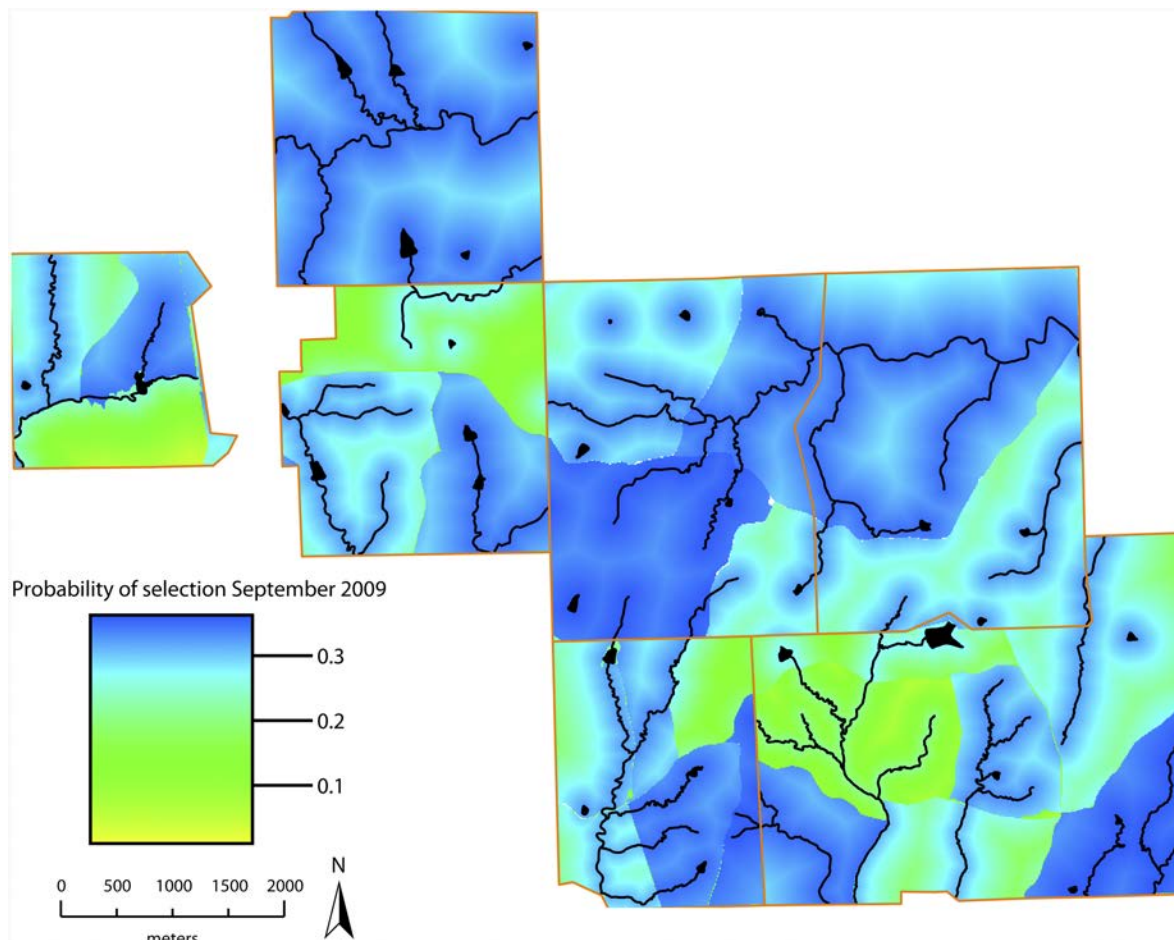


Fig. 4. Probability of selection for cattle at the Tallgrass Prairie Preserve, OK, USA September 2009. Probabilities presented as a function of time since fire, distance to water, and their interaction. Black interior lines and areas represent water sources. Solid orange lines represent perimeter fences. Refer to Fig. 1 for recently burned areas. Cattle prefer recently burned areas and minimize their distance to water. Due to the preference of recently burned areas, probabilities will change as fire is applied and moved around the landscape.

processes are largely lacking.

It is difficult to account for the many factors that may create differences or similarities between bison and cattle, and like all studies of processes on complex landscapes, this study is not without limitations. Though stocking rates were similar between bison and cattle units, cattle were only present during the growing season (April–September), while bison remained throughout the year. Differences in the social and temporal organizations of cattle and bison herds may also confound differences. The bison herd was a mixture of males and females of various ages grazing together, while cattle herds were

yearling stocker steers. A yearlong, cow-calf cattle operation would permit even better comparisons between the two species, particularly with regard to ecological effects. Though treatment units were large and incorporated landscape complexity, they were not of equal size. We could expect that animal behavior would be sensitive to and vary with available area. Smaller units would limit animal movement and behavior, restricting selection and interaction with other environmental factors. Available area would be important particularly regarding cattle preference for water, as smaller units would constrain animals closer to water. While cattle

Table 4. Estimated resource selection function coefficients[†] of the top ranked model for individual bison and cattle at the Tallgrass Prairie Preserve, OK, USA each year of study (2009 and 2010); model parameters include distance to water (water; m), distance to patch edge (edge; m), slope (slope; degrees), northing (north; degrees), easting (east; degrees), wooded area (woody), and time since fire (tsf; days).

Year	tsf	water	slope	edge	woody	north	east	tsf × wtr	tsf × slp	tsf × edge	tsf × wdy
Bison											
2009	-1.69	-0.01	-0.72	-0.55	-2.44	0.01	0.06	0.12	-0.48	-0.78	-1.85
2009	-1.29	0.20	-0.48	-0.12	-2.45	0.00	0.03	0.31	-0.22	-0.34	-1.64
2009	-1.74	0.19	-0.61	-0.50	-1.22	0.01	-0.01	-0.05	-0.35	-0.78	-0.47
2009	-1.16	0.00	-0.63	-0.43	-1.55	-0.03	0.06	0.15	-0.58	-0.59	-0.93
2009	-1.91	0.23	-0.45	-0.40	-2.45	-0.03	0.02	0.30	-0.31	-0.64	-2.38
2009	-1.35	-0.02	-0.62	-0.14	-2.59	-0.02	0.02	0.11	-0.37	-0.39	-2.23
2009	-1.57	0.10	-0.56	-0.36	-1.46	-0.03	0.00	0.00	-0.37	-0.43	-1.19
2010	-1.38	0.13	-0.51	-0.07	-1.38	0.03	0.00	0.20	-0.08	-0.26	0.30
2010	-1.16	0.13	-0.49	-0.14	-1.35	0.00	-0.03	0.10	-0.16	-0.22	0.27
2010	-1.37	0.06	-0.54	-0.25	-0.82	0.01	0.01	0.14	-0.17	-0.37	0.40
2010	-1.52	0.11	-0.51	-0.06	-0.71	0.01	-0.02	0.19	-0.16	-0.20	0.32
2010	-1.46	0.06	-0.57	-0.14	-0.40	0.04	-0.02	0.07	-0.07	-0.38	1.16
2010	-1.38	0.00	-0.79	-0.13	-1.59	0.02	0.00	-0.02	-0.30	-0.33	-0.11
2010	-1.79	-0.15	-0.43	-0.17	-1.21	-0.02	0.03	-0.08	-0.08	-0.32	0.11
Variation [‡]	0.23	0.10	0.10	0.17	0.70	0.02	0.03	0.12	0.16	0.19	1.12
Cattle											
2009	-1.70	-0.05	-0.46	-0.81	-1.66	0.04	-0.01	-0.19	-0.32	-1.20	-1.68
2009	-1.44	-0.33	-0.11	-0.87	2.74	-0.06	-0.02	0.26	0.05	-1.78	-0.23
2009	-1.16	-0.30	-0.02	-0.28	2.37	0.00	-0.01	-0.19	0.18	-0.94	0.18
2009	-0.37	-0.03	-0.15	-0.69	1.61	-0.01	0.01	-0.23	0.00	0.53	-0.47
2009	-0.36	-0.11	-0.25	-0.18	1.42	0.02	0.01	-0.09	-0.12	0.08	0.10
2009	-0.79	-0.22	-0.28	-0.12	1.24	0.00	0.00	-0.25	-0.08	0.03	0.40
2009	-3.35	-0.62	-0.15	-0.61	1.49	0.00	-0.04	-0.95	-0.04	-0.97	0.43
2010	-0.37	-0.09	-0.27	-0.07	1.60	0.01	0.00	-0.81	-0.01	0.00	0.04
2010	-2.72	-0.45	-0.42	-0.82	3.66	0.04	-0.02	-0.55	-0.47	-0.99	1.44
2010	-1.24	-0.38	-0.12	-0.37	1.86	0.05	-0.04	-0.56	0.14	-0.41	-0.72
2010	-1.59	-0.17	-0.02	-0.43	1.24	0.00	0.01	-0.39	-0.10	-0.38	-0.41
2010	-0.48	-0.29	-0.24	-0.32	2.79	-0.05	0.04	-0.44	-0.33	0.18	-0.50
2010	-2.09	-0.21	0.04	-1.18	1.31	-0.03	-0.01	-0.79	-0.03	-0.55	0.44
2010	-1.16	-0.13	-0.40	-0.41	0.82	0.00	-0.01	-0.21	-0.42	-0.39	-0.24
Variation [‡]	0.91	0.17	0.16	0.33	1.22	0.03	0.02	0.33	0.2	0.63	0.71

[†]Standardized variables are shown for coefficient comparison and interaction term interpretation.

[‡]Variation measured by calculating the standard deviation of coefficients within species.

units within the Tallgrass Prairie Preserve are smaller than the bison unit, they are larger than the majority of land holdings within the Great Plains; size likely did not limit the distance to water. This study also compared bison to European cattle breeds that are typical for livestock production objectives on tallgrass prairies. Other breeds of cattle are likely to respond differently (Rook et al. 2004, VanWagoner et al. 2006). Brahman or Texas longhorn breeds, for example, are likely to be adapted to more arid environments where water is limiting and may behave more similarly to bison.

In the Great Plains of North America, bison are reintroduced for primarily two objectives: species conservation and restoration of ecosystem processes. Reintroduction to conservation areas, development of private herds, and recent efforts in identifying pure herds to conserve genetics

have been successful in restoring wild bison populations to many areas. Conservation of this species is a unique success story that deserves acknowledgement. Bison are also reintroduced to restore keystone effects (Knapp et al. 1999). Conservation groups as well as government agencies reintroduce bison to both small prairie remnants and large landscapes to restore historical disturbance patterns. In most cases, this is done without considering the many other factors that influence grazing behavior or effects. While the first objective for reintroduction can be accomplished by building up bison herds throughout the Great Plains, the second objective is not possible without the consideration or reintroduction of other environmental or animal factors. For example, we show that both of these herbivores have a strong preference for recently burned areas. This may suggest that the reintro-

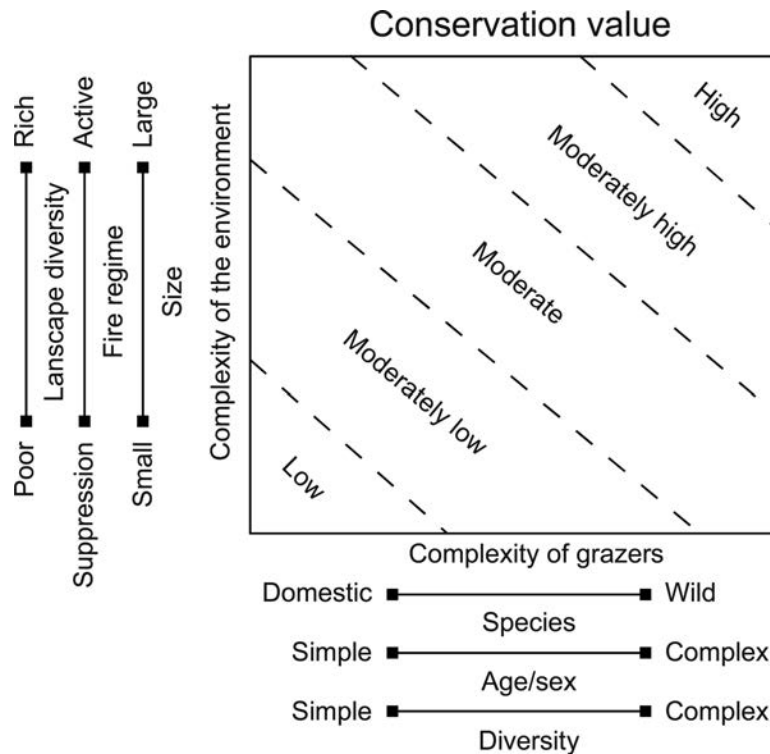


Fig. 5. Conceptual model to evaluate conservation value with respect to animal and environmental factors. Conservation value is defined as the contribution to regional conservation efforts, which includes the promotion of native plants, animals, and ecosystem processes. Species of animal alone does not automatically increase the value in regard to conservation; other factors play an important role in overall conservation value.

duction of bison, or the evaluation of differences between these species, may be largely irrelevant unless fire and other complexities are incorporated (Fuhlendorf et al. 2009). It is likely true that other factors, such as predators, would also greatly alter animal behavior and grazing effects (Ripple and Beschta 2003).

Conservation efforts regarding bison reintroduction should be evaluated to not only see if specific objectives are met, but how efforts contribute to overall conservation. We developed a conceptual model to evaluate the conservation value of different options regarding bison reintroduction (Fig. 5). We define conservation value as the contribution to regional conservation efforts, including promotion of native plants, animals, and ecosystem processes. The model is based on two primary factors that influence grazing behavior and effects, primarily complexity of grazers and the environment. Complexity of grazers refers to factors such as species,

diversity, and social organization that contribute to the overall conservation value. Although this study examined only differences between two species, increasing species diversity with multiple species will add additional complexity to the system and alter the effects of grazing (du Toit and Cumming 1999, Hooper et al. 2005, Burns et al. 2009). Other native species in North American grasslands, such as prairie dogs (*Cynomys* spp.) are also important components of the system; as an example, incorporating prairie dogs will increase conservation value (Coppock et al. 1983).

The social organization of ungulates, particularly age and sex ratios, also contribute to ecosystem functioning, complexity, and conservation (Sheldon and West 2004, Gordon et al. 2004, Milner et al. 2007). Variation in animal factors will also contribute to interactions with the environment. For example, the body size of animals (also related to age and sex) influences

preferences for burned areas, playing an important role in spatiotemporal heterogeneity (Wilsey 1996, Sensenig et al. 2010). Simple social organization, such as the yearling stocker steers within cattle units of this study, limit variability and decrease conservation value. With particular regard to livestock production, complexity of grazers may be improved by increasing individual variation or combining differing breeds or species (VanWagoner et al. 2006, Searle et al. 2010). Historically, bison were a keystone species, but their impacts were dependent upon how they interacted with the environment, disturbances, and other herbivores. Increasing the complexity of grazers (more species diversity, more wild herbivores, etc.) increases the conservation value, but this value is also dependent upon environmental factors. The simple replacement of domestic cattle with bison may contribute to bison conservation, but may have minimal impact on the broader conservation value of ecosystems. In an extreme example, replacing cattle with bison in a small, intensively managed, and simplified livestock production operation (e.g., a feedlot or small pasture) has little conservation value. Restoring other important processes such as fire, predation, etc. are just as important as the large herbivore upon the landscape (Ripple and Beschta 2003, Fuhlendorf et al. 2009).

Conservation value is also dependent upon the environmental complexity of the area. The majority of these factors are independent of the species of herbivore. In mesic grasslands of the Great Plains (tallgrass and mixed grass prairies), fire-grazing interactions have been shown to be a dominant driver of animal distribution and integral ecosystem process (Fuhlendorf and Engle 2004, Vermeire et al. 2004, Anderson et al. 2006). Similar to the example given above, the simple replacement of cattle with bison without a restoration of fire regimes will not result in disturbance patterns that are critical for conservation and biodiversity. In our study, time since fire was a primary driver in bison and cattle grazing behavior. The suppression of fire or the simplification of fire-grazing interactions within fire prone systems will limit conservation value, regardless of the herbivore species. Environmental factors that are critical to grazing effects and other ecosystem processes need to be accounted for in study designs that evaluate the role of

grazing in conservation efforts. In North American grasslands, key environmental factors include fire regimes (Wright and Bailey 1982, Knapp et al. 1998, Brockway et al. 2002), landscape complexity and size (Herkert 1994, With et al. 2008), water distribution (Bailey et al. 1996, Augustine 2010), and woody vegetation (Archer et al. 1995, Briggs et al. 2002). These do not only influence grazing and the resulting effects, but play a broader role in ecosystem functioning. On lands with minimal environmental complexity, any differences between bison and cattle will likely contribute little to conservation value.

Grasslands are endangered worldwide (Hoekstra et al. 2005). While propositions to restore or conserve grasslands regularly focus on native herbivores (e.g., Sanderson et al. 2008), it is often overlooked that the majority of grasslands are privately owned and used for domestic livestock production (particularly true in the Great Plains of North America; Samson and Knopf 1994). Low and high conservation values can be achieved with bison or cattle. Though bison are the iconic symbol of the Great Plains of North America, and it is critical that we conserve the species, there are not enough data to confidently state that landscapes with bison are inherently better than landscapes with cattle for overall conservation or biodiversity. Both species can be mismanaged and cause degradation of habitat as well as ecological processes. Using domestic cattle to achieve some conservation objectives may be more practical or relevant, as cattle currently make up the vast majority of herbivores in many grasslands. Conservation value of productions cattle herds can be improved by increasing the size and complexity of landscape available. Allowing cattle to move at broader spatial scales and to interact with biotic and abiotic factors, may increase conservation value substantially, perhaps more so than replacing cattle with bison at finer scales. Popular management strategies that constrain animal movement and behavior (through use of fencing and rotation) may prevent many important interactions between the animal and environment, potentially reducing conservation value. As more studies effectively and appropriately compare grazing behavior and effects at broad and fine spatial scales, additional reliable conclusions will

be made that may change conservation efforts or directions.

We argue that for future studies and comparisons between bison and cattle (as well as other species) it is critical that we limit our extrapolation with discussions of the abiotic and biotic environment in which these studies occur. Though it is unlikely that we will be able to conduct studies that encompass all possibilities in environmental and herbivore complexity, we must begin to contextualize our discussions and limit our inferences. From a conservation perspective it is important to understand the ecological effects of cattle grazing for livestock production, and explore approaches to alter these patterns to more effectively achieve conservation objectives. It is not productive to look for differences or similarities between bison and cattle to justify certain management objectives or agenda. In the face of the vast variability and complexity in which these species are nested within, generalizations are limited and over inferences likely.

Conservation of bison is important as an iconic species and a keystone herbivore (Knapp et al. 1999). From a broad context, however, conservation efforts need to recognize that cattle will continue to be a dominant feature on the Great Plains and grasslands worldwide, and that some conservation objectives may be met using cattle. It is critical to understand grazing behavior and ecological effects of both species in simple and complex landscapes relevant to conservation. There is an important place for species comparisons, but this is just one aspect of grassland conservation and may not be the most important for future conservation of biodiversity.

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Prairie Dog (*Cynomys ludovicianus*) Influence on Forage Quantity and Quality in a Grazed Grassland-Shrubland Ecotone[☆]

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ABSTRACT

Black-tailed prairie dogs (*Cynomys ludovicianus*) have high dietary overlap with livestock, which can cause forage-centric conflicts between agriculture and conservation. Research suggests prairie dogs can enhance forage quality, but trade-offs between quality and quantity throughout the growing season remain unclear, as well as the degree to which increased forage quality is caused by altered species composition versus altered plant physiology. To assess the effects of prairie dog herbivory on forage in a northern mixed-grass prairie, we collected samples on prairie dog colonies and at sites without prairie dogs during June, July, and August 2016–2017 for forage quality, and August 2015–2017 for herbaceous biomass. To isolate mechanisms affecting forage quality, we collected both composite samples of all herbaceous species and samples of western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve). Across years and plant sample types, crude protein, phosphorus, and fat were 12–44% greater and neutral detergent fiber was 6–10% lower on prairie dog colonies than at sites without prairie dogs. The effects of prairie dogs on forage quality persisted throughout the season for western wheatgrass samples (all treatment*time p-values ≥ 0.4). Across years, aboveground herbaceous biomass did not differ significantly between prairie dog colonies and sites without prairie dogs (on-colony: 933 ± 156 kg/ha, off-colony: 982 ± 117 kg/ha). The effects of prairie dogs on herbaceous biomass were significantly influenced by spring precipitation. In years with dry springs, herbaceous biomass was lower on colonies than sites without prairie dogs and this pattern was reversed in years with wet springs. Our results demonstrate season-long enhanced forage quality on prairie dog colonies, indicating that multiple mechanisms are shaping forage quality in this system, including altered species composition, phenological growth stage, and soil condition. Across years, enhanced forage quality may help to offset reductions in forage quantity for agricultural producers.

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Introduction

Free-roaming herbivores have historically been major drivers of structural and evolutionary patterns and processes in rangeland ecosystems (Frank et al., 1998; Sankaran et al., 2005). In the western United States, rangelands have evolved under grazing and browsing pressure from herds of native free-roaming ungulates that interacted with

small mammal assemblages (Stebbins, 1981). Before European settlement, wild ungulate herbivores included species from the Cervidae (deer and elk), Antilocapridae (American pronghorn), and Bovidae (bison) families (Danell et al., 2006). In the absence or reduction of these large native grazers, domestic livestock now serve as the dominant large herbivore interacting with small mammals on North American rangelands. Contemporary livestock management on rangelands influences animal distribution and competition for forage, creating a unique anthropogenic interaction between large ungulates and small mammals where both agricultural production and the conservation of biodiversity are of concern (Heitschmidt and Stuth, 1991).

In the northern mixed-grass prairie of the United States, black-tailed prairie dogs (*Cynomys ludovicianus*) co-occur with domestic livestock, particularly beef cattle (Koford, 1958). The sympatric distribution of beef cattle and prairie dogs was historically viewed as competitive for forage due to their dietary overlap (~75%) and shared preference for graminoids (Koford, 1958; Summers and Linder, 1978; Uresk, 1984; Miller et al., 2007). Potential competition for perennial grasses between

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cattle and prairie dogs can be heightened when forage attains peak quality and quantity during the growing season of spring and summer, a time when cattle rely solely on pasture forage for sustenance and prairie dogs consume greater quantities of graminoids (Fagerstone et al., 1981; Vermeire et al., 2004; Scasta et al., 2016a; Scasta, 2017). The preferential selection for graminoid forage changes in the fall and winter, when prairie dogs consume greater amounts of forbs, shrubs, seeds, roots, and cacti (Fagerstone et al., 1981) and cattle are typically moved to winter pastures where their diets are supplemented with harvested feed. Thus, dietary overlap and potential competition between beef cattle and prairie dogs are highest in spring and summer.

Competition for shared and limited resources dictates occupancy, distribution, and spatiotemporal use in free-roaming animals on rangelands. Direct competition occurs when a limited resource is exploited to the benefit of one individual or species, rendering the remaining resource insufficient for another species or individual (Gause, 1934). Animals may mitigate interspecific competition by avoiding overlapping resource use in time or space (Rosenzweig, 1995) or by capitalizing on phenologic growth whereby the first herbivory event causes palatable, nutritious regrowth and thus mitigates competition for the second herbivory event. However, modern grazing management practices alter the evolutionary ungulate–prairie dog interaction by imposing artificial restrictions on livestock movement (i.e., fences), which may limit the ability of livestock to mitigate interspecific competition with relatively sedentary small mammals such as prairie dogs.

For perspective, an individual prairie dog consumes the same relative forage as ~0.003 animal units (AUs), or 335 prairie dogs consume the same forage as a 454-kg (1 000-lb) cow with a calf, which is the basis for the AU concept in rangeland grazing management (Koford, 1958). However, the subsequent reduction of herbaceous forage biomass on rangeland landscapes by prairie dogs is also influenced by prairie dog density, which can be highly variable, ranging from 2 to 36 individuals per hectare (Powell et al., 1994; Severson and Plumb, 1998; Johnson and Collinge, 2004; Derner et al., 2006; Eads and Biggins, 2012). In addition, prairie dogs may further deplete aboveground biomass by clipping, but not consuming, standing forage as a vigilance strategy to enhance their ability to see predators (Hoogland, 2006). In both mixed-grass and shortgrass prairies, prairie dogs are capable of decreasing graminoid biomass by half (Fahnestock and Detling, 2002) and causing morphological variation of native graminoids in the form of reduced height and greater prostrate form (Painter et al., 1993). These effects may be exacerbated in low-production grasslands (Derner et al., 2006; Lauenroth and Burke, 2008) or mitigated by spring precipitation and colony characteristics such as occupancy and colony age (Augustine and Springer, 2013).

Prairie dogs have the ability to negatively affect cattle weight gains, but the magnitude of such an effect is highly dependent on colony scale, spatial overlap of colonies with livestock pastures, instantaneous intake rate of the ruminant, site-specific grass species, soil type, and spring precipitation (Derner et al., 2006; Augustine and Springer, 2013). Indeed, these results alone suggest that prairie dogs are in direct competition with cattle for forage. However, effects of prairie dogs on livestock may be mitigated by enhanced forage quality found on prairie dog colonies, where grass regrowth following defoliation is tender and highly nutritious (Chipault and Detling, 2013).

Currently, few studies are available that directly examined the trade-offs between prairie dog effects on forage quantity (likely negative) and their effects on forage quality (likely neutral to positive). Augustine and Springer (2013) found prairie dogs in northern mixed-grass prairie sites reduced herbaceous biomass of commonly grazed species by 63–94%, but in the shortgrass prairie there was little to no significant reduction in herbaceous biomass at one site and substantial reductions at another. Under dry conditions, reductions of forage biomass were substantial but effects on forage digestibility were nonexistent or very small. Under wet conditions, forage biomass was not reduced at one shortgrass prairie

site but was reduced at a northern mixed-grass prairie site, and both sites had enhanced forage digestibility and nitrogen content. The authors of this study concluded that the interactive effects of prairie dogs on forage quantity and quality were highly variable across space and time, and competition between cattle and prairie dogs may be evident under dry conditions but offset under wet conditions (Augustine and Springer, 2013).

To better understand the potential for forage-centric competition between livestock and prairie dogs, we investigated the effects of prairie dog herbivory on aboveground herbaceous biomass and forage quality in the northern mixed-grass prairie and sagebrush steppe ecotone in northeastern Wyoming. Specifically, we assessed how prairie dog herbivory, across variable colony characteristics, livestock stocking rates, and interannual precipitation, influenced forage biomass and quality throughout the growing season and across years. In order to distinguish between prairie dog effects on plant phenology and plant species composition, we examined forage quality of composite herbaceous samples and the dominant, palatable perennial grass species in this ecosystem.

Methods

Study Area

Our study occurred in the Thunder Basin National Grassland (Thunder Basin), a 6 880-km² northern mixed-grass prairie and sagebrush steppe ecotone in northeastern Wyoming (497013.101, 4830298.439 m, UTM Zone 13; Fig. 1). Long-term mean annual precipitation (1981–2010) was 320 mm (PRISM Climate Group, 2017), and long-term mean growing-season precipitation was 177 mm (April–June 1981–2010; Derner and Hart, 2007; WRCC, 2016). Mean growing-season precipitation at our sampling sites during the study period was above average in 2015, below average in 2016, and very close to average in 2017 (308 mm, 125 mm, and 171 mm, respectively; PRISM Climate Group, 2017). Sampling sites were constrained to loamy soils, which dominate 33% of the landscape (Ecological Site R058BY122WY, USDA-NRCS), and elevation ranged from 1 328 to 1 511 m (PRISM Climate Group, 2017). Sampling sites were located on both private land and public land managed by the US Forest Service.

Vegetation was dominated by Wyoming big sagebrush (*Artemisia tridentata* spp. *Wyomingensis* [Beetle & Young]), and common perennial grasses included blue grama (*Bouteloua gracilis* [H.B.K.] Lag. Ex Griffiths), western wheatgrass (*Pascopyrum smithii* [Rydb.] Å. Löve), prairie junegrass (*Koeleria macrantha* [Ledeb.] Schult.), threadleaf sedge (*Carex filifolia* Nutt.), Sandberg bluegrass (*Poa secunda* J. Presl), and needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth). Annual grasses included exotic bromes (*Bromus arvensis* and *B. tectorum* [L.]) and the native sixweeks fescue (*Vulpia octoflora* (Walter) Rydb) (Porensky and Blumenthal, 2016). Plains pricklypear cactus (*Opuntia polyacantha* [Haw.]) was also common throughout the landscape.

Study Design

We randomly selected four 16-km² sites in Thunder Basin (see Fig. 1). Each site was selected a priori as part of a larger study to encompass three types of disturbance history: a black-tailed prairie dog colony, a historic wildfire (results presented in a separate manuscript; Connell et al., 2018), and an adjacent undisturbed control (hereafter: sites without prairie dogs). The experiment had a blocked design with each of the three disturbances present in each of the four sites ($n = 12$). Within each site, large candidate areas were selected within each disturbance so that sampling areas were matched in terms of soil type, slope, aspect, and topographic wetness index (an indicator of landscape

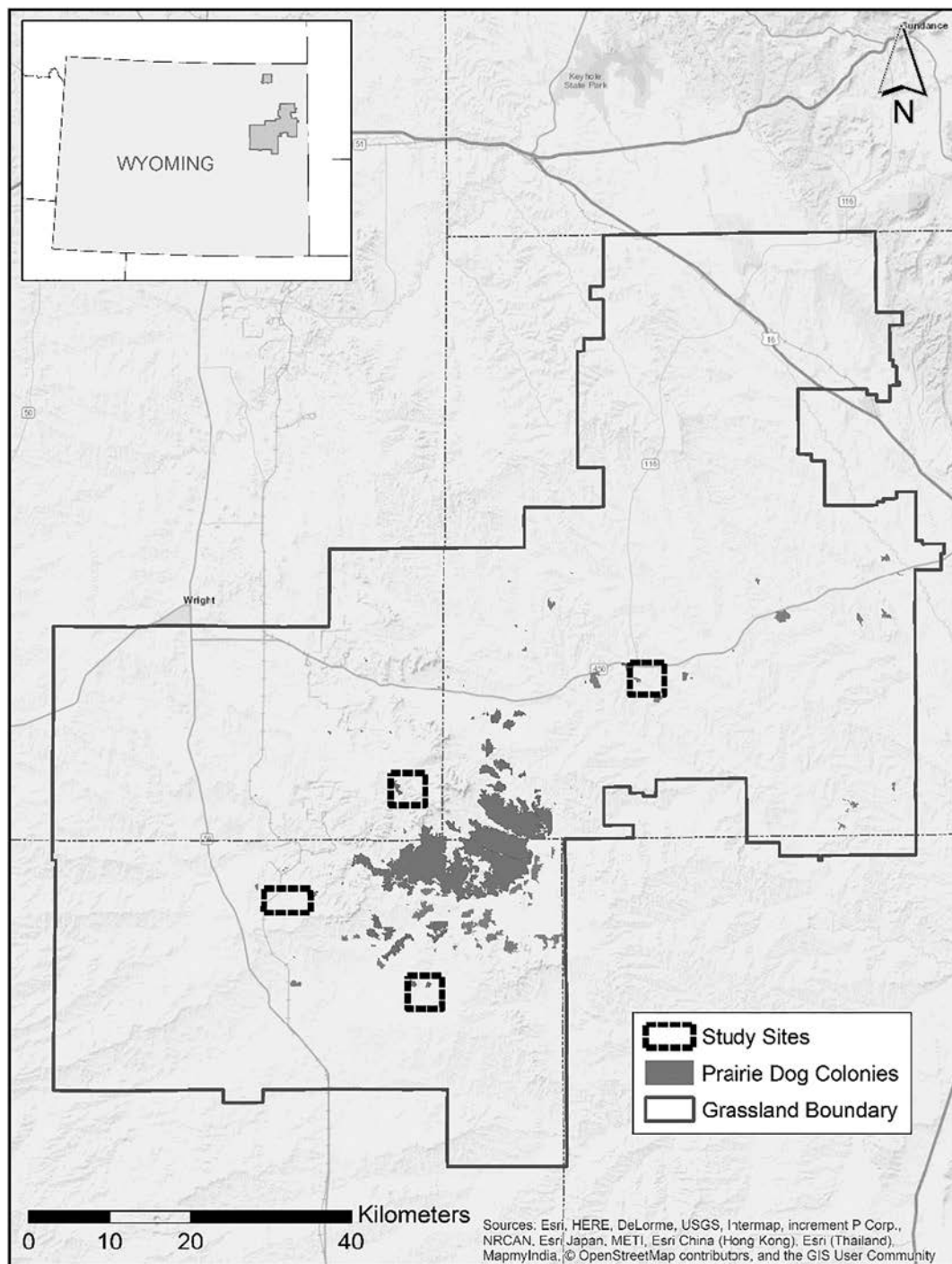


Figure 1. We established four study sites in Thunder Basin National Grassland, Wyoming. Each study site contained 1) a black-tailed prairie dog colony, 2) a historical wildfire (not pictured; data represented in a separate manuscript), and 3) an undisturbed site without prairie dogs or fires (control). Study sites were located on public land managed by the US Forest Service and privately owned property.

position). At each site, we permanently established paired 20-m monitoring stations (transects) randomly located within the prairie dog colony or sites without prairie dogs (≥ 280 m from colony edge; $n = 4$ paired stations across sites). Monitoring stations were fully accessible to livestock, wild ungulate, and small mammal grazing. Livestock grazing, which included cow-calves, cows, bulls, yearling steers, ewes-lambs, and ewes, was variable between pastures and years. Across livestock class, grazing ranged from 0.1 to 0.4 AU mo $\cdot$ ha $^{-1}$ $\cdot$ yr throughout the study period, with a median of 0.2 (Table 1; see Appendix A for greater detail). Prairie dog colonies at our sites ranged in time since

settlement (9 – 20 + yr), size (48 – 69 ha), and occupied density (7 – 25 individuals $\cdot$ ha $^{-1}$; Table 1; see Data Collection for methodology).

Data Collection

To determine how soil nutrients differed between prairie dog colonies and sites without prairie dogs, we collected soil samples in June 2015 along one side of each monitoring station at distances of 5, 10, 15, and 20 m with a 7-cm diameter soil auger. At each sampling station, we collected soil at two depths (0–10 cm and 10–30 cm) and pooled soil

Table 1

Characteristics of black-tailed prairie dog colonies at study sites in Thunder Basin National Grassland, Wyoming. Colony age (total and continuous years), size, and year of colony size were derived maps of colony boundaries created annually by the US Department of Agriculture Forest Service. Active prairie dog burrows were estimated at each site in 2017. Livestock grazing information provided by the Thunder Basin Grazing Association.

Location	Colony age (total yr) ¹	Active burrows / ha	Prairie dogs / ha	Colony size (ha) ²	Yr of colony size	Avg. animal unit mo • ha ⁻¹ (yr) ³	Site description
Site 1	9	142	25	47.63	2016	0.2 (2015) 0.4 (2016) 0.1 (2017)	Prairie dog colony
—	—	—	—	—	—	0.1 (2015) 0.2 (2016) 0.3 (2017)	Site without prairie dog colony
Site 2	15	67	12	20.31	2016	0.2 (2015) 0.1 (2016) 0.2 (2017)	⁴ Pasture contains prairie dog colony and site without prairie dogs
Site 3	20	133	24	68.63	2016	0.1 (2015) 0.1 (2016) 0.1 (2017)	⁴ Pasture contains prairie dog colony and site without prairie dogs
Site 4 ⁵	11	42	7	34.72	2014	0.2 (2015) 0.2 (2016) 0.3 (2017)	⁴ Pasture contains prairie dog colony and site without prairie dogs

¹ Colony age was determined by colony mapping conducted by the US Forest Service beginning in 1997. The colony at Site 3 was present at this time and therefore this colony may be older.

² Estimate of colony limited to areas contained on public land. Values represent a conservative estimate of colony size.

³ See Appendix A for greater detail of livestock grazing type and animal unit months by pasture size and site.

⁴ Pastures containing both prairie dog colonies and site without prairie dogs were large (≥ 1137 ha) and sampling stations were spatially distinct (sites without prairie dogs were ≥ 280 m from colony edge).

⁵ Colony last mapped in 2014 and does not reflect growth experienced 2015–2016. Values represent a conservative estimate of colony size.

samples across sampling distances to generate two composite soil samples per monitoring station (one per depth by station combination). Soil samples were passed through a 2-mm sieve and then analyzed for total C and N (Matejovic, 1997). Organic carbon (%) was determined with a modified pressure-calimeter method (Sherrod et al., 2002).

To determine how forage quantity differed between prairie dog colonies and sites without prairie dogs, we clipped peak standing herbaceous biomass at each monitoring station according to peak plant maturity each year (the first week of August in 2015, 2016, and during the third week of July in 2017). We collected three subsamples at each monitoring station by randomly locating a 0.5-m² hoop within 20 m of the monitoring station and clipping all herbaceous vegetation rooted within the hoop to ground level ($n = 24$ per yr). Samples were oven-dried at 60°C for 48 hr before weighing and averaged by sampling event and monitoring station prior to analysis ($n = 8$ per sampling event; Elgersma et al., 2014).

We collected forage quality samples at each monitoring station during the first week of June, July, and August in 2016 and 2017. For each sampling event, we collected two forage quality sample types: 1) a composite of all herbaceous vegetation (i.e., COMP) obtained by randomly tossing and clipping vegetation inside a 0.5-m² hoop and 2) a sample of western wheatgrass (*Pascopyrum smithii* [Rydb.] Á. Löve) (i.e., PASM), a palatable C3 perennial grass, obtained by collecting 30–50 individual plants as close to the random hoop position as possible. We collected three subsamples of each forage sample type, within a 100-m² area surrounding each monitoring station. We chose to collect these two sample types to isolate the mechanisms driving forage quality, which could be caused by species composition, the presence or absence of standing dead material, or phenological growth stage. We clipped samples to the soil surface and excluded ground litter while including standing-dead vegetation that was intermingled with live material at the bite scale.

Samples were stored in paper bags and oven-dried at 60°C for 48 hr and analyzed at Ward Laboratories, Kearney, Nebraska, a facility certified by the National Forage Testing Association. Samples were evaluated with near infrared reflectance spectrometry (NIRS) using a Foss 2500 at 850- and 2500-nm wavelengths to quantify presence of key forage quality factors (Marten et al., 1989; Schutte and Lauriault, 2015). We assessed forage quality by evaluating specific quality metrics within 3 general categories of quality, which are typically evaluated by producers to determine supplementation needs: 1) protein, energy, and

fat (crude protein [CP], total digestible nutrients [TDN], and crude fat); 2) digestibility (acid detergent fiber [ADF], *in-vitro* true dry matter digestibility [IVTMD 48-hr], neutral detergent fiber [NDF], and percent lignin), and 3) minerals (ash, calcium [Ca], magnesium [Mg], phosphorous [P], and potassium [K]). Samples were passed through a 1-mm sieve by Ward Laboratories before analysis and results are reported on a dry matter basis.

We estimated prairie dog densities in July 2017 by counting the density of prairie dog burrow entrances as a surrogate for estimating prairie dog populations (see Table 1; Biggins et al. in Fish and Wildlife Service, 1993). At each site, we conducted surveys within a 20 × 20 m area at three randomly and permanently established survey points for a total survey area of 1200 m² and reported mean burrow density by site. We assessed burrow entrance activity based on signs of activity during the growing season, as this represents their peak population and colony density before a collapse from plague in midsummer 2017. Signs of active burrows include fresh scat, vegetation clipping near burrow, and pathways worn in vegetation, while signs of inactive burrows include multiple layers of spider webs and vegetation overgrowth near burrow entrance (Andelt and Hopper, 2016).

Statistical Analyses

We evaluated the effects of prairie dog herbivory on herbaceous biomass across and within years using linear mixed effects models (LMMs). Our response variable was mean herbaceous biomass pooled by site and treatment, and our fixed effect was prairie dog presence (prairie dog colonies vs. sites without prairie dogs; henceforth “Site Type”). We included site, monitoring station nested within site, and spring precipitation and year (when examining effects across years) as random effects to account for site-specific variation and repeated measurements across years.

To better understand how environmental variation modulates prairie dog effects, we used an LMM to determine whether spring precipitation altered the relationship between prairie dog presence and herbaceous biomass. Our response variable was mean herbaceous biomass pooled by site and treatment. We estimated spring precipitation, received 1 April–30 June, by averaging the total monthly precipitation received at the four corners of each site (Derner and Hart, 2007; PRISM Climate Group). We included spring precipitation of each site and year as a fixed effect, as well as prairie dog presence, and the prairie

dog $\times$ precipitation interaction. We included site, monitoring station nested within site, and year as random effects to account for site-specific variation and repeated measurements across years, and to identify robust patterns that could be generalized across spatial and temporal variability.

We used multiple LMMs to determine whether prairie dog presence affected the forage quality of composite and western wheatgrass samples. Forage-quality response metrics were evaluated separately and included 1) protein, energy, and fat metrics (crude protein [CP], total digestible nutrients [TDN], and fat); 2) digestibility metrics (acid detergent fiber [ADF], *in-vitro* true dry matter digestibility [IVTMD 48-hr], neutral detergent fiber [NDF], and percent lignin); and 3) mineral metrics (ash, calcium [Ca], magnesium [Mg], phosphorous [P], and potassium [K]). All nutrients were evaluated as percent dry matter content. Our fixed effects included prairie dog presence, month (treated as a categorical variable with three levels to account for potentially

nonlinear responses through the growing season), and the interaction of prairie dog presence by month. We included site, monitoring station nested within site, and year as random effects to account for site-specific variation and repeated measurements across years. When evaluating the composite sample for *in-vitro* true dry matter digestibility, we included year as a fixed effect to assist in model convergence.

To further understand the potential tradeoff between forage quantity and quality, as well as to directly relate the two, we calculated $\text{kg CP} \cdot \text{ha}^{-1}$ by multiplying peak-season herbaceous biomass by the corresponding percent CP from the composite sample (data collected in August 2016–2017). We then evaluated the effects of prairie dogs on $\text{kg CP} \cdot \text{ha}^{-1}$ across and within years by using LMMs. Our response variable was $\text{kg CP} \cdot \text{ha}^{-1}$, and prairie dog presence was our fixed model effect. We included site, monitoring station nested within site, and year (when analyzing trends across years) as random effects. All linear mixed effects models were executed in JMP (JMP, Cary, NC,

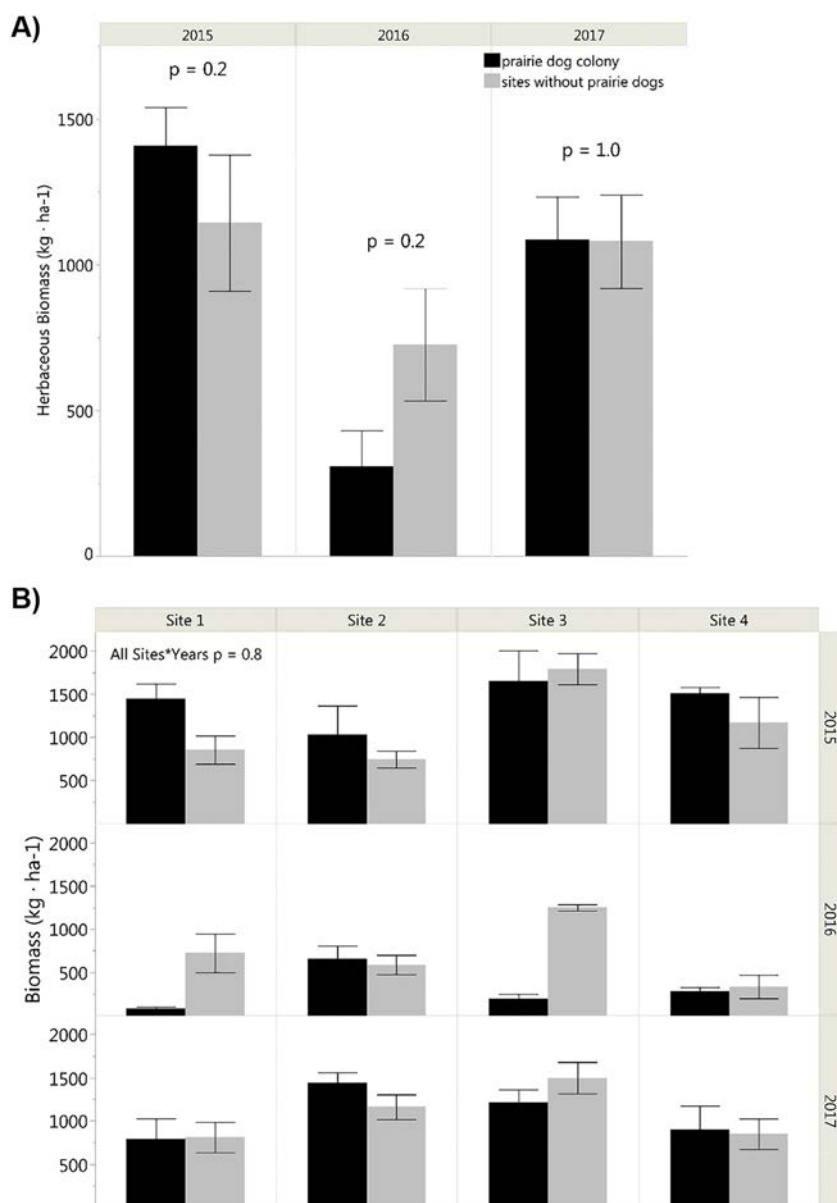


Figure 2. Effects of black-tailed prairie dogs on herbaceous biomass in Thunder Basin National Grassland, Wyoming. Biomass was measured during peak growing season (17 July–10 August). Results reflect effects of prairie dogs on (A) herbaceous biomass across four sites, over 3 yr (error bars in Panel A are $\pm$ SE from means across sites) and (B) herbaceous biomass at four sites, over 2 yr (error bars in Panel A are $\pm$ SE from subsamples).

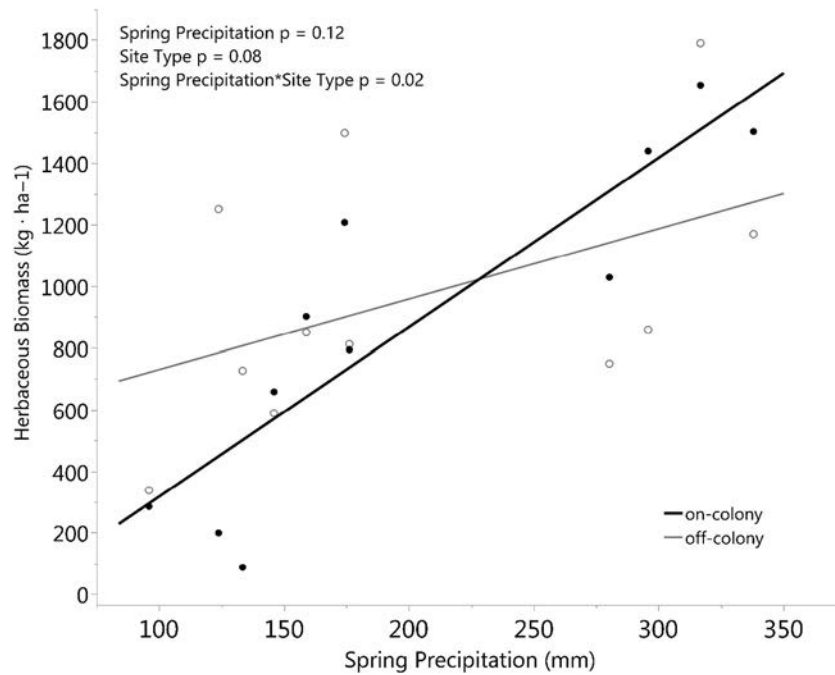


Figure 3. Herbaceous biomass response to spring precipitation, across four study sites and 3 yr, in Thunder Basin National Grassland, Wyoming. Closed circles and black lines represent data from sites on prairie dog colonies while open circles and gray lines represent data from sites without prairie dogs.

version 12.0.1). Data were transformed when necessary to meet model assumptions of normality and homoscedasticity, and results are presented as means $\pm$ SE.

We used a constrained form of principal components analysis—a partially constrained redundancy analysis (RDA) to further understand the complexity of forage quality composition and the influence of abiotic factors and seasonality on multiple aspects of forage quality. We chose this method because it allows for comparison of response variables of differing units and is ideal for short-term studies where treatments are the explanatory variables (Šmilauer and Lepš, 2014; Ordination Methods for Ecologists). This ordination technique is a direct gradient ordination of forage quality response metrics and was constrained by abiotic and temporal factors. Ordination variables in our partially constrained RDA included soil nutrients (% nitrogen and % organic carbon) at variable depths (0–10 cm and 10–30 cm), metrics of forage quality (previously described), site, month, and sample type. Year was a covariate of the RDA to account for interannual variation in forage quality. All constrained axes were tested for significance ($P \leq 0.05$) using a permutation test with 999 iterations and random seed number generator. Ordination analyses were conducted in CANOCO 5 version 5.04 (ter Braak and Šmilauer, 2012). To examine and account for forage quality as it relates to peak-season herbaceous biomass, we performed a second partially constrained RDA on herbaceous biomass coupled with August forage quality data. This second analysis used the same constraints and covariates as described earlier, with the additional metric of $\text{kg CP} \cdot \text{ha}^{-1}$.

Results

Aboveground Herbaceous Biomass

Aboveground herbaceous biomass did not differ between prairie dog colonies and sites without prairie dogs across three growing seasons (prairie dog colonies: $933 \pm 156 \text{ kg} \cdot \text{ha}^{-1}$, sites without prairie dogs: $982 \pm 117 \text{ kg} \cdot \text{ha}^{-1}$, $P = 0.8$; Fig. 2A). Results were similar when each year was analyzed individually (prairie dog presence by year, all P values ≥ 0.2 ; see Fig. 2A). Effects of prairie dog presence on

herbaceous biomass differed among colonies and years (Fig. 2B) and were contingent on spring precipitation (prairie dog presence $\times$ precipitation $F_{1,12} = 7.72$, $P = 0.02$; Fig. 3). For years and sites with dry spring seasons, herbaceous biomass tended to be lower on colonies than at sites without prairie dogs. However, this pattern was reversed for years and sites with wet spring seasons (see Fig. 3).

Forage Quality: Protein, Energy, and Fat

Crude protein (CP) was $1.4\times$ higher on prairie dog colonies (12.33 ± 0.81) than sites without prairie dogs (8.7 ± 0.38 ; $P = 0.04$) across years for composite samples (Fig. 4A; Table 2), but the strength of this effect varied by month (Month $\times$ Site Type $P = 0.009$). In June, CP of composite samples was significantly greater on prairie dog colonies than on sites without prairie dogs, but in July and August, CP did not differ significantly between sites with prairie dogs and sites without prairie dogs (see Fig. 4A). For both site types, CP was significantly higher in June than July or August (see Fig. 4A). Western wheatgrass samples contained $1.4\times$ higher CP on prairie dog colonies (12.66 ± 0.72) than sites without prairie dogs (8.79 ± 0.61 ; $P = 0.008$; see Table 2), and this difference was maintained across all 3 mo (Month $\times$ Site Type $P = 0.4$). CP in western wheatgrass samples was higher in June than July or August (Month $P < 0.0001$; see Fig. 4A).

Total digestible nutrients (TDN) was $1.1\times$ higher on prairie dog colonies (61.95 ± 0.90) than sites without prairie dogs (57.0 ± 0.74 ; $P = 0.02$) for composite samples (see Fig. 4B and Table 2), and this difference was maintained across all 3 mo (Month $\times$ Site Type $P = 0.2$). TDN of composite samples was lower in August than June or July across both site types (Month $P < 0.0001$). In contrast, TDN of western wheatgrass samples was not significantly different between prairie dog colonies (62.84 ± 0.70) and sites without prairie dogs (60.46 ± 0.58 ; Site Type $P = 0.1$; Month $\times$ Site Type $P = 0.6$; see Fig. 4B). TDN was lower in August than June or July (Month $P < 0.0001$).

Fat content (%) was $1.3\times$ higher on prairie dog colonies (3.14 ± 0.15) than sites without prairie dogs (2.44 ± 0.09 ; $P = 0.04$) across years for composite samples (see Fig. 4C and Table 2), and this difference was maintained across all 3 mo (Month $\times$ Site Type $P = 0.2$). Fat content

of composite samples was significantly higher in July than in June, likely due to peak seed production of forbs and graminoids midseason, while August had intermediate values (Month $P < 0.001$). Similarly, western wheatgrass samples contained $1.1 \times$ higher fat content on prairie dog colonies (3.53 ± 0.16) than sites without prairie dogs (3.15 ± 0.13 ; $P = 0.02$; see Table 2), and this difference was maintained across all 3 mo (Month $\times$ Site Type $P = 0.4$). Fat content was significantly higher in July than August and June (Month $P < 0.0001$; see Fig 4C).

Forage Quality: Digestibility

Neutral detergent fiber (NDF) was 9% lower on prairie dog colonies (62.36 ± 1.15) than sites without prairie dogs (68.88 ± 1.04) and marginally significant ($P = 0.07$) for composite samples. Differences were not affected by the month $\times$ site type interaction (Month $\times$ Site Type $P = 0.2$; Fig. 5; see Table 2). NDF was significantly higher in August than July and significantly higher in July than June (Month $P < 0.0001$).

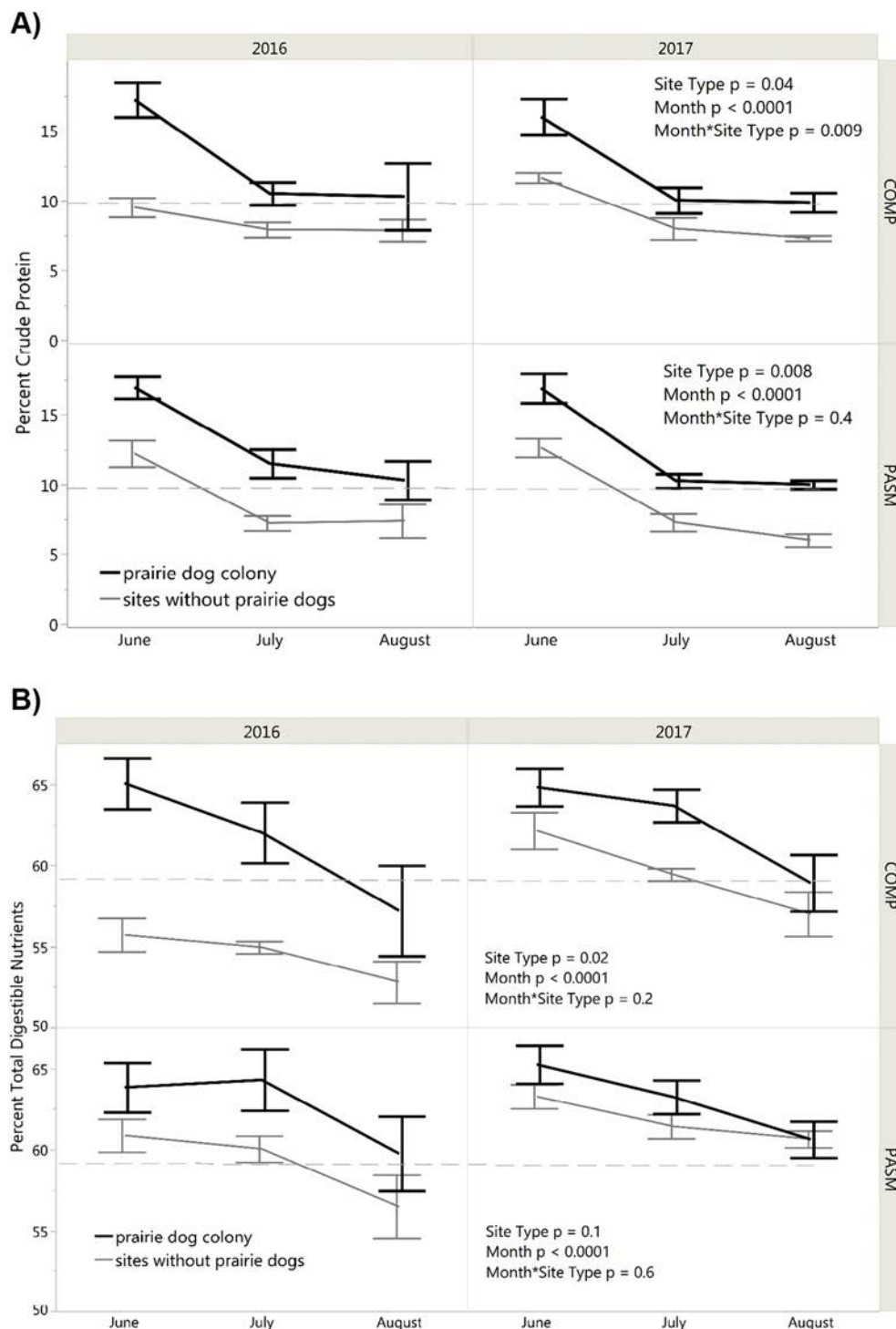


Figure 4. Effects of black-tailed prairie dog herbivory on metrics of (A) crude protein (CP, % dry matter), (B) energy (total digestible nutrients [TDN] % dry matter), and (C) fat (% dry matter) across four sites in Thunder Basin National Grassland, Wyoming. Prairie dog colonies and sites without prairie dogs are denoted in model results by “Disturbance Type.” Dashed line indicates the CP and TDN requirements for an average lactating beef cow of moderate size, 3–4 months postpartum. Error bars show $\pm$ SE.

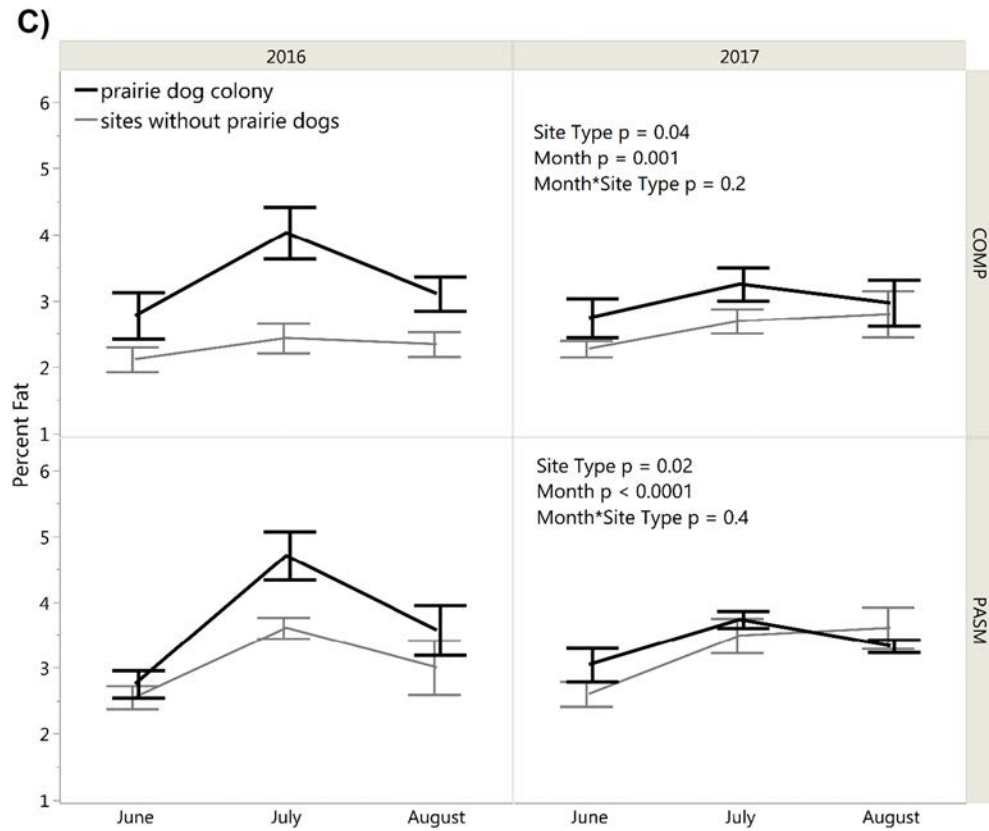


Figure 4 (continued).

Western wheatgrass samples contained 6% less NDF on prairie dog colonies (64.01 ± 0.82) than sites without prairie dogs (67.80 ± 0.84 ; $P = 0.006$), and this difference was maintained across all 3 mo (Month $\times$ Site Type $P = 0.5$). NDF was higher in August than June or July (Month $P = 0.001$; see Fig. 5).

Acid detergent fiber (ADF) was 11% lower on prairie dog colonies (35.61 ± 0.78) when compared with sites without prairie dogs (39.95 ± 0.64 ; $P = 0.02$) across years for composite samples, and these differences were maintained throughout the season (Month $\times$

Site Type $P = 0.2$; see Table 2). ADF was higher in August than June or July (Month $P < 0.0001$). However, western wheatgrass samples contained similar ADF on prairie dog colonies (34.83 ± 0.62) as sites without prairie dogs (36.92 ± 0.50 ; Site Type $P = 0.1$; Month $\times$ Site Type $P = 0.6$). For western wheatgrass samples, ADF was higher in August than June or July (Month $P < 0.0001$).

In-vitro true dry matter digestibility (IVTDM) was $1.03\times$ higher on prairie dog colonies (70.93 ± 1.20) than sites without prairie dogs (68.29 ± 0.65 ; $P = 0.004$) across years for composite samples, but the

Table 2

Select summary of forage quality nutrients at paired sites (with and without prairie dogs) across month (June, July, and August) and yr (2016–2017) in northeastern Wyoming. Statistically significant values ($P < 0.05$) are denoted in bold print. All month effects were significant ($P \leq 0.003$).

% Nutrient from dry matter	Composite forage samples				Western wheatgrass forage samples			
	On-colony (mean $\pm$ SE)	Off-colony (mean $\pm$ SE)	Site type ² <i>P</i> value	Month $\times$ Site type <i>P</i> value	On-colony (mean $\pm$ SE)	Off-colony (mean $\pm$ SE)	Site type ² <i>P</i> value	Month $\times$ Site type <i>P</i> value
<i>Metrics of protein, energy, and fat</i>								
Crude protein	12.33 $\pm$ 0.81	8.7 $\pm$ 0.38	0.041	0.009	12.66 $\pm$ 0.72	8.79 $\pm$ 0.61	0.008	0.409
Kilograms of crude protein per hectare ¹	73.93 $\pm$ 13.20	61.34 $\pm$ 5.14	0.5	n/a				
Total digestible nutrients	61.95 $\pm$ 0.90	57 $\pm$ 0.74	0.017	0.161	62.83 $\pm$ 0.70	60.46 $\pm$ 0.58	0.119	0.600
Fat	3.14 $\pm$ 0.15	2.44 $\pm$ 0.09	0.037	0.182	3.53 $\pm$ 0.16	3.15 $\pm$ 0.13	0.022	0.380
<i>Metrics of digestibility</i>								
Acid detergent fiber	35.61 $\pm$ 0.78	39.95 $\pm$ 0.64	0.017	0.164	34.84 $\pm$ 0.62	36.92 $\pm$ 0.50	0.120	0.603
<i>In-vitro</i> true dry matter digestibility	70.93 $\pm$ 1.2	68.29 $\pm$ 0.65	0.004	0.016	71.77 $\pm$ 0.78	69.4 $\pm$ 0.66	0.163	0.437
Neutral detergent fiber	62.36 $\pm$ 1.15	68.88 $\pm$ 1.04	0.068	0.213	64.01 $\pm$ 0.82	67.8 $\pm$ 0.84	0.006	0.478
Neutral detergent fiber digestibility	49.75 $\pm$ 2.21	51.79 $\pm$ 1.00	0.284	0.068	55.57 $\pm$ 1.31	54.69 $\pm$ 1.24	0.646	0.863
Lignin	4.12 $\pm$ 0.27	4.01 $\pm$ 0.12	0.969	0.350	3.3 $\pm$ 0.12	3.36 $\pm$ 0.11	0.702	0.041
<i>Metrics of minerals</i>								
Ash	8.06 $\pm$ 0.70	6.47 $\pm$ 0.42	0.379	0.685	6.9 $\pm$ 0.43	4.84 $\pm$ 0.36	0.151	0.568
Calcium	0.56 $\pm$ 0.04	0.41 $\pm$ 0.03	0.358	0.747	0.4 $\pm$ 0.02	0.3 $\pm$ 0.02	0.034	0.474
Magnesium	0.2 $\pm$ 0.01	0.11 $\pm$ 0.01	0.031	0.243	0.18 $\pm$ 0.01	0.15 $\pm$ 0.01	0.148	0.995
Phosphorus	0.2 $\pm$ 0.01	0.14 $\pm$ 0.01	0.006	0.074	0.23 $\pm$ 0.01	0.19 $\pm$ 0.01	0.049	0.740
Potassium	1.32 $\pm$ 0.13	0.9 $\pm$ 0.07	0.090	0.090	1.55 $\pm$ 0.12	1.28 $\pm$ 0.10	0.094	0.315

¹ Kilograms of crude protein $\cdot$ ha⁻¹ was estimated for composite samples only to reflect field conditions of species composition in our study sites.

² Site type indicates sites with prairie dogs versus sites without prairie dogs.

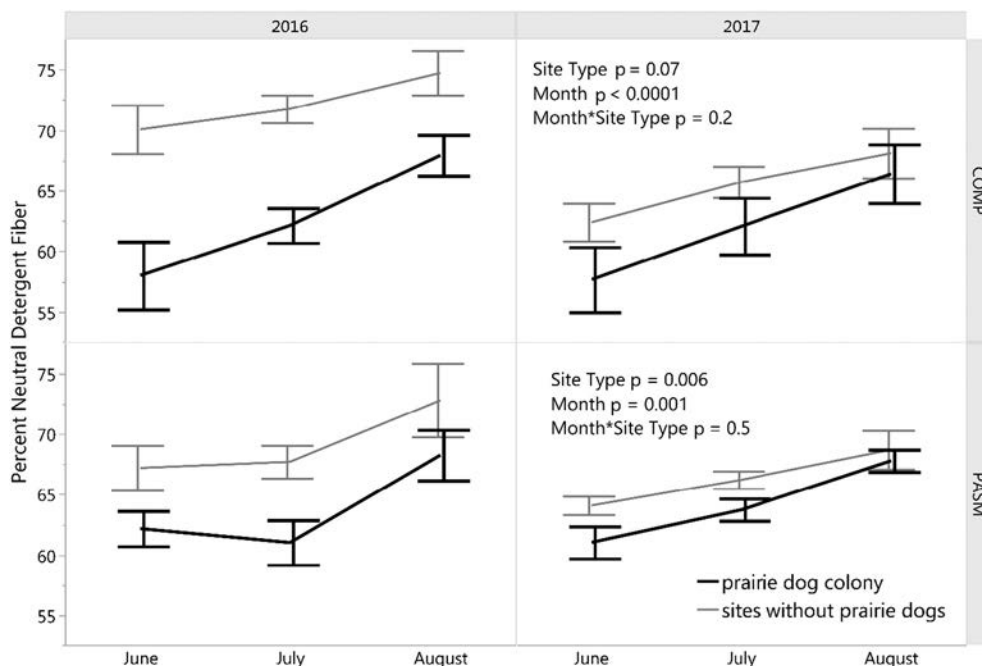


Figure 5. Effects of black-tailed prairie dog herbivory on neutral detergent fiber (NDF; % dry matter), across four sites and 2 yr, in Thunder Basin National Grassland, Wyoming. Prairie dog colonies and sites without prairie dogs are denoted in model results by “Disturbance Type.” Error bars show $\pm$ SE.

strength of this effect varied by month (Month $\times$ Site Type $P = 0.02$; see Table 2). In June, IVTDMD of composite samples was significantly greater on prairie dog colonies than on sites without prairie dogs, but in July and August, IVTDMD did not differ significantly between sites with prairie dogs and sites without prairie dogs. For both site types, IVTDMD was significantly higher in June than July or August. Across years, western wheatgrass samples contained similar IVTDMD on prairie dog colonies (71.77 ± 0.78) as sites without prairie dogs (69.40 ± 0.66 ; Site Type $P = 0.2$; Month $\times$ Site Type $P = 0.4$).

IVTDMD in western wheatgrass samples was significantly higher in June than July and significantly higher in July than August (Month $P < 0.0001$).

For composite samples, lignin was not different between prairie dog colonies (4.12 ± 0.27) and sites without prairie dogs (4.01 ± 0.12 ; Site Type $P = 1.0$; Month $\times$ Site Type $P = 0.4$; see Table 2). Lignin in composite samples was significantly higher in July than June, while August had intermediate values (Month $P < 0.003$). Western wheatgrass samples contained similar amounts of lignin on prairie dog colonies ($3.30 \pm$

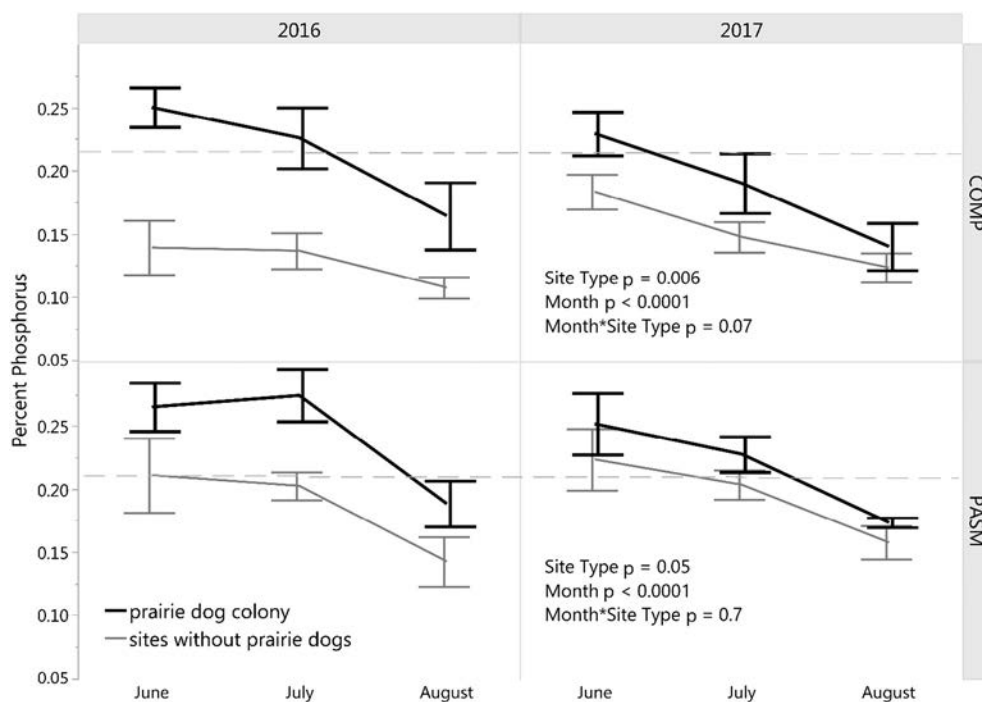


Figure 6. Effects of black-tailed prairie dog herbivory on phosphorus (P; % dry matter), across four sites and 2 yr, in Thunder Basin National Grassland, Wyoming. Dashed line indicates the phosphorus requirements for an average milking beef cow of moderate size, 3–4 mo postpartum. Error bars $\pm$ SE.

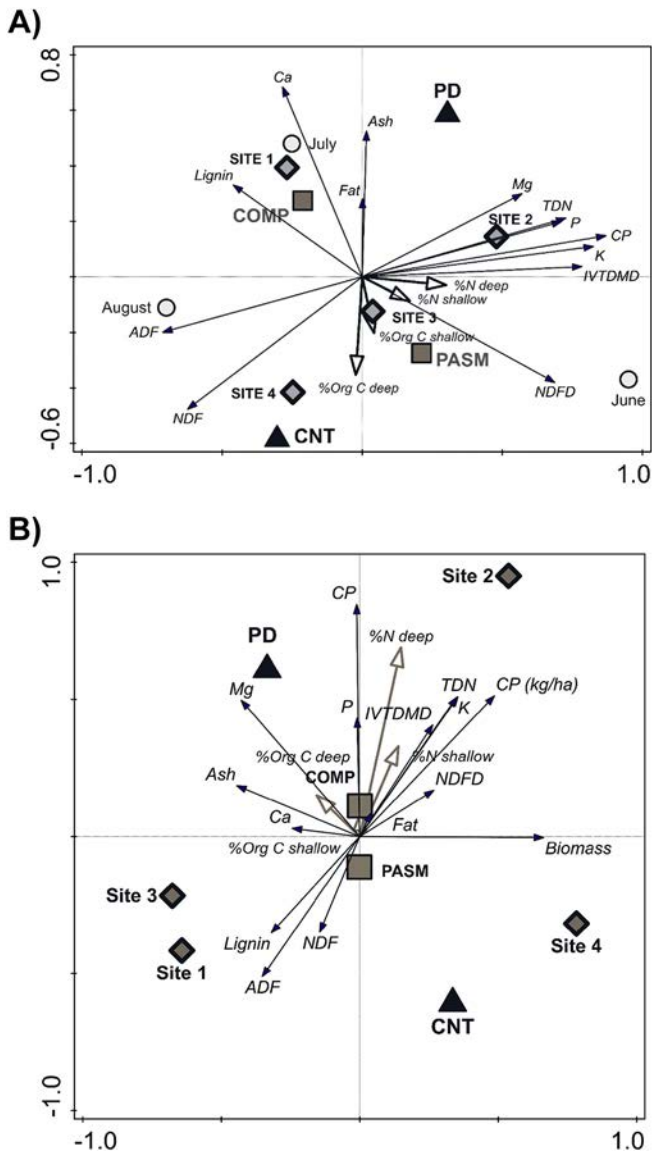


Figure 7. (A) Partially constrained RDA ordination of all forage quality metrics collected June–August 2016–2017 and soil nutrient content collected June 2015. Axis 1 explained 73.22% of the fitted variation, and Axis 2 explained 17.9% of the fitted variation. Triangles indicate site type; “PD” stands for prairie dog colonies and “CNT” stands for control (sites without prairie dogs). “%Org C” and “%N” represent percent organic soil carbon and percent soil nitrogen, respectively; “shallow” represents samples from 0 to 10 cm, and “deep” indicates soils from 10 to 30 cm. (B) Partially constrained RDA ordination of biomass and forage quality metrics collected August 2016–2017 and soil nutrient content collected June 2015. Axis 1 explained 99.41% of the fitted variation. Axis 2 explained an additional 0.54% of the fitted variation. Triangles indicate site type; “PD” stands for prairie dog colonies, and “CNT” stands for control (sites without prairie dogs). “%Org C” and “%N” represent percent organic soil carbon and percent soil nitrogen, respectively; “shallow” represents samples from 0 to 10 cm and “deep” indicates soils from 10 to 30 cm.

0.12) as sites without prairie dogs (3.36 ± 0.11 ; $P = 0.7$), but seasonal patterns varied between site types (Month $\times$ Site Type $P = 0.04$). On sites without prairie dogs, lignin values were significantly lower in June than July or August, but lignin values on prairie dog colonies did not differ significantly across months.

Forage Quality: Minerals

Phosphorous was $1.4\times$ higher on prairie dog colonies (0.20 ± 0.01) than sites without prairie dogs (0.14 ± 0.01 ; $P = 0.006$) across years for

composite samples, though the strength of this effect varied marginally by month (Month $\times$ Site Type $P = 0.07$; Fig. 6, see Table 2). Across site types, phosphorous was higher in June than July and higher in July than August (Month $P < 0.0001$). Western wheatgrass samples contained $1.2\times$ greater phosphorous on prairie dog colonies (0.23 ± 0.01) than sites without prairie dogs (0.19 ± 0.01 ; $P = 0.05$; see Table 2), and this difference was maintained across all 3 mo (Month $\times$ Site Type $P = 0.7$). For western wheatgrass samples, phosphorous was lower in August than June or July (Month $P < 0.0001$; see Fig. 6).

Calcium did not differ between prairie dog colonies (0.56 ± 0.04) and sites without prairie dogs (0.41 ± 0.03 ; Site Type $P = 0.4$; Month $\times$ Site Type $P = 0.7$; see Table 2) across years for composite samples. Calcium in composite samples was significantly higher in July than June, while August had intermediate values (Month $P < 0.006$). In contrast, western wheatgrass samples contained $1.3\times$ higher Calcium on prairie dog colonies (0.40 ± 0.02) than sites without prairie dogs (0.30 ± 0.02 ; $P = 0.03$), and this difference was maintained across all 3 mo (Month $\times$ Site Type $P = 0.5$). Calcium in western wheatgrass samples was lower in June than July or August (Month $P < 0.0001$).

Magnesium was $1.8\times$ higher on prairie dog colonies (0.20 ± 0.01) than sites without prairie dogs (0.11 ± 0.01 ; $P = 0.03$) across years for composite samples, and these differences were maintained across all 3 mo (Month $\times$ Site Type $P = 0.2$; see Table 2). Magnesium in composite samples was higher in June than July or August (Month $P < 0.0001$). In contrast, western wheatgrass samples contained similar amounts of Mg on prairie dog colonies (0.18 ± 0.01) and sites without prairie dogs (0.15 ± 0.01 ; $P = 0.1$; Month $\times$ Site Type $P = 1.0$). Magnesium values in western wheatgrass samples were higher in June than July or August (Month $P < 0.0001$).

Available Crude Protein ($\text{kg} \cdot \text{ha}^{-1}$)

In 2016, a drier than average year, $\text{kg CP} \cdot \text{ha}^{-1}$ on prairie dog colonies (38.0 ± 14.3) did not differ from sites without prairie dogs (52.1 ± 6.8 ; $P = 0.3$; see Table 2). In contrast, in 2017, an average precipitation year, $\text{kg CP} \cdot \text{ha}^{-1}$ was $1.5\times$ greater on prairie dog colonies (109.8 ± 13.2) than sites without prairie dogs (70.6 ± 6.5 ; $P = 0.04$). Across years, $\text{kg CP} \cdot \text{ha}^{-1}$ did not differ between prairie dog colonies (73.9 ± 13.2) and sites without prairie dogs (61.3 ± 5.1 ; $P = 0.5$; see Table 2). The variances in available crude protein are likely due to high variability in herbaceous biomass among sites.

Forage Quality Composition Relative to Site, Seasonality, and Biotic/Abiotic Factors

Our partially constrained RDA of forage quality composition for June–August in 2016 and 2017 revealed Axis 1 explained 73.22% of the fitted variation and was associated with growing season, site type, and sample type. Minerals and digestibility were associated with early growing season (June) samples, prairie dog colony samples, and western wheatgrass samples on the right side of the ordination diagram, while metrics associated with plant maturity were associated with later growing season (August) samples, composite samples, and samples from sites without prairie dogs on the left side of the ordination diagram (Fig. 7a). Forage quality response variables associated with early plant growth stage, prairie dog colonies, and western wheatgrass include IVDMD and CP, whereas NDF and ADF were associated with increasing plant maturity, sites without prairie dogs, and composite samples. Abiotic response variables associated with Axis 1 included % N (0–10 cm and 10–30 cm). The second axis was largely a function of site and sample type, with fat, ash, Ca, Mg, TDN, and P associated with prairie dog colonies

and composite samples, whereas % organic C (0–10 and 10–30 cm), ADF, and NDF were associated with western wheatgrass samples and sites without prairie dogs. The permutation test for significance of all constrained axis was significant (pseudo- F 18.5; $P = 0.001$), suggesting growing season, site type (prairie dog colonies vs. sites without prairie dogs), and sample type explained a significant amount of variation in our forage quality metrics. Overall, our data show strong differences in site type (prairie dog colony vs. sites without prairie dogs) and sample type (composite vs. western wheatgrass) and reinforce the unique characteristics associated with these features.

In our partially constrained RDA for herbaceous biomass and forage quality composition during peak-seasonal biomass (August) of 2016 and 2017, Axis 1 explained 99.41% of the fitted variation and was a function of August peak standing herbaceous biomass, site variation, and site type (see Fig. 7b). Sites without prairie dogs were associated with higher herbaceous biomass and lower mineral content compared with prairie dog colonies. The second axis explained 0.54% of the remaining fitted variation for a total of 99.95% of the fitted variation explained by Axis 1 and 2. The second axis was largely a function of site type, with metrics of nutrition and digestibility (CP, P, Mg, TDN, and K) more strongly associated with prairie dog colonies, whereas metrics of plant maturity and nondigestibility (NDF, ADF, and lignin) were more closely associated with sites without prairie dogs. Forage quality was not strongly influenced by sample type (western wheatgrass vs. herbaceous composite) in August (as indicated by proximity in ordination space in Fig. 7b). The permutation test for significance of all constrained axis was significant (pseudo- F 11.3; $P = 0.001$), suggesting site variability and site type (prairie dog colonies vs. sites without prairie dogs) explained the majority of variation in our herbaceous biomass data.

Discussion

We used a replicated, paired design to compare herbaceous forage quality and quantity on prairie dog colonies and sites without prairie dogs across three growing seasons. We found that during the spring and summer, when livestock diets are most heavily dependent on grasses, forage produced on prairie dog colonies was consistently higher in nutrition for many metrics associated with livestock and native ungulate growth and weight gain (see Table 2). For composite samples in our study site, the average lactating beef cow, which produces 5 kg of milk $\cdot$ day⁻¹ at 3–4 mo postpartum and weighs 450 kg, could potentially meet their nutritional requirements of TDN, CP, Ca, and P for part or all of the growing season on prairie dog colonies (Figs. 4, 5; The National Research Council, 2000). Similarly, Ca requirements could be met on prairie dog colonies throughout most months and years, and P requirements could be met for an additional month on colonies (although, we note a deficiency for the composite sample in 2017; Fig. 6). Access to enhanced fat via foraging on prairie dog colonies is advantageous to maintain body condition and reproductive status (Scasta et al., 2016b). Finally, the role of dormant plant material and neutral detergent fiber (NDF) has implications for animal intake rates because NDF, a metric of forage bulk, limits maximum forage dry matter intake rate to 1.1% of a cow's body weight (Belyea et al., 1993). Although clipping methods may not be analogous to animal foraging decisions at multiple scales within a pasture, our study clearly demonstrates that forage resources available to grazing animals at the bite scale differ between sites occupied and unoccupied by prairie dogs.

In northern mixed-grass prairies, vegetation community composition and cover change within 3–4 yr following prairie dog colonization, whereby graminoids become displaced by annual forbs (Coppock et al., 1983; Archer et al., 1987). Our composite samples included a diverse assemblage of plant functional groups that were capable of mechanistically structuring nutritional composition. For example, nutritional content at different times during the growing season may be influenced

by the relative abundance of warm- versus cool-season grasses. The warm-season species blue grama, which was present in our composite samples, can contain lower CP than western wheatgrass early in the growing season but greater CP later in the growing season and generally has greater digestibility most of the year (Scasta, 2017). Foliar cover of warm-season grasses was greater on sites without prairie dogs in 2015–2016 and did not differ strongly between site types in 2017 (Fig. S1, available online at <https://doi.org/10.1016/j.rama.2018.10.004>). Forb abundance could also drive compositionally induced quality differences depending on the timing of sampling. Foliar cover of short-lived forbs, which typically reach peak performance and nutritional quality in June, was higher on prairie dog colonies than sites without prairie dogs (see Fig. S1). Despite these compositional considerations, we observed differences in metrics of forage quality on prairie dog colonies in both our composite (multispecies) and western wheatgrass (single-species) samples. Repeated herbivory by prairie dogs causes plants to regrow new, tender leaves that are more nutritious and palatable (Detling and Painter, 1983). By isolating western wheatgrass, we removed the confounding influence of variable species composition and isolated a smaller subset of potential mechanisms contributing to increased forage quality on prairie dog colonies. Western wheatgrass results suggest that repeated herbivory by prairie dogs can maintain higher forage quality within a single species by reducing standing dead material at the bite scale or by maintaining plants in an earlier phenological growth stage due to compensatory regrowth. Forage quality often differed between our composite and western wheatgrass samples, indicating that multiple mechanisms are shaping forage quality in this system (e.g., species composition, phenological growth stage, or soil condition changes). Moreover, both composite and western wheatgrass samples contained standing dead material, which is 2–4 $\times$ lower on prairie dog colonies (Whicker and Detling, 1988). The removal of standing dead material is another important mechanism through which prairie dogs may directly enhance forage quality on colonies.

Surprisingly, the expected effect of prairie dog herbivory on herbaceous biomass was not statistically different between sites with and without prairie dogs and remained highly variable throughout our study period due to site and precipitation variability. Our experiment assessed forage characteristics within the context of working landscapes where prairie dogs, other wildlife, and livestock are fully interacting. We compared forage characteristics on sites with and without prairie dogs in the presence of wildlife and livestock grazing, and variability in stocking rates and season of use may have contributed to observed results (see Table 1). Each year, we documented greater herbaceous biomass on one or more sites with prairie dog colonies than sites without prairie dogs. This increase in herbaceous biomass on prairie dog colonies may be an inherent site characteristic of prairie dogs, as they are known to select habitat generally free of shrubs (Hoogland, 1995); thus, herbaceous forage on colonies experiences decreased competition (Lett and Knapp, 2003). However, the influential role of precipitation and interactions of precipitation and prairie dog herbivory at the local site scale may also explain the variable effects prairie dogs can have on herbaceous biomass (Augustine and Springer, 2013).

Our regression of aboveground herbaceous biomass response to spring precipitation illustrates the influential role of spring precipitation on the effect of prairie dog herbivory. For example, in 2015 when herbaceous biomass was 23% higher on prairie dog colonies than undisturbed sites, our study sites received spring precipitation (April–June) 13.1 cm greater than the average long-term spring precipitation. In contrast, herbaceous aboveground biomass was reduced by 58% in 2016, when our study sites received spring precipitation 5.2 cm below the long-term average. Livestock and native ungulates may also contribute to observed biomass reductions during dry periods via potentially increased utilization of higher-quality forage on prairie dog colonies. Following this trend, herbaceous biomass was similar at sites with versus without prairie dogs in 2017, when spring precipitation nearly matched the long-term average (0.6 cm below long-term average).

Thus, the interaction of prairie dog herbivory with the spatiotemporal distribution of precipitation across the landscape and the subsequent effect on herbaceous biomass are more informative than the overly simplistic view that prairie dogs always are antagonistic to livestock production (see also Augustine, 2010; Augustine and Springer, 2013).

Complex trade-offs between forage quality and quantity were further illustrated by the interactive effects of prairie dog herbivory and spring precipitation on $\text{kg CP} \cdot \text{ha}^{-1}$, a metric that accounts for both biomass and forage quality simultaneously. In 2016, when spring precipitation was below average, $\text{kg CP} \cdot \text{ha}^{-1}$ was similar between sites with prairie dogs and those without prairie dogs; however, with near-average spring precipitation in 2017, prairie dog colonies contained greater $\text{kg CP} \cdot \text{ha}^{-1}$ than sites without prairie dogs. These findings have direct implications for livestock enterprises and livestock production and performance.

Our research has identified several topics concerning livestock and forage performance within areas occupied by prairie dogs that are in need of further investigation. We suggest further research is needed: 1) to more directly quantify the potential benefits of consuming digestible organic matter in the absence of standing dead material (as observed on prairie dog colonies). We recommend feeding trials or *in-situ* foraging studies that use fecal NIRS or similar methods to assess direct digestibility; 2) to directly assess the effect of prairie dogs on animal performance, specifically cattle weight gain in the presence and absence of prairie dogs at varying level of pasture occupancy, in a grassland-shrubland ecotone; and 3) to directly assess how prairie dog density and colony age may have contributed to the variable effects of prairie dogs on herbaceous biomass that we observed in this study. We suggest future research should quantify herbaceous biomass across a broad gradient of prairie dog densities over multiple years with variable precipitation.

Vegetation of low forage quality requires herbivores to spend additional time and effort foraging to increase net biomass intake to achieve desired nutrition concentrations (Fryxell, 1991). Plant nutrition and digestibility is negatively associated with maturation and biomass (Van Soest, 1994), and thus plants that experience repeated herbivory, as in the case of forage on prairie dog colonies, express decreased herbaceous biomass and increased forage quality, specifically for CP and digestibility measurements, because of their immature phenological growth stage. In these circumstances, large herbivores are faced with a trade-off to 1) maximize time spent searching a habitat patch for forage that is low in biomass but high in nutrition (necessitating increased foraging time to achieve base requirements of ruminant intake) or 2) conserve energy through decreased foraging behavior and maximize time by consuming readily available vegetation that is greater in biomass but lower in nutritional quality and digestibility (Charnov, 1976; Bergman et al., 2001).

Our results, coupled with foraging theory, begin to address the questions: 1) does the effect of prairie dog herbivory on forage quantity and quality create trade-offs between a limited quantity of a resource at a higher quality? And 2) can cattle mitigate this interspecific competition by strategic distributional decisions (Rosenzweig, 1995)? Trade-offs between forage quantity and quality are addressed by scientific studies in northwestern Mexico, which demonstrated both bison and cattle used black-tailed prairie dog colonies in disproportionate amounts when compared with their availability (Chipault and Detling, 2013; Sierra-Corona et al., 2015; but see Guenther and Detling, 2003). This preferential grazing on prairie dog colonies, coupled with our study results, suggests increased forage quality on prairie dog colonies might facilitate large ungulate distribution and foraging strategies and provide benefits to livestock in times of above-average spring precipitation. Conversely, prolonged periods of below-average precipitation can eliminate beneficial effects of prairie dog colonies by limiting instantaneous intake rate of forage and livestock may need to spend additional time foraging in areas without prairie dogs to compensate for biomass reduction (Vermeire et al., 2004; Augustine and Springer, 2013).

In the Northern Plains, rangeland-based livestock operations are heavily reliant on rainfall events and remain susceptible to year-to-year variability and long-term climatic changes (Derner et al., 2018). Thus, the mitigating effect of prairie dogs on forage quality and herbaceous biomass, which is closely related to spring precipitation, is also subject to uncertainty. Forecasted climate change models for this region project increased winter and spring precipitation, with rising temperatures that can lengthen growing seasons (Shafer et al., 2014). Drought forecasts predict an increase in the maximum precipitation received in a single day, while the annual longest consecutive dry-day period is expected to remain similar or even decrease over the next 30–70 yr; these predictions are notably unique compared with the rest of the United States (Derner et al., 2018). Increasing atmospheric CO_2 is also predicted to increase total forage production while negatively affecting digestibility of forage (Augustine et al., 2018). These trends could potentially lead to increased utilization of prairie dog colonies by livestock and native ungulates seeking improved forage quality.

Implications

Black-tailed prairie dogs generally compete with livestock for graminoid forage, but in years of average or above-average rainfall prairie dog herbivory may not significantly reduce herbaceous biomass. Moreover, prairie dogs increased most forage quality metrics of nutrition, including digestibility, with many of these positive effects extending through the growing season. These findings suggest livestock can sometimes benefit from access to prairie dog colonies, similar to pre-European bison-prairie dog interactions, which may have conservation implications for the black-tailed prairie dog. The conservation of prairie dogs within their native grassland habitat is important for ensuring the continued provisioning increased groundwater recharge and benefits to soil (Martínez-Estévez et al., 2013), grassland biodiversity (see Augustine and Baker, 2013 for implications specific to our region of study), and other benefits provided via the ecosystem engineering activities of this unique burrowing mammal (Kotliar et al., 1999).

These benefits, coupled with comparable herbaceous biomass on prairie dog colonies in years with average or above-average spring precipitation, could serve to mitigate direct competition with livestock for forage and therefore alleviate forage-centric tensions surrounding the presence of prairie dogs on rangelands. In fact, given current climate projections for this region, the long-term maintenance of native rangelands that can provide high-quality nutrition for livestock may be facilitated by conservation of the black-tailed prairie dog. However, benefits are dependent on spring precipitation; in years of average spring precipitation, livestock may require periodic access to areas without prairie dogs to meet bulk intake requirements, and in years of below-average spring precipitation livestock may not be able to meet their bulk forage intake requirements solely on prairie dog colonies. In addition, when prairie dogs occupy the majority of a pasture during seasons of below-average precipitation, cattle weight gain can be negatively affected (Derner et al., 2006). Producers should be especially cognizant in years of below-average precipitation when prairie dog-induced reductions of herbaceous biomass become pronounced.

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Appendix A

Livestock grazing utilization during the study period (2015–2017) in Thunder Basin National Grasslands, Wyoming. We collected data at sites with prairie dog colonies and from separate, spatially distinct areas without prairie dogs (≥ 280 m from colony edge). Livestock grazing information provided by the Thunder Basin Grazing Association.

Site	Prairie dogs presence or absent	Pasture size (ha)	Date in	Date out	Livestock type	Animal unit months
1	Prairie dogs present	874	7/16/2015	9/20/2015	Cows/calves	177
			8/1/2016	8/31/2016	Cows/calves	46
			9/1/2016	9/20/2016	Ewes	124
			9/28/2016	10/4/2016	Cows	30
			8/1/2016	9/20/2016	Cows/calves	132
			9/28/2016	10/4/2016	Ewes	44
			8/1/2017	9/20/2017	Cows/calves	131
1	Prairie Dogs Absent	660	5/8/2015	5/15/2015	Cows	32
			7/2/2015	8/3/2015	Ewes/lambs	52
			5/10/2016	5/30/2016	Cows/calves	14
			5/10/2016	5/30/2016	Yearling steers	31
			8/2/2016	9/4/2016	Ewes/lambs	68
			5/8/2017	5/11/2017	Cows/calves	16
			7/16/2017	8/26/2017	Ewes/lambs	70
			12/9/2017	2/15/2018	Cows/calves	82
2	Prairie dogs present + absent	12 655	1/1/2015	6/11/2015	Cows/calves	2 025
			12/20/2015	3/18/2016	Cows/bulls	1 631
			12/10/2016	3/3/2017	Cows	1 683
			11/18/2017	12/31/2017	Cows	911
			1/1/2015	6/1/2015	Bulls	155
3	Prairie dogs present + absent	2 809	9/1/2015	5/1/2016	Bulls	248
			9/1/2016	5/1/2017	Bulls	196
			9/1/2017	12/31/2017	Bulls	140
			5/10/2015	7/4/2015	Cows/calves	877
4	Prairie dogs present + absent	3 650	5/25/2016	8/2/2016	Cows/calves	864
			5/20/2017	7/13/2017	Cows/calves	904
			6/12/2017	7/13/2017	Bulls	32

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RESEARCH ARTICLE OPEN ACCESS

Potential Landscapes for Conservation of the Black-Tailed Prairie Dog Ecosystem

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ABSTRACT

Aim: To identify potential landscapes for the conservation of the black-tailed prairie dog (*Cynomys ludovicianus*; BTPD) ecosystem, across their historical geographical range within the United States.

Location: Central Grasslands of the United States.

Methods: We used a structured decision analysis approach to identify landscapes with high conservation potential (HCP) for the BTPD ecosystem. Our analysis incorporated ecological, political and social factors, along with changing climate and land use to maximise long-term conservation potential.

Results: The landscapes we identified with HCP (top 30% rangewide) represented 22% of the historical distribution of BTPDs and remained strongholds under projected climate change. We provide a suite of HCP area scenarios to help inform different conservation and management interests, including those that consider projected climate change and jurisdictional (state-level) boundaries.

Main Conclusions: Our findings highlight the large conservation potential for BTPDs and associated species, and the maps we generated can be incorporated into other large-scale, multispecies conservation planning efforts being developed for the Central Grasslands of North America.

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1 | Introduction

Conservation planning involves identifying where, when and how to allocate limited conservation resources to maximise the preservation of biodiversity (Pressey et al. 2007). Of central importance to determining areas with high conservation potential (hereafter, HCP) is identifying the most ecologically suitable habitat for the species or communities of interest—the biophysical landscape. However, for conservation goals to be effectively implemented on the ground, understanding the human landscape is also critical (Knight et al. 2008). Systematic conservation planning (Margules and Pressey 2000) has evolved over the last several decades, going beyond the biophysical landscape, to holistically incorporate biodiversity processes, habitat connectivity, ecosystem services, climate change, dynamic threats, economics and political and social landscapes (Pressey et al. 2007). Yet, incorporating human dimensions into a spatial landscape to inform conservation planning remains a challenge and has been limited in its application (Knight and Cowling 2007; Knight et al. 2008; Whitehead et al. 2014; Williamson et al. 2018). Insights into the human dimensions are especially needed for species that have large, transformative effects on ecosystems and are consequently often in conflict with human activities, such as prairie dogs (*Cynomys* spp.), beavers, wolves (*Canis lupus*), and bison (*Bison bison*) (Miller et al. 2007; Pilliod et al. 2018; Niemiec et al. 2021; Pejchar et al. 2021; Livieri et al. 2022). Even if the biophysical landscape is highly suitable for conservation or recovery of these high-conflict species, the human sociocultural landscape might prohibit on-the-ground success (Knight et al. 2008; Niemiec et al. 2021).

North America's Central Grasslands are among the most endangered ecosystems in the world and face a suite of conservation challenges associated with habitat loss, transformation and fragmentation (Samson, Knopf, and Ostlie 2004; Olimb and Robinson 2019; Lark et al. 2020; Augustine et al. 2021). Millions of bison, pronghorn and elk historically inhabited the Central Grasslands, along with wolves and grizzly bears, once rivalling the wildlife abundance of Africa's Serengeti (Samson, Knopf, and Ostlie 2004; Dan Flores 2017). The region since has been converted to a highly domesticated landscape, with fences, livestock, crops and complex jurisdictional boundaries making large-scale conservation efforts and planning challenging (Augustine et al. 2021). The impact of human activities on the Central Grasslands has resulted in widespread declines in native wildlife, including >95% declines in bison and prairie dogs, >50% decline in grassland birds, and near extirpation of wolves and grizzly bears (Hoogland 2006; Sanderson et al. 2008; Rosenberg et al. 2019). Recent awareness of the plight of the Central Grasslands and associated species has inspired new conservation initiatives like the *Central Grasslands Roadmap*, *Great Plains Summit*, WAFWA's *Western Grasslands Initiative* and *The North American Grasslands Conservation Act of 2024* recently introduced in the U.S. Congress (Western Association of Fish and Wildlife Agencies 2011; Finch 2018; Heady and Child 2019; Lark 2020; Haaland et al. 2021; Central Grasslands Roadmap 2022; Mace 2024). One of the conservation strategies taken by these and other initiatives is to focus prioritisation efforts on umbrella species, whose conservation results in protecting suites of associated species or entire ecosystems (Carroll, Dunk, and Moilanen 2010; Gary et al. 2022).

Black-tailed prairie dogs are often at the centre of many conservation efforts throughout the Central Grasslands because of the disproportionate ecological role they play (Davidson, Detling, and Brown 2012; Hoogland 2006). Prairie dogs transform the grassland landscape through their burrowing and herbivory, creating islands of open grassland habitat dotted with numerous mounds that are linked to extensive burrow systems tunnelling deep underground (Davidson, Detling, and Brown 2012; Hoogland 2006). Their colonies attract grassland animals that prefer open habitats and utilise their burrows for homes and shelter, including mountain plovers and burrowing owls, lizards, snakes, numerous arthropods, rabbits and other rodents (Augustine and Baker 2013; Augustine and Derner 2012; Davidson, Detling, and Brown 2012; Duchardt, Augustine, and Beck 2019). Pollinators are also attracted to their colonies because of the greater floral abundance and open bare soil for oviposition sites (Hardwicke 2006), and large herbivores like bison and cattle are attracted to the more nutritious forage that can be found in their colonies (Kotliar et al. 2006; Bayless and Beier 2011; Connell, Porensky, and Scasta 2019). Prairie dogs also provide an important source of prey for numerous predators, including coyotes (*Canis latrans*), American badgers (*Taxidea taxus*), raptors [e.g. golden eagles (*Aquila chrysaetos*), ferruginous hawks (*Buteo regalis*)] and the highly endangered black-footed ferret (*Mustela nigripes*) (Davidson, Detling, and Brown 2012; Eads and Biggins 2015; Eads, Biggins, Grassel, et al. 2016; Goodrich and Buskirk 1998; Grassel, Rachlow, and Williams 2015; Kotliar et al. 2006).

Yet, prairie dog populations have declined dramatically since the early 1900s due to widespread extermination efforts, introduced plague, shooting and habitat loss. The declines of prairie dogs rangewide, and locally following cyclic plague events, has resulted in cascading declines in associated species (Cully et al. 2010; Eads and Biggins 2015; Davidson et al. 2022; Duchardt et al. 2023). The black-footed ferret, for example, is considered North America's most endangered mammal largely as a result of the dramatic decline in prairie dogs, their primary prey (U.S. Fish and Wildlife Service 2013; Livieri et al. 2022). These declines in prairie dogs and associated species underscore the need for conserving the prairie dog ecosystem by identifying potential landscapes for conservation both now and into the future. And—critically—such areas need to be considered within the context of the social, environmental and economic factors that influence where prairie dog complexes can be conserved and expanded across large blocks of continuous habitat so that they can support numerous grassland species (Davidson, Detling, and Brown 2012; Duchardt, Augustine, and Beck 2019; Livieri et al. 2022).

Here, we use a systematic spatial conservation prioritisation approach (Moilanen, Kujala, and Leathwick 2009) to determine HCP areas for the conservation of the prairie dog ecosystem. Our approach provides a structured decision analysis (*sensu* Gregory et al. 2012) that disentangles the complex biophysical and sociopolitical landscapes of North America's Central Grasslands and illuminates areas with the greatest potential for conservation successes. We provide a suite of HCP area scenarios to help inform different conservation and management interests, including those that consider projected climate change and jurisdictional (state-level) boundaries.

2 | Methods

2.1 | Spatial Data Layers Used in Conservation Prioritisation Analysis

We used the spatial conservation prioritisation method and Zonation software (Moilanen et al. 2005) to evaluate how landscapes varied in their potential for prairie dog ecosystem conservation and restoration across the full range of species in the United States. Our analysis included a total of 23 environmental input datasets for the full study area, based on the data sources described in Table 1. The most important layer we used to inform our analysis was the BTPD habitat suitability model, as it provided the basis for where, ecologically, the best places are to conserve and restore the BTPD ecosystem (Davidson et al. 2023). This habitat suitability model (HSM) was based on presence and absence data for BTPD occurrences across their geographical range within the United States (McDonald et al. 2015), and quantified how prairie dog occurrences related to climate, soils, topography and land cover (see Davidson et al. 2023 for details). We also utilised HSMs for BTPDs under two future climate scenarios: (1) warm and wet and (2) hot and dry, to inform where the most ecologically suitable habitat will likely be located under a warming climate (Davidson et al. 2023).

However, the goal of our analysis was to not only determine potential landscapes for conservation based on local habitat suitability but also to examine how the distribution and connectivity of native grassland habitat at broad spatial scales, the distribution of threats to prairie dog habitat (such as development and conversion to cropland) and the political and social landscape collectively influence opportunities to conserve and restore the BTPD ecosystem (Table 1; Figure S1). We used the 2016 National Land Cover Database (NLCD) to inform on the location, extent and connectivity of favourable habitats (grassland/shrubland), versus unfavourable habitats (forest/woodland and emergent wetland) for prairie dogs (USGS 2019a). We also created a landscape fragmentation layer by mapping the degree of rangeland fragmentation across the historical BTPD range. To do this, we followed the methods of Augustine et al. (2021), except that we used the 2016 NLCD as the source data layer rather than a combination of the 2011 NLCD and USDA Cropland Data Layers. Briefly, every pixel was classified as either (1) rangeland, which we defined as grassland, shrubland and improved pasture/hay cover types, (2) a fragmenting land cover type, which we defined as forest, cropland or developed lands or (3) neutral land cover types which were not rangeland, but also did not fragment adjacent rangelands. In the final fragmentation map, we set all pixels mapped as either a fragmenting or a neutral land cover type to a value of zero and then calculated the distance to the nearest fragmenting land cover type for each rangeland pixel (e.g. Figure 3 of Augustine et al. 2021). Additionally, we incorporated spatial data on land use: oil and gas well locations, distance to transmission lines, wind turbine count, and road density (Homeland Security Infrastructure Program (HSIP) 2020; United States Census Bureau 2020; Federal Aviation Administration 2021; WellDatabase 2021). These land use data layers provide information on anthropogenic activity that reflects the presence of humans and habitat quality. Areas that have higher levels of human activity may be less favourable for the BTPD ecosystem because of the increased potential for shooting of prairie dogs, impacts on associated species through behavioural

modification, and habitat degradation. We also included spatial layers on projected habitat loss. The tillage risk layer (Olimb and Robinson 2019) informs where habitat is most likely to be lost to cropland. Further, we included scenarios of overall landcover change projected into the future (Sohl et al. 2018), with a focus on areas that would retain the greatest amount of favourable grassland habitat. We then obtained PAD-US (USGS 2019b), National Conservation Easement Database (NCED; Ducks Unlimited and The Trust for Public Land 2021) and other private conservation land data to determine the landownership of identified HCP areas (Table 1). We also obtained data from Carlson, Bevins, and Schmid (2022; Wildlife model presented in Figure 1) to relate HCP areas to plague risk.

We also included social and political spatial data in our analysis. We collated percent of Conservation Reserve Program (CRP) grasslands per county and the League of Conservation Voters Conservation Score Card (LCVCSC) to reflect political and social support for the environment (on a per county basis) (USDA Farm Service Agency 2020; League of Conservation Voters 2022). We also included data from a novel survey of wildlife governance preferences delivered to Canadian, Mexican and American residents (Williamson et al. 2023a, 2023b) to determine the probability that a region would support increases in prairie dog populations or support federal or private incentives for prairie dog conservation. Census tract level estimates were generated using a Bayesian multilevel regression with poststratification wherein the demographics of survey respondents were used to map the probability to census geographies based on the demographic composition of the Census tracts (Williamson et al. 2023b; Gelman 2007; Hanretty 2020). Finally, we created a spatial layer of the count of Land and Water Conservation Fund (LWCF) projects (The Wilderness Society 2015) to reflect a regions' institutional capacity to actualise conservation.

2.2 | Data Preparation

To prepare the underlying data for Zonation, the data layers were integrated into a nested hexagon framework (NHF). A NHF grid is based around a 1 km² hexagon unit that is aggregated up by units of 7 to generate coarser scale cells of 7 km² (cogs), 49 km² (wheels) and 343 km² (rings), allowing for cross-scale multidisciplinary analysis while obscuring precise sensitive location data.

A total of 31 data layers representing point, polygon and raster formats were processed and summarised into the NHF for consideration in the Zonation analysis (Table S1). While the exact process used to integrate the data layers into the NHF and subsequently into raster files for the Zonation analysis was slightly different for each data layer, the general process was the same. All GIS data processing was done using ESRI ArcMap 10.7 software. Input data layers were intersected with the NHF and the data layers were summarised per NHF hexagon cell using Zonal Statistics, Tabulate Area or other similar geoprocessing tools to generate a summary of the source layer data per hexagon. Examples of the resulting tabular summaries conveyed the area of each landcover class per hexagon cell (later converted to a percent), the mean tillage risk, majority landscape condition, the sum of the metres of road or number of wells within a cell, or the presence of wind turbines within each 1 km² hexagon cell.

TABLE 1 | Data layers used in the Zonation analysis and in post hoc analyses, and the original data sources.

Data layer	Source dataset	In final Zonation analysis
Fine-scale habitat suitability		
BTPD habitat suitability model (HSM)	Ensemble model of BTPD habitat potential, under current climate (Davidson et al. 2023)	Yes
BTPD non-habitat mask ^a	Mask layers of unsuitable habitat, based on the BTPD HSMs (Davidson et al. 2023) ^a	Yes
Habitat suitability under climate change	BTPD HSM under future climate (2100), warm and wet scenario (Davidson et al. 2023)	Yes
Habitat suitability under climate change	BTPD HSM under future climate (2100), hot and dry scenario (Davidson et al. 2023)	Yes
Landscape scale land use/land cover		
Percent cover grassland/shrubland	2016 NLCD (land cover class: 52, 71, 81; USGS 2019a)	Yes
Percent cover emergent wetland	2016 NLCD (land cover class: 95; USGS 2019a)	Yes
Percent cover of forests/woodlands	NLCD trees (USGS 2019a) + USFS % tree cover (United States Forest Service 2019) + PLJV cedar and mesquite (Playa Lakes Joint Venture)	Yes
Percent cover of grassland/shrubland in the 6 adjacent hexagons	Raster surface of % grass/shrub from NLCD (land cover class: 52, 71, 81; USGS 2019a) within 1 mile	Yes
Landscape fragmentation	Modified from Augustine et al. (2021) ^b	Yes
Oil/gas wells (well count)	Welldatabase (Welldatabase 2021)	Yes
Distance to transmission lines	(Homeland Security Infrastructure Program 2020)	Yes
Wind turbine count	FAA obstruction database (Federal Aviation Administration 2021)	Yes
Road density (primary and secondary)	US Census Tiger Roads (United States Census Bureau 2020)	Yes
Risk of future habitat loss		
Tillage risk	Olimb tillage risk (Olimb and Robinson 2019)	Yes
Land cover change	Scenario A2, projected 2050; Sohl et al. (2018)	Yes
Land cover change	Scenario A2, projected 2100; Sohl et al. (2018)	Yes
Land cover change	Scenario B2, projected 2050; Sohl et al. (2018)	Yes
Land cover change	Scenario B2, projected 2100; Sohl et al. (2018)	Yes
Land ownership		
Protected area	PAD-US (USGS 2019a)	No, Posthoc
Private lands conservation	NCED (Ducks Unlimited and The Trust for Public Land 2021) + Turner ^c + SPLT ^d + APR ^e properties	No, Posthoc
Social environment		
Political support for the environment	League of Conservation Voters Conservation Scorecard (League of Conservation Voters 2022)	Yes
Preference for prairie dog population increases	Prairie dog survey ^f (Williamson et al. 2023a, 2023b)	Yes

(Continues)

TABLE 1 | (Continued)

Data layer	Source dataset	In final Zonation analysis
Preference for federal economic incentives for prairie dog conservation	Prairie dog survey ^f (Williamson et al. 2023a, 2023b)	No, Posthoc
Preference for private economic incentives for prairie dog conservation	Prairie dog survey ^f (Williamson et al. 2023a, 2023b)	No, Posthoc
% (Conservation Reserve Program) CRP	County level CRP (USDA Farm Service Agency 2020)	Yes
Institutional capacity to actualise conservation	Count of Land and Water Conservation Fund projects (The Wilderness Society 2015)	Yes

^aBTPD non-habitat mask: We created a layer to mask out highly unsuitable habitats. We classified highly unsuitable habitats as those areas where suitability was in the 10th (lowest) percentile for each of the BTPD HSMs generated under the current and future climate scenarios, and where soils were comprised of 90% or greater of sand.

^bLandscape fragmentation layer: We mapped the degree of rangeland fragmentation across the historic BTPD range following the methods of Augustine et al. (2021), except that we used the 2016 NLCD as the source data layer, rather than a combination of the 2011 NLCD and USDA Cropland Data Layers. Briefly, every pixel was classified as (1) rangeland, which we defined as grassland, shrubland and improved pasture/hay cover types, (2) a fragmenting land cover type, which we defined as forest, cropland or developed lands or (3) neutral land cover types which were not rangeland, but also did not fragment adjacent rangelands. In the final fragmentation map, we set all pixels mapped as either a fragmenting or a neutral land cover type to a value of zero and then calculated the distance to the nearest fragmenting land cover type for each rangeland pixel (e.g. Figure 3 of Augustine et al. 2021).

^cTurner Ranches. <https://www.tedturner.com/turner-ranches/>.

^dSouthern plains land trust properties. <https://southernplains.org/en/>.

^eAmerican Prairie (AP) properties. <https://americanprairie.org/>.

^fPrairie dog survey (Williamson et al. 2023a, 2023b): The probability that a region would support increases in prairie dog populations or support federal incentives for prairie dog conservation was based on survey responses from over 29,000 North American residents. Census tract level estimates were generated using a Bayesian multilevel regression with poststratification wherein the demographics of survey respondents were used to map the probability to Census geographies based on the demographic composition of the Census tracts.

Within the attribute table of the hexagon feature class, a series of new attribute fields were created to convey the newly summarised data (e.g. % grassland, number of wells). Using the unique hexagon IDs, the data tables of the summarised information were joined with the feature class attribute table, and the summarised data were copied into the newly created hexagon attribute fields using the 'calculate field' process. Due to the number of hexagons (over 2 million record rows) being calculated, this process often took several days so researchers later began using a python script to 'update cursor' that proved much faster than join/calculate field process. The resulting attribute table of the NHF 1-km cells provided a summary of the datasets integrated, all presummarised to the same framework for compatibility and easy use (Table S1). Some source data layers like percent of CRP and the political voting data were originally in coarse (county/voting district) spatial resolutions. As a result of summarising these datasets to hexagons, the results displayed a false level of spatial precision regarding the data values conveyed. In cases where coarse data were summarised and displayed at a higher spatial resolution, many individual hexagons share the same value that originally represented the district/county as a whole, not a specific hexagon.

The hexagon feature class data were exported to a series of raster layers using the ArcMap Feature to Raster function to accommodate the conservation prioritisation software requirements that all input data be in a raster format. Output raster layers were specified to have a 90-m resolution, were snapped to the same 90-m pixels as the ensemble habitat suitability models, and the raster values were derived from the values in each of the feature class attribute fields representing the 1-km² hexagon summarised data. The intersect, calculate field and convert to raster processes were done in batches using the 5×5 degree

NHF tile or by regional groupings of seven tiles for the northern half of the range and nine tiles for the southern half of the range for efficient processing. After each tile was converted to a raster layer, they were mosaiced together to create a series of range-wide raster layers and then clipped to the BTPD range boundary (Figure S2).

2.3 | Prioritisation Analysis

We used Zonation, an approach and software for spatial conservation prioritisation, to select HCP areas for the conservation of the prairie dog ecosystem. Zonation produces a hierarchical spatial priority ranking of the study region, accounting for complementarity by considering the local representation of the biodiversity features (species, ecosystem types, etc.; Moilanen et al. 2005). Zonation iteratively removes cells whose removal causes the smallest loss in feature representation across the overall remaining region until no cells are left in the region. The hierarchical conservation rank of the region is based on the order of cell removal, which is recorded and can be used later to select any given top fraction (e.g. best 25%) of the region. We used the additive benefit function (ABF) removal rule, which is based on the sum of the features represented in each cell, favouring places containing high habitat quality for a large number of biodiversity features.

The relative weighting of data layers is an important component of the Zonation algorithm and impacts the order in which cells are removed from the prioritisation landscape. Cells that contain a high-weight feature are kept longer in the analysis than cells with only low-weight features. Features with a negative weight are considered undesirable. Consequently, they

Conservation Potential only considering Habitat Suitability

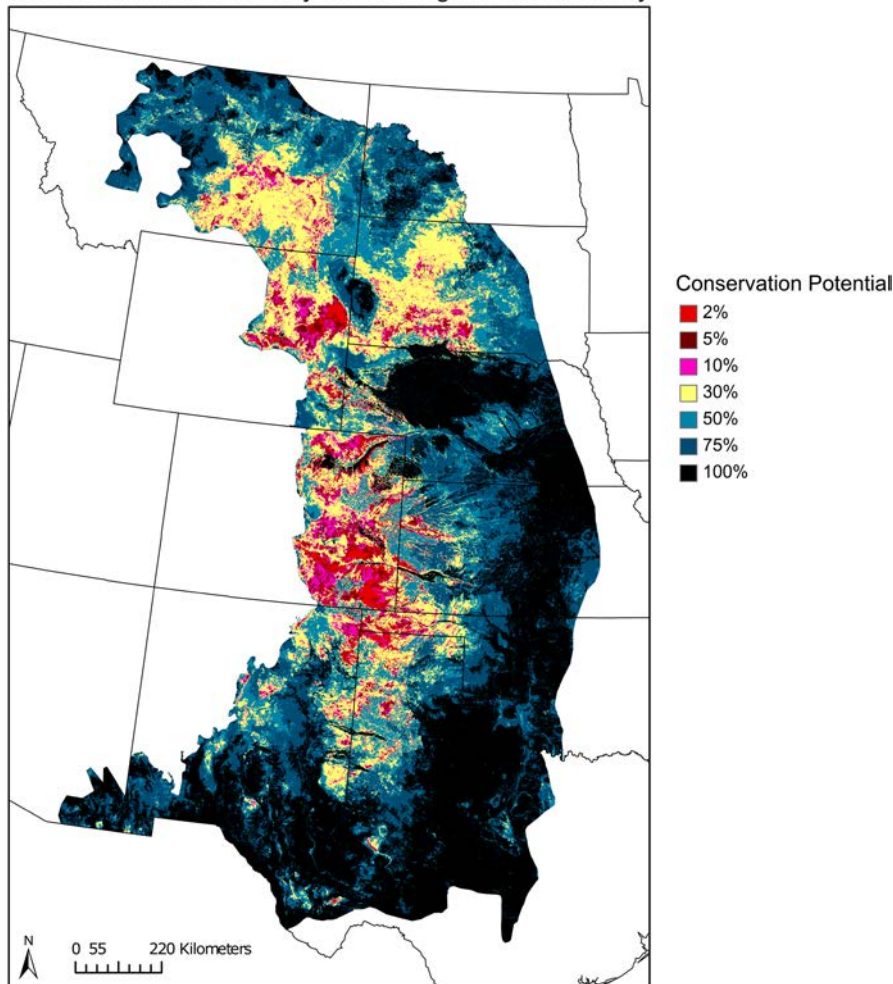


FIGURE 1 | Map of conservation potential across the black-tailed prairie dog (BTPD) geographical range within the United States, considering only habitat suitability and current climate. The priority rankings are as follows: 2% (from 0.98 to 1 of priority rank) Light red; 5% (from 0.95 to 0.979 of priority rank) Dark red; 10% (from 0.90 to 0.949 of priority rank) Pink; 30% (from 0.70 to 0.89 of priority rank) Yellow; 50% (from 0.50 to 0.79 of priority rank) Light blue; 75% (from 0.25 to 0.499 of priority rank) Dark blue; 100% (from 0.00 to 0.249 of priority rank) Black.

are found among the cells with low conservation priority and removed from the landscape early in the analysis. To identify those areas with the highest potential for prairie dog ecosystem conservation, we used a weight of 10 for spatial layers describing habitat suitability for BTPDs, a weight of 1 for landscape-scale land use/land cover features that have a positive influence on conservation potential and a weight of 1 for social environment layers with a positive influence on conservation potential. The spatial layers were considered as features in the analysis with positive values (i.e. higher values indicated favourable places for BTPD conservation). Because suitable habitat is ultimately the most important variable for conservation, we assigned habitat suitability features with the highest weighting among all positive features. We also considered land use in the selection of priorities, aiming to avoid places with high intensity of anthropogenic activities and potential conservation conflicts. Those layers within the landscape-scale land use/land cover and risk of habitat loss categories that negatively affect conservation potential were given negative weights (-4). These areas consequently had low values of conservation priority and were removed from the study region early in the analysis. Details on each feature used can be found in Table 1. Areas with low habitat suitability

or high sandy soil ($>90\%$) were masked out of the analysis using an area mask file, where cells with value '1' were included in the analysis, while cells with value '0' were excluded (Table 1).

We used Zonation to evaluate conservation potential under various scenarios. First, we evaluated HCP areas across the geographical range of BTPDs using suitable habitats under the current climate. Next, we created scenarios that involved current and future projected suitable BTPD habitat, across the BTPD range within the United States. To do this, we used the interaction function that induces connectivity of suitable sites for the interacting features to account for distribution shifts due to climate change. Additionally, because conservation policies and funding decisions are often made by political entities, we also identified conservation priorities within each state, under both present and projected future climate. For this, we used the administrative units (ADMU) function in Zonation to also select state-level priorities in the final conservation ranking (Moilanen and Arponen 2011).

Finally, we conducted several post hoc analyses to help illuminate: (1) those areas where habitat, anthropogenic threats and the social landscape changed the priority ranking and (2) where

conservation incentives may help facilitate prairie dog ecosystem conservation. We evaluated changes in priority ranking by calculating the priority value per cell when habitat, threats or social layers were included in the Zonation analysis minus the priority value of each cell when habitat, threats or social layers were excluded, respectively (see Table 1). The habitat layer was based on the percent of grass (in the NLCD and in the future projections by Sohl et al. 2018), tree and wetland cover and landscape fragmentation (i.e. mean distance to fragmenting feature). The threats layer was based on mean tillage risk, number of active wells, wind turbine count, distance to transmission lines and the density of primary and secondary roads. The social layer was based on the LCV Conservation Scorecard, percent of county-level CRP land, count of LWCF projects and the social survey by Williamson et al. (2023a, 2023b). Lastly, we evaluated the overlap of conservation priority rankings with responses from survey participants' willingness to support federal or private conservation incentives for prairie dog conservation.

3 | Results

We show extensive regions with HCP for the BTPD ecosystem when considering only habitat suitability under the current climate (Figure 1). When we considered all spatial variables (Table 1), in addition to habitat suitability, we found 96,944 km² (top 10%) and 359,425 km² (top 30%) of lands that have high conservation potential for the BTPD ecosystem across all climate scenarios (Figure 2d,e); these areas have high-quality habitat for BTPDs, intact grassland, high habitat connectivity and low threats. This represents 6% (top 10%) and 22% (top 30%), respectively, of the historical BTPD range; the entire prairie dog geographical range boundary within the United States, encompasses 1,645,749 km², not all of which is suitable habitat (Davidson et al. 2023). Land with the lowest conservation potential includes high elevation and urban landscapes, the Nebraska sandhills (high-quality grassland habitat, but unsuitable sandy soils) and grassland that has been converted to or is severely fragmented by cropland (much of the eastern portion of the BTPD range).

We found that landscapes with the highest conservation potential for the BTPD ecosystem were largely distributed across the western portion of the current/historical BTPD range (Figures 1, 2 and 4a). Northeastern New Mexico, eastern Colorado, eastern Wyoming, eastern Montana, far western Nebraska and western South Dakota harboured the greatest amount of HCP habitat now and into the future. Much of (but not all) of the high HCP habitat in Arizona, southern New Mexico and Texas under today's climate does not maintain such status under future climate scenarios (Figure 2d). From a rangewide perspective, the states with the largest amount of HCP habitat (top 10%) were as follows: Colorado, Montana, South Dakota, and Wyoming respectively (Table 2). These four states harbour 87% of the lands with the highest conservation potential for the BTPD ecosystem, both now and into the future.

The priorities changed dramatically when we looked by state, instead of across the entire BTPD range (Figure 3). This is to be expected because we were specifically selecting for HCP habitat *within* each state, whereby each state had its own suite of lands with high, medium and low conservation potential. In these

state-based scenarios, much of the high HCP habitats in Arizona, New Mexico and Texas remained HCP under the future climate scenarios.

Rangewide, there were large differences in the amount of HCP lands across different landownership types. Most of the areas with HCP into the future (top 10%) were located on private land (65%; 63,447 km²) (Table 3, Figure 4b). Whereas 24% (23,467 km²) of lands with HCP were public, with 14.5% on Federal and 9.6% on State lands. Some of the strongholds (top 10%) on public land included State Trust Lands, lands managed by Bureau of Land Management (BLM) and National Grasslands (NGs) managed by the US Forest Service: Thunder Basin NG in Wyoming; Comanche NG in Colorado; Pawnee NG in Colorado; Oglala NG in Nebraska; Kiowa and Rita Blanca NGs in New Mexico, Texas and Oklahoma. Indigenous lands also supported considerable HCP area habitat (8%; 7,779 km²). Other long-term hotspots included those on Private Conservation Lands (2%; 2,250 km²), such as ranches managed by: American Prairie in Montana; Southern Plains Land Trust in southeastern Colorado; Turner Enterprises Inc. (multistate); The Nature Conservancy (multistate) and Malpai Border Lands Group in Arizona. Less than 4% of the top 30% of land with HCP (shown in Figures 2e and 4a) is currently protected (4,643 km²; 1.29% of lands with PAD-US Gap 1 and Gap 2 status and 8,818.24 km²; 2.45% of Private Conservation Lands).

Plague risk (Carlson, Bevins, and Schmid 2022) was high across most landscapes identified as having HCP (Figure 5). Indeed, 87% of the top 30% of landscapes with HCP occurred where plague risk was medium to high (Figure 5b). Few areas with HCP in the top 10% overlapped with low plague risk, these included the eastern portion of Standing Rock and Cheyenne River Reservations in South Dakota, northeastern Colorado and Arizona. Overall, the most suitable, intact habitat for the prairie dog ecosystem overlapped with medium to high plague risk (Figures 1 and 5; see also Davidson et al. 2023).

Figure 6 illuminates how priority rankings changed due to the inclusion versus exclusion of habitat, threat and social layers in the conservation prioritisation analysis. For the habitat layer (Figure 6a), intact grassland (current and future) had a strong, positive influence on conservation potential, especially throughout New Mexico, southeast Colorado, Montana, the Conata Basin region of South Dakota and the desert grasslands of southwest Arizona. Indeed, the western distribution of the BTPD range had the most extensive grassland both now and projected into the future and the least fragmented habitat overall, except for northeastern Colorado and northern Montana (Figure S1). The areas that lost priority rankings due to habitat were largely because of mountainous terrain and/or tree cover (Figure 6a). For the threats layer (Figure 6b), we found cropland development and consequent loss of intact grassland to be the most extensive habitat threat across the BTPD range both today and under projected land use change (Figure S1). The eastern portion of their range was the most impacted by cropland development, especially across the Central and Southern Plains in Texas, Oklahoma and Kansas, and across parts of the Northern Plains in Montana and North Dakota. Oil and gas development was extensive across southeast New Mexico, Texas, Oklahoma, Kansas, northeast Colorado, northwest Wyoming and some parts

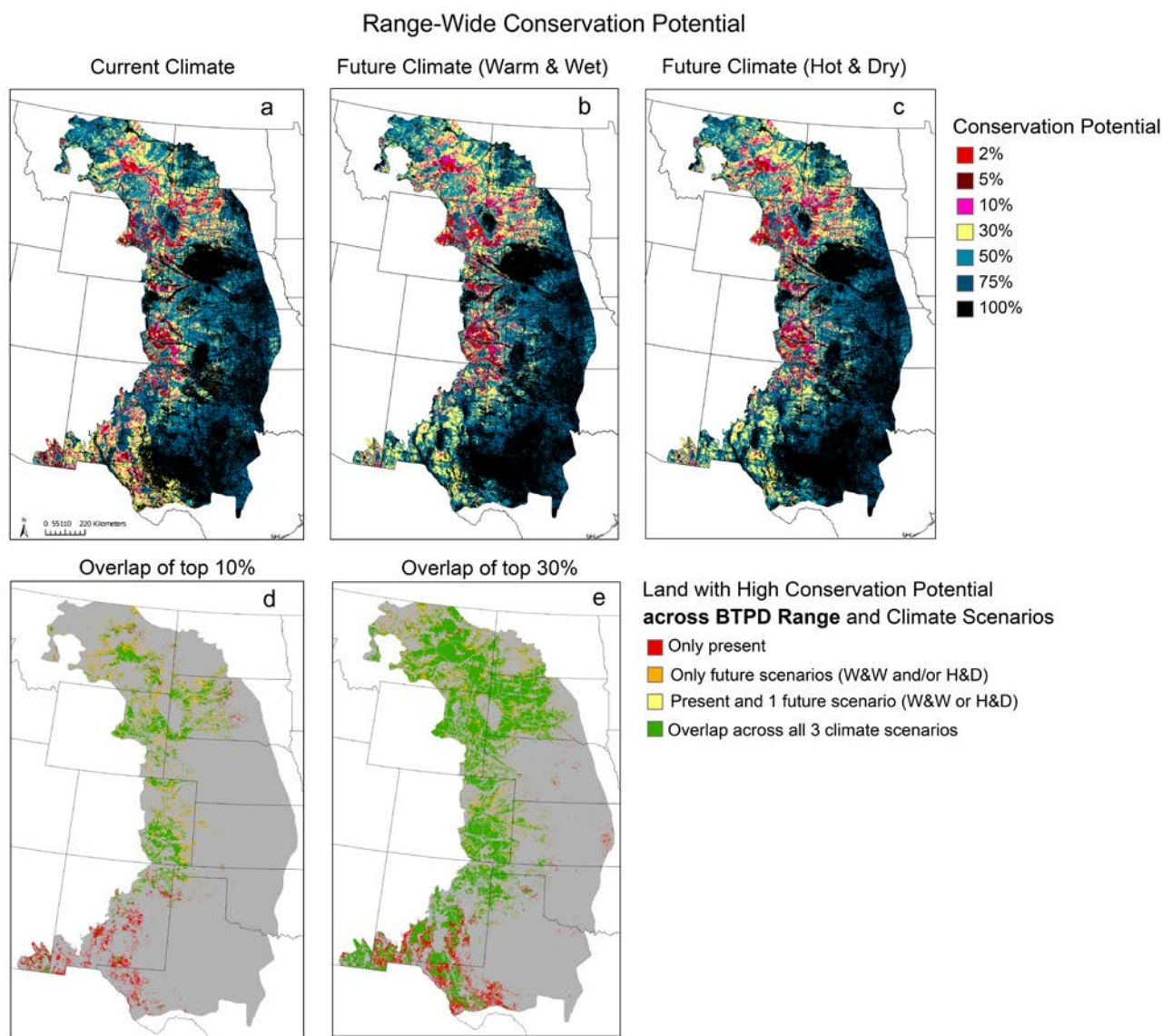


FIGURE 2 | Maps showing conservation potential across the black-tailed prairie dog geographical range under current and future climate scenarios, considering all spatial variables (see Table 1). (a) Conservation potential under the current climate; (b) conservation potential under the warm and wet (W&W) future climate scenario; (c) conservation potential under the hot and dry (H&D) future climate scenario; (d) overlap of the top 10% of lands with high conservation potential across the present and future climate scenarios; (e) overlap of the top 30% of lands with high conservation potential across the present and future climate scenarios. The priority rankings in panels a, b and c are as follows: 2% (from 0.98 to 1 of priority rank) Light red; 5% (from 0.95 to 0.979 of priority rank) Dark red; 10% (from 0.90 to 0.949 of priority rank) Pink; 30% (from 0.70 to 0.89 of priority rank) Yellow; 50% (from 0.50 to 0.79 of priority rank) Light blue; 75% (from 0.25 to 0.499 of priority rank) Dark blue; 100% (from 0.00 to 0.249 of priority rank) Black.

of Montana and North Dakota. Road densities, wind farm development and transmission lines were especially high across Texas, Oklahoma and Kansas, and across the eastern distribution of the BTPD range in general. Areas that lost priority rankings due to threats included the Texas-Oklahoma panhandle region, southwest Kansas, much of eastern Colorado and Wyoming. For the social layer (Figure 6c), a few areas exhibited positive social support for prairie dog conservation, such as in northeast New Mexico and southeast Arizona, and increased in priority rank. Unsurprisingly, there was low social support for BTPD conservation across most of the BTPD range.

Lastly, Figure S3 shows places where conservation incentives may be helpful for securing HCP habitat. These areas (in maroon) included the Thunder Basin ecoregion of northwestern

Wyoming, southeast Arizona, New Mexico, southwest Texas and the panhandle, eastern Colorado, parts of Montana and South Dakota. The places in blue indicate where incentives are likely to be adopted but may fail to secure meaningful conservation, and yellow represents HCP areas that are not likely to be successfully secured with incentives. Overall, we found generally greater support for private than federal conservation incentives throughout much of the lands with HCP.

4 | Discussion

We identify extensive areas of high conservation potential habitat for BTPD ecosystem conservation, especially across the western portion of the BTPD geographical range. These HCP areas

TABLE 2 | Shows how much of the top 10% of lands with high conservation potential (identified in Figures 2d and 4a) occurs within each state.

State	Area (km ²)	%
Total	96,944	100
Colorado	24,084	24.8
Montana	19,401	20.0
South Dakota	19,331	19.9
Wyoming	18,947	19.5
New Mexico	7,082	7.3
Nebraska	2,525	2.6
Arizona	1,845	1.9
Texas	1,552	1.6
Oklahoma	1,059	1.1
North Dakota	699	0.7
Kansas	420	0.4

represent 6% (top 10%) and 22% (top 30%) of their historical distribution within the United States and remain strongholds under projected climate change. Davidson et al. (2023) identified 20.8 million hectares of suitable grassland habitat for the BTPD ecosystem, of which only 9% is currently occupied by prairie dogs (see also BTPD population estimates; McDonald et al. 2015). Here, we build on this work, showing that of the suitable habitat, 96,944 km² have the greatest conservation potential (the top 10%; Figures 2d and 4a) when also considering the threat, social and political landscapes, future climate and habitat connectivity. Our findings highlight the large conservation potential for BTPDs and associated species, especially those that depend on extensive prairie dog colony complexes and intact habitat to support their populations.

Much of the HCP habitat is located across regions where extensive, intact grassland habitat remains. These areas were also located where climate, soils and topography were most suitable for BTPDs. The suitable soils had medium to high clay content, organic matter, pH and low sand content (Davidson et al. 2023), which reflects their preference for clayey-loam soils when burrowing and mound building (Augustine et al. 2012). Regions like the Nebraska Sandhills have extensive, intact grasslands, but have unsuitable soils for prairie dogs (Davidson et al. 2023). The HCP habitats we found were located in areas that also had low topographical ruggedness (Davidson et al. 2023), as BTPDs do not associate with montane habitats and are often found around 700–1700 m elevation (Hoogland 1995). HCP areas were located where a suitable climate exists for the BTPD ecosystem, which is characterised by intermediate levels of net primary productivity, with relatively high winter–spring precipitation, and moderate summer–fall precipitation (Davidson et al. 2023). These climate variables reflect the importance of forage resources during offspring production in the spring (Zaks et al. 2007; Davidson et al. 2014; Hayes, Talbot, and Wolf 2016) and the need for sufficient forage resources for overwinter survival, while too much

summer–fall precipitation can result in tall vegetation that can hamper colony growth (Grassel, Rachlow, and Williams 2016; Bruggeman and Licht 2020).

The HCP areas we identified expanded significantly across the northern distribution of their range under the future climate projections (Davidson et al. 2023). In contrast, the southern distribution of their range became less optimal habitat in the future (Davidson et al. 2023), which is the underlying driver for the HCP area shifts under a changing climate in our analysis (Figure 2). Indeed, prairie dog colonies in the southern distribution of the BTPD range are already in decline in part due to increasing intensity and frequency of drought under climate change (Ceballos et al. 2010; Facka et al. 2010; Hale, Koprowski, and Hicks 2013; Davidson et al. 2014, 2018; Hayes, Talbot, and Wolf 2016). We suggest BTPD conservation might be best maximised by focusing on those areas we highlight in Figure 4a that have HCP under both current and projected future climate. Our analysis also highlights HCP areas in the southern part of the range, such as northeastern New Mexico, that may remain priorities well into the future and be worthy of conservation investment from a rangewide perspective.

Plague risk was relatively high across much of the land we identified as having HCP, as well as where grassland habitat for the prairie dog ecosystem was most suitable and intact (Carlson, Bevins, and Schmid 2022; Figure 5). We evaluated plague risk post hoc, instead of as a variable in our conservation planning analysis, because plague is now endemic across much of the remaining habitat for the prairie dog ecosystem (Davidson et al. 2023; Carlson, Bevins, and Schmid 2022). Additionally, the plague-prairie dog system is complex and poorly understood, creating too much uncertainty when identifying lands with HCP now and into the future. Epizootics are a result of a suite of interactions among climate, landscape connectivity, colony sizes, metapopulation dynamics and host and vector population densities (Collinge et al. 2005; Snäll et al. 2008; Johnson et al. 2011; George et al. 2013; Eads, Biggins, Long et al. 2016; Eads and Hoogland 2017; Biggins and Eads 2019; Barrile et al. 2023), and there remains different hypotheses about how future climate change might alter plague dynamics across the BTPD range (Snäll, Benestad, and Stenseth 2009; Eads and Biggins 2017; Eads and Hoogland 2017; Carlson, Bevins, and Schmid 2022). But, it appears climate change is increasing plague risk across the BTPD range (Carlson, Bevins, and Schmid 2022). Conservation planning for the BTPD system would benefit from a better understanding of plague dynamics in general and from a rangewide perspective of where plague vulnerability is greatest today and where it may increase or decrease under a changing climate. There is a suite of tools currently available to mitigate the impact of plague, often administered in areas considered high priority for BTPD ecosystem conservation and black-footed ferret recovery. These include administering deltamethrin dust to BTPD burrows and/or fipronil grain bait to reduce flea abundance, and/or the oral sylvatic plague vaccine for prairie dogs (Rocke et al. 2017; Biggins, Godbey, and Eads 2021; Eads et al. 2022). Our work, here, highlights that such plague mitigation efforts will be important for colonies selected for conservation prioritisation across most of the habitat that has been identified as having HCP, with a few potential exceptions (Figure 5). Future research might explore how the HCP areas and the spatial

State-Level Conservation Potential

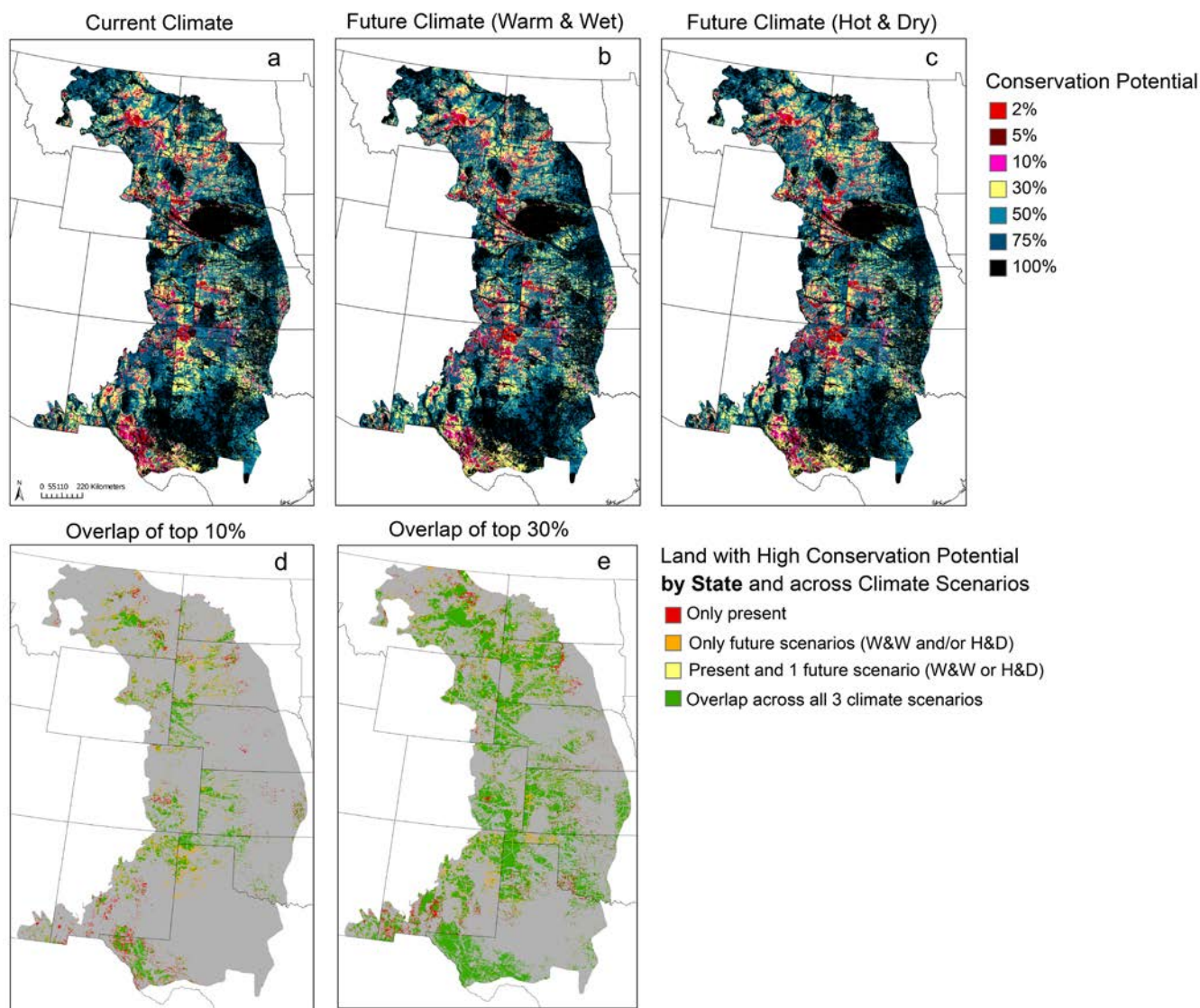


FIGURE 3 | Maps showing state-level conservation potential across the black-tailed prairie dog geographical range under current and future climate scenarios, considering all spatial variables (see Table 1). (a) Conservation potential under the current climate; (b) conservation priorities under the warm and wet (W&W) future climate scenario; (c) conservation potential under the hot and dry (H&D) future climate scenario; (d) overlap of the top 10% of lands with high conservation potential across the present and future climate scenarios; (e) overlap of the top 30% of lands with high conservation potential across the present and future climate scenarios. The priority rankings in panels a, b and c are as follows: 2% (from 0.98 to 1 of priority rank) Light red; 5% (from 0.95 to 0.979 of priority rank) Dark red; 10% (from 0.90 to 0.949 of priority rank) Pink; 30% (from 0.70 to 0.89 of priority rank) Yellow; 50% (from 0.50 to 0.79 of priority rank) Light blue; 75% (from 0.25 to 0.499 of priority rank) Dark blue; 100% (from 0.00 to 0.249 of priority rank) Black.

plague model (Carlson, Bevins, and Schmid 2022) could be used to help inform which areas have the greatest need for plague mitigation and how to best focus such efforts.

State-based conservation priorities differed considerably from rangewide priorities, under both current and future climate scenarios. The largest difference was among the southern states (Arizona, New Mexico and Texas), where climate change reduces the conservation priorities across this region more when viewed from a rangewide perspective than when viewed from a state-level perspective. Additionally, from a rangewide perspective, the

eastern states have fewer areas with HCP compared to the western states within the BTPD range, but when viewed from a state-level perspective there are considerably more areas with HCP. We expected such differences because our question was aimed at understanding the HCP areas within each state, so the analysis sought conservation solutions within each of the states' boundaries. Identifying state-based conservation priorities is important because funding sources and management priorities are often focused at the state level, and not rangewide (Meretsky et al. 2012; Lacher and Wilkerson 2013; Riley et al. 2020). This way, each state has information on conservation priorities within its own

jurisdictional boundaries. We suggest each state focus conservation efforts for the BTPD ecosystem, especially in those areas highlighted in green in Figure 3d,e that remain priorities into the future at the state level, while also considering those priorities identified within their state under the rangewide perspective (Figure 2d,e).

The BTPD ecosystem faces a suite of extrinsic threats. Plague is perhaps the greatest threat facing their populations and that of

TABLE 3 | Shows how much high potential conservation habitat (top 10%, identified in Figures 2d and 4a) overlaps with different landownership categories, across the black-tailed prairie dog geographical range (based on PADUS, NCED and our private conservation lands layer; see Table 1).

Landownership	Area (km ²)	%
Total	96,944	100.0
Private	63,447	65.4
Federal	14,021	14.5
State	9,347	9.6
Indigenous lands	7,779	8.0
NGO/private conservation	2,250	2.3
Local/regional	100	0.1

associated species, followed by lethal control, shooting and habitat loss (Hoogland 2006). We found that the conversion of grasslands to croplands and consequent fragmentation was the overwhelming threat causing habitat loss across the BTPD range (Figure S1). Indeed, the loss of native prairie to agriculture has been and is predicted to be greatest across the eastern part of the BTPD range (Davidson et al. 2023; Sohl et al. 2012; Lark et al. 2020; Augustine et al. 2021; Olimb et al. 2022). Our analysis does not explicitly evaluate the loss of grassland habitat through desertification, as conversion of grasslands to shrublands across the southern distribution of their range has occurred prior to the spatial data on landcover that we used (from 2016; USGS 2019a). But, we know that extensive regions where prairie dogs formerly were abundant across the southwest and northern Mexico are no longer occupied by the BTPD ecosystem (Weltzin, Archer, and Heitschmidt 1997; Ceballos et al. 2010; Hale, Koprowski, and Hicks 2013; Davidson et al. 2014). These desert grasslands continue to be vulnerable to desertification with the ongoing combination of overgrazing by livestock and warming climate, reducing their long-term potential as HCP habitat (Ceballos et al. 2010; Gutzler and Robbins 2010; Hale, Koprowski, and Hicks 2013; Davidson et al. 2014). Although prairie dogs themselves probably are not that impacted by oil and gas development, wind farms, roads and transmission lines (especially common across the eastern distribution of their range), they all increase grassland fragmentation and the presence of humans (Augustine et al. 2021). Smaller, fragmented colonies are less able to support the populations of species that

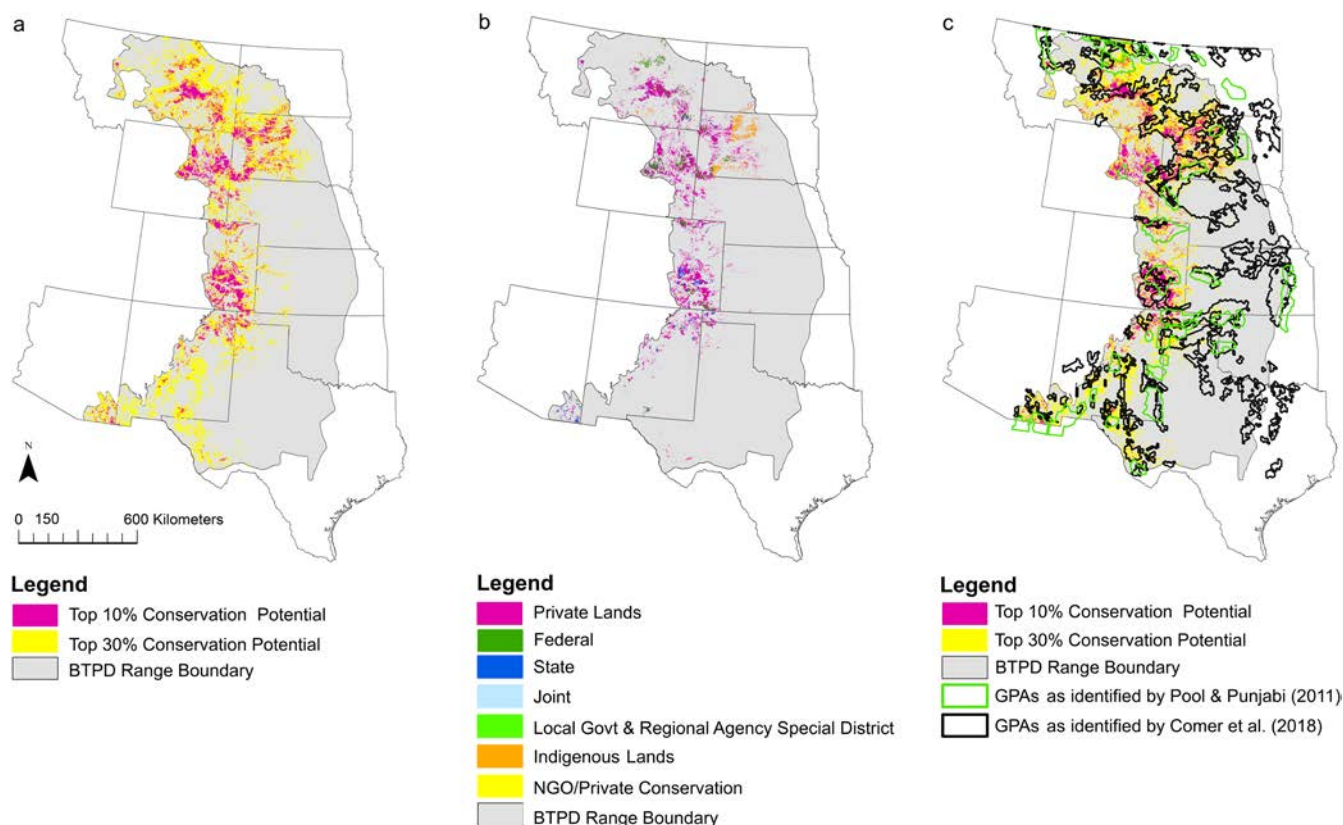


FIGURE 4 | Maps of (a) the intersection of the top 10% and 30% of areas with high conservation potential for the black-tailed prairie dog ecosystem (across the three climate scenarios (Figure 2 respectively)), (b) those same top 10% of areas with high conservation potential intersected with different landownership types (data are from PAD-US (USGS 2019b) and NCED and other Private Land Conservation areas, Table 1; see also Table 3) and (c) the top 10% and 30% of areas with high conservation potential (as in panel a) overlapped with grassland priority areas (GPAs) for the Central Grasslands identified by Pool and Panjabi (2011) and by Comer et al. (2018).

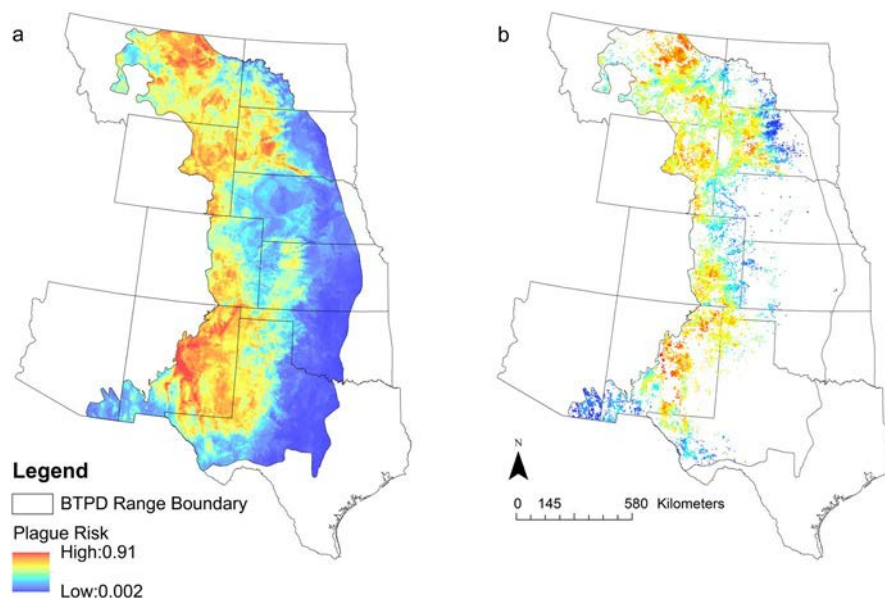


FIGURE 5 | Maps of plague risk (a) across the black-tailed prairie dog geographical range within the United States (data from wildlife model presented in Figure 1 of Carlson, Bevins, and Schmid 2022) and (b) within the top 30% of areas with high conservation potential.

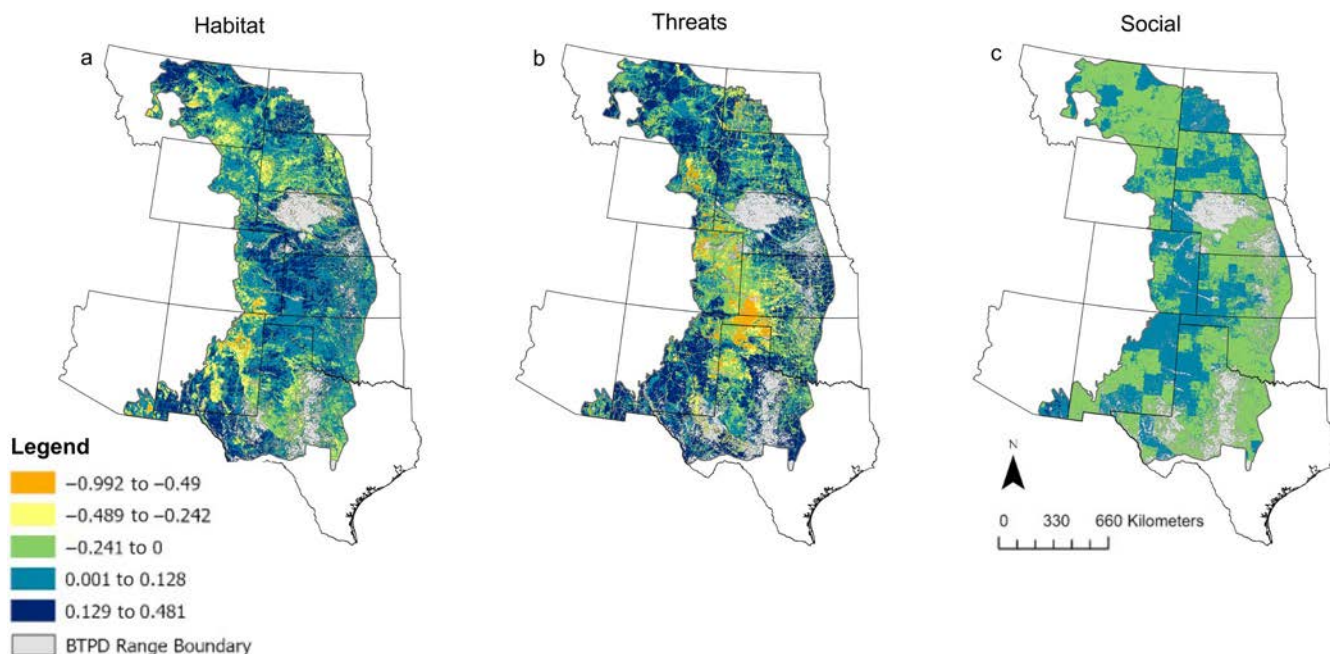


FIGURE 6 | Maps show the change in the conservation potential when (a) habitat (b) anthropogenic threats and (c) social layers were included versus excluded from the analysis shown in Figure 2a. Change in conservation potential was calculated by obtaining priority value per cell when (a) habitat (b) threats and (c) social layers were included in the model minus the priority values when (a) habitat (b) threats and (c) social layers were excluded respectively. The positive values show places where conservation potential (represented in Figure 2a) was increased by the presence of (a) quality habitat (b) low threats and (c) social support for prairie dog conservation, whereas negative values show areas that lost conservation potential due to (a) poor habitat quality (b) high threats and (c) low social support for prairie dog conservation. The original social data are from Williamson et al. (2023a, 2023b). Grey areas represent masked-out regions of unsuitable habitat (see Table S1).

depend on large, connected prairie dog colony complexes, such as mountain plovers, black-footed ferrets and other mesocarnivores and raptors (Duchardt et al. 2023; Augustine and Baker 2013; Augustine and Skagen 2014; Davidson, Detling, and Brown 2012; Duchardt, Beck, and Augustine 2020; Livieri et al. 2022; U.S. Fish

and Wildlife Service 2013). Additionally, the greater presence of humans increases the likelihood of prairie dogs being shot and occurrence of plague epizootics, and high levels of development and anthropogenic activity may negatively impact the behaviour and populations of associated species (Pauli and Buskirk 2007;

Lendrum, Crooks, and Wittemyer 2017; Biggins and Eads 2019; Chalfoun 2021).

Somewhat surprisingly, we found that general spatial patterns of HCP areas, across present and future climate scenarios, were not strongly impacted by the social and political data layers used in our analysis. Indeed, most of the HCP areas we identified remained priorities when we removed the social layers in our analysis, even when we increased the weightings of the social data in our analysis. Habitat suitability, habitat connectivity and threats played a larger role in determining the potential landscapes for conservation priority in our analysis. This makes good sense, as the primary goal when identifying conservation priorities for on-the-ground implementation should be to protect and restore habitat that is most suitable, followed by the surrounding landscape potential and threat presence (Margules and Pressey 2000; Watson et al. 2011). Secondary to this should be the relative ease or difficulty in securing those HCP habitats (Watson et al. 2011). For example, when evaluating two high-quality patches of habitat, managers might choose to focus their efforts in areas with greater social support and institutional capacity for actualising conservation action (Figure 5c and Figure S3; Watson et al. 2011).

The social landscape was relatively similar across the BTPD range, with regard to social support for their conservation (Figure S1). This lack of large variability in social support likely explains why the social data in our analysis did not have a larger influence on the HCP area locations. Additionally, the social data we used may not have captured the full depth of the social and political landscapes well enough; indeed, reflecting human attitudes and perspectives in a spatial framework is complex and challenging (Ban et al. 2013). Nevertheless, our conservation planning analysis provides a novel assessment of priorities by including social and political spatial data, and spatial social data specific to BTPDs (Williamson et al. 2023a, 2023b). Inclusion of such data layers is lacking in most spatial conservation planning efforts, largely because of the paucity of available data and difficulty of obtaining it in a meaningful way (Knight and Cowling 2007; Knight et al. 2008; Ban et al. 2013; Whitehead et al. 2014). We strongly encourage more research in this area to gain much needed insights into the social and political landscapes for future spatial conservation planning, as it has the potential to provide much needed insights for on-the-ground conservation implementation.

Landownership also plays an important role in on-the-ground conservation potential (Table 3, Figure 4b; Burger et al. 2019; Dawson et al. 2019; Maxwell et al. 2020; Augustine et al. 2021). Most (65%) of the top 10% of land with HCP, across all three climate scenarios, were located on private land, compared to public land (24%). However, across the western distribution of the BTPD range, there remains considerable public land, especially federal and state land, and indigenous land (8%) that may provide valuable opportunities for conservation of the BTPD ecosystem. Yet, the extent to which private, public and indigenous lands will support BTPD ecosystem conservation, is strongly influenced by the social and political landscapes within which they are embedded. While the prairie dog ecosystem faces numerous threats from plague and habitat loss, the social landscape is often considered the greatest and most challenging barrier to successful conservation of the BTPD ecosystem (Miller et al. 2007; Augustine et al. 2021). To facilitate co-existence

between BTPDs and humans, incentive programmes, grass banks to mitigate economic losses from ranching during droughts and other local community-based conservation solutions are needed (Augustine and Derner 2021; Crow et al. 2022). Our maps can be used to guide where might be best to focus conservation incentive programmes with private landowners, for example, such as the NRCS incentive programme that pays private landowners for maintaining BTPD colonies to support black-footed ferret recovery (NRCS 2023). Managers can identify which landowners to include in the incentive programme, based on where they occur within the HCP landscapes. Likewise, funds and efforts to create grassbanks can be focused on those lands that are in HCP hotspots. The landownership maps and their relationship to the HCP landscapes we identify underscore the importance of working with private landowners and local communities when implementing conservation measures to support BTPD ecosystem conservation.

Most (> 96%) of the HCP habitat we identify is not located within already protected areas. This assessment is based on those areas that have been identified as Gap 1 or Gap 2 status within the Protected Areas Database (USGS 2019b). Examples of Gap 1 protected areas include National Parks and Wilderness Areas, and of Gap 2 include National Wildlife Refuges, State Parks and The Nature Conservancy Preserves. Our assessment also includes those lands we identify as 'Private Conservation Lands', which included properties owned by the American Prairie, Turner Enterprises Inc. and Southern Plains Land Trust because they are private lands properties with a focus on BTPD ecosystem conservation. National Forests, BLM Lands, State Forests and some State Parks, are under Gap Status 3, and while some of these lands, as well as Tribal lands, may be partially managed for conservation, we did not include them in our assessment of how Protected Areas overlap with the HCP areas we identify. There are numerous conservation easements on private lands throughout our study region that also are not included in our assessment, because we found the data to be inconsistent and unreliable (see also Ducks Unlimited and Trust for Public Land 2023). Yet, even if a private lands property has a conservation easement, this does not necessarily translate into BTPD ecosystem protection. Despite the limitations of our protected areas assessment, our analysis shows that most grasslands throughout the BTPD currently lack an explicit mandate to promote the conservation of the BTPD ecosystem.

The HCP areas we identify encompassed or overlapped with many of the regions also identified in other landscape-level conservation priority analysis for the Central Grasslands (Comer et al. 2018; Pool and Panjabi 2011), but we also illuminate extensive, additional regions of grassland priority. NatureServe identified potential conservation areas (PCAs) based on long-term trends, species of concern, current level of protection and landscape intactness and connectivity, across the Central Grasslands (Comer et al. 2018). Our HCP areas overlapped with these PCAs across much of the intact western grasslands within the BTPD range (Figure 4c). They also overlapped with many of the grassland priority conservation areas (GPCAs) identified by the Commission for Environmental Cooperation and The Nature Conservancy, based on ecoregion representation, condition of native grassland and 20 focal grassland-dependent species (BTPDs and 18 species of grassland birds) (Pool and Panjabi 2011). Again, most of the areas of overlap were across the western distribution of the BTPD range (see Pool and Panjabi 2011). Differences

among these more generalised grassland conservation priorities with those of the BTPD ecosystem were mostly in the eastern portion of the historic BTPD range where their suitable habitat declines under today's existing grassland landscape (Augustine et al. 2021; Davidson et al. 2023).

5 | Conservation Implications and Conclusions

Prairie dogs are a keystone species of the central grasslands of North America, and consequently, they are often at the centre of grassland conservation efforts. Yet, conservation of the BTPD ecosystem is fraught with complex challenges that include: (1) the non-native disease, plague, that devastates BTPD populations and that of some associated species (Cully et al. 2010; USFWS 2013; Eads and Biggins 2015); (2) widespread habitat loss (Davidson et al. 2023; Augustine et al. 2021) and (3) high conflict with human activities, especially ranching (Detling 2006; Miller et al. 2007; Augustine and Derner 2021; Crow et al. 2022). The duality of being ecologically important while also being in high conflict with humans creates one of the greatest conservation challenges facing North America's Central Grasslands. Finding solutions to facilitate the co-existence of BTPDs and humans is central to the conservation of the BTPD ecosystem, but to date remains largely lacking and remarkably inadequate.

Here, we provide maps that identify the best locations to focus limited conservation resources for the BTPD ecosystem, both now and into the future. These maps can be explored down to 90m resolution. The algorithm we used in our conservation planning analysis created a conservation value for each cell across the gridded geographical landscape of the BTPD range, based on climate, land use, habitat suitability and social and institutional support for conservation. Through this insight, our maps provide decision support for where limited conservation resources might best be invested and where conservation goals have the best chance of being actualised. Furthermore, the maps can inform efforts like the Central Grasslands Roadmap, and be overlaid with priority landscapes identified for other umbrella species or functional groups, such as the lesser prairie-chicken (*Tympanuchus pallidicinctus*), greater sage-grouse (*Centrocercus urophasianus*), grassland birds, bison and biodiversity conservation in general (Sanderson et al. 2008; Van Pelt et al. 2013; Reeves et al. 2014; Jenkins et al. 2015; Gary et al. 2019; Central Grasslands Roadmap 2022; Dreiss et al. 2024), in addition to those identified by (Pool and Panjabi 2011 and Comer et al. 2018). Doing so, can provide a more complete picture of where to focus conservation resources across the Central Grasslands and inform efforts aimed at conserving 30% of United States lands and waters by the year 2030 (EOP 2021).

Author Contributions

Ana D. Davidson: conceptualization, data curation, methodology, formal analysis, writing – original draft, editing and review, visualization, supervision, project administration. **Fernanda Thiesen Brum:** methodology, formal analysis, writing – editing and review. **Michael Houts:** data curation, methodology, formal analysis, writing – review. **Michael Menefee:** conceptualization, visualization, writing – review. **Matt Williamson:** methodology, visualization, writing – review. **Lindsey Sterling Krank:** conceptualization, visualization, project administration,

funding acquisition, writing – review. **Bill Van Pelt:** funding acquisition, visualization, writing –review. **David J. Augustine:** conceptualization, visualization, methodology, writing – editing and review.

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Conflicts of Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data Availability Statement

The data that support the findings of this study are openly available through Data Dryad: <https://doi.org/10.5061/dryad.wpzgmsbr5>.

The Homes on the Range project web page can be found here, where the data also is publically available for download: <https://cnhp.colostate.edu/projects/hotr/>.

Additionally, an interactive web page is available for users to explore the maps without having to download the data: <https://kars.geoplatform.ku.edu/maps/KU::black-tailed-prairie-dog-ecosystem-priority-conservation-areas/about>.

Peer Review

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ddi.13945>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.



Present and future suitable habitat for the black-tailed prairie dog ecosystem

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ABSTRACT

The black-tailed prairie dog (BTPD) ecosystem is an important component of North America's Central Grasslands, which are highly imperiled. Here, we develop a habitat suitability model (HSM) for the BTPD ecosystem across their historical geographic range within the United States to support conservation planning in the region. We used an ensemble HSM approach and spatial analysis combining ecological and climatic variables to quantify suitability of habitat for the black-tailed prairie dog ecosystem, both under today's current climate and projected into the future. We identified 20.8 million hectares of suitable grassland habitat for the black-tailed prairie dog ecosystem, indicating that large areas of quality habitat remain across the western half of their historic range. We also identified a significant northward expansion of their geographic range with future climate change scenarios, with a concomitant decline in habitat suitability across the southern Central Grasslands. Our results show that there is substantial conservation potential for the BTPD ecosystem, given the large amount of remaining available habitat, especially across the western portion of their historical range. Currently, however, we estimate that only ca. 782,521 hectares (3.8 %) of this habitat are occupied by BTPDs. The recovery of the black-tailed prairie dog ecosystem is a complex, multidimensional, socio-ecological challenge. The maps we generated in this analysis provide the basis to carry out spatial analyses that also consider the social, political, and threat landscapes and to incorporate such findings into other large-scale, multi-species conservation planning efforts being developed for the Central Grasslands of North America.

1. Introduction

Temperate grasslands are the most imperiled and least protected of the world's terrestrial biomes (Bardgett et al., 2021; Carbutt et al., 2017; Jacobson et al., 2019). North America's Central Grasslands have undergone some of the greatest ongoing losses, transformed by agriculture, oil and gas development, desertification and woody plant encroachment, fencing, urbanization, and altered surface water distribution (Allred et al., 2015; Augustine et al., 2021; Morford et al., 2022; Olimb and Robinson, 2019; Van Auken, 2000; Weltzin et al., 1997). The abundance of wildlife that historically occurred across the Central Grasslands once rivaled Africa's Serengeti, but the pervasive

anthropogenic impacts have resulted in widespread declines in grassland habitat and wildlife (Knowles et al., 2002; Lark et al., 2020; Samson et al., 2004; Sanderson et al., 2008). Awareness of the plight of the Central Grasslands has been increasing, especially over the last several years, with initiatives like the Central Grasslands Roadmap, Great Plains Summit, WAFWA's Western Grasslands Initiative, and introduction of The North American Grasslands Conservation Act of 2022 to the U.S. Congress (Central Grasslands Roadmap [WWW Document], 2022; Comer et al., 2018; Finch, 2018; Haaland et al., 2021; Heady and Child, 2021; Lark et al., 2020; Western Association of Fish and Wildlife Agencies, 2011; Wyden, 2022). These efforts, and others, aim to focus limited conservation resources (Gary et al., 2022). One key approach centers on

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identifying species that serve as umbrellas for suites of other species, such as management focused on protecting the lesser prairie chicken (*Tympanuchus pallidicinctus*), which provides a conservation benefit for 84 % of other co-occurring at-risk species (Gary et al., 2022). The umbrella concept naturally extends to ecosystem engineers that play large and unique ecological roles, such that conservation efforts centered on them consequently encompass habitats they create and the species associated with them (Johnson et al., 2017).

The black-tailed prairie dog ecosystem is an important component of North America's Central Grasslands (Davidson et al., 2012; Hoogland, 2006). The prairie dog ecosystem is characterized by unique islands of open grassland habitat, dotted with burrow mounds, and occupied by a suite of associated species (Davidson et al., 2012; Whicker and Detling, 1988). The extensive burrow systems prairie dogs engineer provide critical refugia for a suite of invertebrates, amphibians, reptiles, birds and other mammals (Davidson et al., 2012; Whicker and Detling, 1988) and their colonies attract numerous species that prefer open grassland habitat that the prairie dogs meticulously maintain, such as burrowing owls (*Athene cunicularia*) and mountain plovers (*Charadrius montanus*) (Augustine and Baker, 2013; Augustine and Derner, 2012; Davidson et al., 2012; Duchardt et al., 2023). Pollinators also are 2–3 times more abundant on colonies than off because of the greater abundance of forbs and availability of oviposition sites (Hardwicke, 2006). Large herbivores, like bison (*Bison bison*) and cattle (*Bos taurus*), also are attracted to their colonies because of the more nutritious forage available compared to off colony (Bayless and Beier, 2011; Connell et al., 2019; Kotliar et al., 2006). Additionally, prairie dogs are an abundant and reliable source of prey for many predators including coyotes (*Canis latrans*), American badgers (*Taxidea taxus*), raptors [e.g., golden eagles (*Aquila chrysaetos*), ferruginous hawks (*Buteo regalis*)], and the highly endangered black-footed ferret (*Mustela nigripes*) (Davidson et al., 2012; Eads et al., 2016; Eads and Biggins, 2015; Goodrich and Buskirk, 1998; Grassel et al., 2015; Kotliar et al., 2006).

Prior to European settlement and the introduction of plague, prairie dog colony complexes were abundant across the Central Grasslands of North America, stretching from the northern plains in southern Canada to the desert grasslands of northern Mexico (Augustine et al., 2008a; Davidson et al., 2012; Eads and Biggins, 2015; Knowles et al., 2002; Kotliar et al., 2006). Through their burrowing and herbivory, prairie dogs transformed and shaped these grasslands, but today, their populations have declined by over 95 % across their range, along with consequent declines in associated species (Davidson et al., 2012; Hoogland, 2006). Once large, stable features across the grasslands, prairie dog colonies are now much smaller and highly unstable, largely due to widespread poisoning that began in the early 1900s and the introduction of plague, a non-native disease from Asia that causes collapses in populations of prairie dog and associated species (Augustine et al., 2008a, b; Davidson et al., 2022; Duchardt et al., 2023; Eads and Biggins, 2015; Livieri et al., 2022). Today, plague is probably the greatest threat to the prairie dog ecosystem across most of the BTPD range (Barrile et al., 2023; Cully et al., 2010; Eads and Biggins, 2015). Across the southern part of their range, increasing frequency and intensity of drought under a changing climate also is a significant threat in this region, causing declines in prairie dogs and associated species, and challenging restoration efforts (Avila-Flores et al., 2012; Davidson et al., 2014; Davidson et al., 2010; Facka et al., 2010). Analyses to assess how climate change could affect the broad-scale distribution of black-tailed prairie dogs are needed.

The USFWS identified “the single, most feasible action that would benefit black-footed ferret recovery is to improve prairie dog conservation” (U.S. Fish and Wildlife Service, 2013). Identifying where to focus conservation efforts for the prairie dog ecosystem requires understanding where the most ecologically suitable habitat is located and the broader landscape within which it is embedded (Crawford et al., 2020; Dufnot et al., 2018; Gary et al., 2022; Olimb et al., 2022). Also critical for long-term conservation planning is understanding how areas

that are identified as suitable habitat today might change in the future under a rapidly warming climate (Reside et al., 2018). Here, we develop the first range-wide habitat suitability model (HSM) for the black-tailed prairie dog ecosystem under both current and future climate to help inform conservation efforts for North America's Central Grasslands. Our HSM is based on presence and absence data for prairie dog occurrences across the geographic range of the BTPD within the United States, and quantifies how prairie dog occurrences relate to climate, soils, topography, and land cover. We also project the BTPD HSM under two future climate scenarios: 1) warm and wet and 2) hot and dry.

2. Methods

We obtained range-wide prairie dog occurrence data from Western EcoSystems Technology, Inc. (WEST, Inc.; Hereafter, “WEST data”) to use for our primary HSM analysis because colony data was systematically collected across the BTPD range over a consistent time period (McDonald et al., 2015). The WEST data are based on prairie dog colonies identified using National Agriculture Imagery Program (NAIP) imagery (1m² resolution) from a stratified random sample of 3.2 by 3.2 km grid cells distributed across the BTPD range within the United States (Table S1). We provide a brief overview here of the methods used by McDonald et al. (2015), but see report for full details. Two independent, trained observers visually and systematically searched each grid cell for prairie dog colonies at a scale of 1:4000. Observers identified colonies based on detection of burrow mounds, reduced vegetation height, “clip lines” around colony edges (indicating where vegetation had been clipped by prairie dogs), and vegetation texture that contrasted from off colony vegetation. Observers then digitized the boundaries of each colony and calculated their acreage across a sample of 20 % of the grid cells across Arizona, 1000 grid cells across each other state evaluated, and about 10 % of grid cells across lands managed by the Bureau of Land Management. Researchers adjusted their estimates for false negatives (missed colonies) by modeling the probability of detection of potential colonies. Range-wide estimates for colony acreage and number of colonies had coefficients of variation of 2.4 % and 4.9 %, respectively. To account for the higher level of sampling effort by McDonald et al. (2015) in Wyoming and Colorado, we subsampled grid cells in these two states in order to obtain an equal density of grid cells in each state across the BTPD geographic range.

We transformed the WEST data into a set of BTPD presence and absence points to make it suitable for data analyses. For each colony polygon detected within a given grid cell, we randomly selected one presence point per colony hectare. We then randomly selected one absence point for every 15 ha within the remaining portion of the grid cell where no colonies were found. All points were at least 60 m (two 30 × 30 m raster cells) away from each other, and all absence points were at least 500 m from any presence point. This produced approximately 86,300 presence points and 315,000 absence points, from which we randomly selected the same number of absence points as presence points to use in the HSM analysis.

Our BTPD range boundary is based on current and historical distribution. To determine current range, we largely followed the WEST (McDonald et al., 2015) boundary and extended the range boundary where appropriate to reflect the historical range distribution based on museum specimens. Each state's Western Association of Fish and Wildlife Agencies (WAFWA) Prairie Dog Conservation Team (PDCT) member approved the final BTPD boundary for their state, and GPS point locations for all museum specimens we used to create the boundary were stored in the project database along with detailed metadata for each.

Next, we identified the most current spatial data layers available for soils, climate, topography, and land cover (Table 1 and Fig. 1). We downloaded and processed data for analyses (described below) and identified suitable land cover types and patch metrics. These efforts yielded a total of 25 environmental input datasets for the full study area,

Table 1

Spatial data layers and their sources used in the black-tailed prairie dog (BTPD) habitat suitability model.

Variable	Spatial Data Layer for Habitat Suitability Model
BTPD colony occurrences	Prairie dog occurrences from WEST survey (McDonald et al., 2015).
Land Cover	USGS National Land Cover Database 2016 (USGS, 2019).
Soils	POLARIS 30-m resolution database (Chaney et al., 2019a, b). Metrics: bulk density to 100 cm, Sand to 100 cm, %Clay to 100 cm, % organic matter to 100 cm, pH to 100 cm.
Slope & elevation	National Elevation Dataset (USGS, 2018). Metrics: Topographic Wetness Index, Topographic Ruggedness Index, slope, aspect.
Climate – current	Current climate (1994–2014), using gridMet (Abatzoglou, 2013). Metrics: Mean annual precipitation (mm), winter + spring + summer + fall precipitation, max summer temperature, potential evapotranspiration, growing degree days.
Climate – future (used only for HSMs projected into the future)	Future climate (2100), using MACAv2_METDATA (Abatzoglou and Brown, 2012; “MACAv2 METDATA”). Metrics: Mean annual precipitation (mm), winter + spring + summer + fall precipitation, max summer temperature, potential evapotranspiration, growing degree days.

based on the data sources in Table 1. First, we used the 2016 National Land Cover Database (NLCD), which was released by USGS in May of 2019. This 2016 database represents a major improvement from the 2011 NLCD, as it incorporates new data derived from the USDA's Cropland Data Layers for 2011–2016 and implemented new algorithms for identifying developed and paved surfaces. Second, rather than using the National Soil Survey's SSURGO database to map soil types across the BTPD range, we used a new digital soil map of the U.S., POLARIS (Chaney et al., 2019a, b), that builds upon SSURGO. It includes improved interpolation of soil texture and other attributes down to a 30-m pixel resolution. One limitation is that this improved soil model did not include depth to bedrock, which is an important factor influencing BTPD burrowing. We attempted to use the latest SSURGO soils data (Soil Survey Staff, 2016) for the depth to bedrock metric, compiling depth to bedrock values from individual statewide datasets and averaged over map unit components. Many map units had no bedrock depth measure in SSURGO, so we estimated missing data using a component-weighted average of maximum horizon depth. POLARIS soils data (Chaney et al., 2019a, b) are available as individual 1-degree tiles per metric per depth, so we downloaded, depth-weighted, and merged the POLARIS data by soil metric over the study area. The most recent National Elevation Data (NED; USGS, 2018) was likewise downloaded as individual 1-degree tiles and merged over the study area. We corrected the

NED by identifying and removing as many sink artifacts as possible, while preserving true sinks such as playas and perennial water bodies. Next, we used the software TauDEM (Tarboton, 2015) to calculate a Topographic Wetness Index and a Terrain Ruggedness Index at a 30 × 30 m pixel resolution for the entire BTPD range. The NED was also used to create information on aspect as a function of 'northness' and 'eastness'. We used the 2016 NLCD (USGS, 2019) to classify each pixel as one of 10 land cover categories (cropland, developed, developed open space, forest, grassland, shrubland, pasture/hay, water, wetland, and other), with shrubland used as the reference category in all models. We also used the NLCD to calculate several land cover type metrics including patch size, distance to patch edge, and nearest edge type. Finally, current climate data metrics were calculated from raw daily gridded meteorological data (Abatzoglou, 2013) averaged over 1994–2014. All continuous datasets were normalized to be between 0 and 1 (−1 to +1 in the case of the northness and eastness measures) so that inputs had equivalent scales. We used one-hot encoding to convert categorical data (primarily land cover) to one-hot 'dummy' variables for use in modeling algorithms that cannot accept categorical inputs. The Python and R scripting code written for many of the above calculations is available at https://github.com/mmink/HOTR_Code. TauDEM, which is written in C++, is available at <http://hydrology.usu.edu/taudem/taudem5/>. The remaining data processing was done in ESRI ArcGIS. During iterative

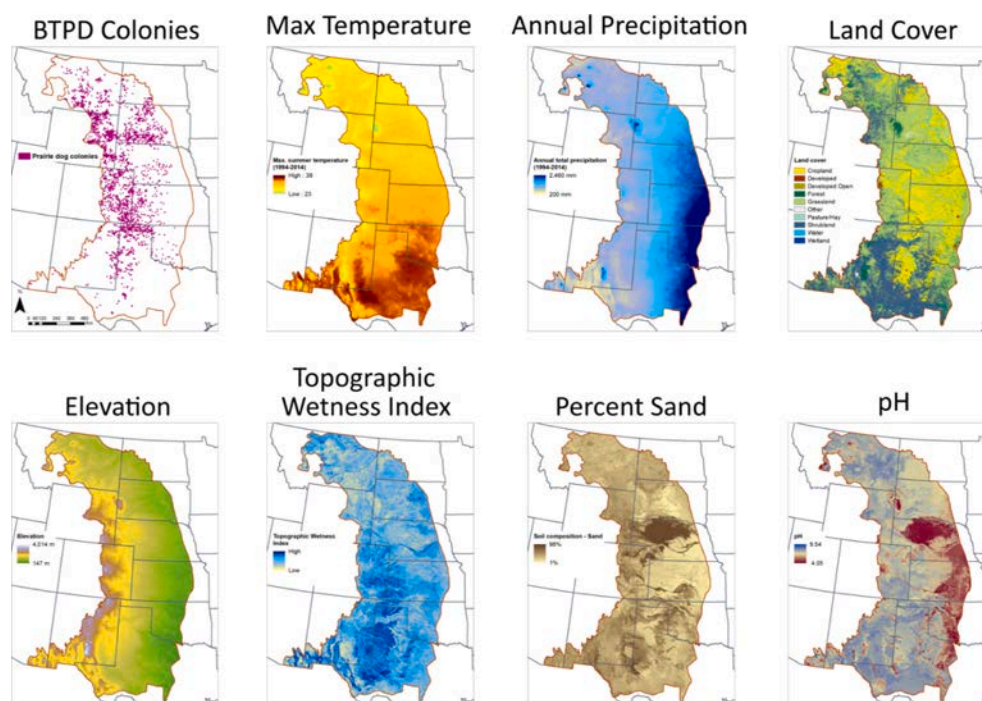


Fig. 1. Some of the spatial layers created for the black-tailed prairie dog (BTPD) habitat suitability model, based on BTPD occurrence (McDonald et al., 2015), climate (Abatzoglou, 2013), land cover (USGS, 2019), topography (USGS, 2018), and soils (Chaney et al., 2019a, b).

Table 2
Post-hoc analysis of the percentage of ground-truthed and ground-mapped black-tailed prairie dog colonies that occurred within habitat that was predicted to be low, medium, or high suitability. Last row of table shows total occupied area (ha) across all ground-truthed and ground-mapped colonies and for each site. Over 92 % of all ground-truthed and ground-mapped colonies fell into habitat that was predicted to be of medium or high suitability, based on a weighted average of occupied colony area at each site.

Habitat Suitability	ALL Colonies	Kiowa NG, New Mexico	Vermejo Park Ranch, New Mexico	State of Colorado	Pawnee NG, Colorado	Comanche NG, Colorado	Thunder Basin NG, Wyoming	Rita Blanca NG, Texas & Oklahoma	Cimarron NG, Kansas	Oglala NG, Nebraska	Conata Basin, South Dakota	Bad River Ranch, South Dakota	American Prairie, Montana
Low	7.48 %	0.80 %	25.97 %	3.46 %	3.22 %	15.85 %	0.89 %	1.74 %	2.67 %	6.05 %	7.39 %	14.14 %	22.51 %
Medium	15.68 %	13.60 %	27.42 %	9.98 %	26.24 %	19.57 %	6.16 %	19.08 %	7.66 %	50.33 %	14.24 %	46.62 %	61.80 %
High	76.66 %	85.58 %	46.61 %	86.56 %	70.54 %	64.59 %	92.94 %	79.18 %	89.67 %	43.61 %	78.37 %	39.24 %	15.68 %
Medium + high	92.52 %	99.18 %	74.03 %	96.54 %	96.78 %	84.16 %	99.10 %	98.26 %	97.33 %	93.94 %	92.61 %	85.86 %	77.48 %
Area (ha)	63,298	864	4114	13,987	1892	8622	11,767	3057	2249	857	14,313	974	1560

modeling, we narrowed down environmental inputs based on covariate correlation, proportion of deviance explained, and effect on model performance (Table S2). We dropped the SSURGO-derived depth to bedrock input due to the large amount of data coded as zeroes (indicating no real depth data available), which was biasing model output.

To determine the best-fit habitat suitability model for our data, we evaluated the performance of several different independent models and an ensemble model (Araújo et al., 2019; Guisan et al., 2017). Specifically, we created BTPD habitat suitability models using: 1) Generalized Linear Mixed Models (GLMM), 2) Random Forest models (RF), 3) Boosted Regression Trees models (BRT, also known as Generalized Boosted Models or GBM), and 4) an ensemble model that combined the outputs of the GLMM, RF, and BRT0. HSMs. Models were created using the R packages *lme4* (Bates et al., 2015), *randomForest* (Liaw and Wiener, 2002), and *dismo* (Hijmans et al., 2017). The GLMM used the identity of the 3.2×3.2 km sampling grid cell that each presence or absence point fell within as a random factor. All R code used for modeling is available at the previously mentioned GitHub repository.

For model training, we randomly selected 70 % of the 3.2×3.2 km grid cells sampled by McDonald et al. (2015), and used the presence and absence points within them. This approach maintained equal numbers of presence and absence points in the training dataset. Half of the remaining data (15 %) were used to evaluate RF and BRT model performance during tuning of the calling parameters (such as number of trees). The final 15 % of withheld data ("Testing dataset") were then used to evaluate all four final models (Table S3, Fig. S1). All sampling of presence/absence points was done at the level of the grid cell (i.e., the cells were randomly sampled, not the points within them). We selected 95 % Sensitivity for model fitting because our primary goal was to correctly identify prairie dog habitat.

The ensemble model was created as a weighted average of the final GLMM, RF, and BRT models. Using the *mean* of Sensitivity = 0.95, weights were calculated by averaging six performance metrics [Area under the Curve (AUC), True Skills Statistic (TSS), Percent Correctly Classified (PCC), kappa, Sensitivity, and Specificity], which were themselves averaged over a 10-fold cross-validation of the models built on the Training dataset. This gave the higher performing models more influence over the ensemble. For the cross-fold validation, each fold randomly sampled 10 % of the sampling grid cells in the training dataset, so that if a sampling grid cell was selected, all presence and absence points within that cell were assigned to that fold. The ensemble was evaluated against the Testing dataset as well (Table S3).

We also conducted a post-hoc analysis of the percentage of predicted suitable habitat of low, medium, and high quality that fell within colonies that were ground-truthed and/or ground-mapped across the BTPD range (Table 2). These colonies were not used to train our model, so provide complementary insight into the accuracy of our HSM. The colonies in this dataset were mapped: across the state of Colorado (2016); Vermejo Park Ranch, NM (2017); Bad River Ranch, SD (2010); American Prairie, MT (2020); Cimarron National Grassland (NG), KS (2004); Comanche NG, CO (2014); Rita Blanca NG, TX and OK (2014); Kiowa NG, NM (2004); Conata Basin, SD (2007); Thunder Basin NG, WY (2014); Oglala NG, NE (2010); Pawnee NG, CO (2011). If multiple years of colony data were available at a given site, we selected a year (shown in parentheses above) when colony areas were at their largest extents, but not necessarily at their largest (peak). We did this to capture the greater area that prairie dogs will utilize, while not necessarily the lower quality habitat they are more likely to expand into during peak years. We defined three classes of habitat suitability (low, medium, and high). Specifying how different probability values predicted by the ensemble model correspond to classes of suitable versus unsuitable habitat depends upon the level and types of error that one is willing to accept. Given the design of our sampling, where locations of BTPD colonies represent used habitat and locations lacking BTPD colonies represent available habitat, the "available" habitat is likely to include both areas of high quality (or potentially suitable) habitat that has not yet been

colonized, and areas of low quality (or unsuitable) habitat that is being avoided by colonizing prairie dogs. In this view, false negative model predictions (i.e., where pixels occurring within known BTPD colony locations are predicted to not have BTPDs present) are a more egregious error than false positive model predictions (i.e., where pixels within “available” habitat are predicted to have BTPD present). We therefore defined “low quality habitat” as those pixels where the probability values predicted by the ensemble model were below the cutoff for a 5 % false negative rate. In contrast, we define “high quality habitat” as areas where probabilities predicted by the ensemble model were above the cutoff associated with a 5 % false positive rate. Medium quality habitat was defined as areas with probabilities in between these two cutoff values.

2.1. BTPD habitat suitability model under future climate

Next, we projected our BTPD HSM into the future (2100) under two different climate scenarios: 1) warm and wet (IPSL-CM5A-LR_r1i1p1_rcp45); and 2) hot and dry (MIROC5_r1i1p1_rcp85). These climate scenarios were selected because they represent two different ends of the spectrum for scenarios across our study region. The future climate model scenarios were obtained from [MACAv2.METDATA \[WWW Document\], 2020](#), and were averaged over 2076–2099 (Table S2). All other model inputs remained the same. From the MACA website, “Climate forcings in the MACAv2-METDATA were drawn from a statistical downscaling of global climate model (GCM) data from the Coupled Model Intercomparison Project 5 (CMIP5, [Taylor et al., 2012](#)) utilizing the Multivariate Adaptive Constructed Analogs (MACA; [Abatzoglou and Brown, 2012](#)) method with the METDATA ([Abatzoglou, 2013](#)) observational dataset as training data.”

2.2. Ensemble model review

During summer 2020, our team met with biologists from each state individually and with other experts on the prairie dog ecosystem to provide detailed state-level review of the ensemble habitat suitability map. After extensive review, our team worked to address each of the comments we received. One challenge was modeling the desert grasslands of the American Southwest (Arizona, southern New Mexico, southwestern Texas), where prairie dogs occurred historically, and considerable grassland remains. Throughout this region, prairie dogs were extensively exterminated over the last century and their populations have not recovered as in other parts of their range, likely due to the increasingly arid climate and grassland desertification ([Davidson et al., 2018](#); [Davidson et al., 2014](#); [Facka et al., 2010](#); [Hale et al., 2013](#)). Nevertheless, extensive grassland remains in the region and colonies do exist, just not in high enough abundance to be well-sampled by [McDonald et al. \(2015\)](#). To address this, we obtained additional, recent data (within the last ca. 10 years) for Arizona, New Mexico, and Texas from within the desert grassland ecoregion ([The Nature Conservancy, 2008](#)) to add to the occurrence locations identified in the WEST data. This allowed us to better model habitat conditions where BTPDs occur across the desert grassland ecoregion. We randomly selected the same number of grid cells in the WEST data and traded them out with the new grid cells ($N = 12$) covering the additional occurrence data. Thus, the dataset retained the same density of grid samples within each state. We also removed false positives in occurrence data identified during the reviews by biologists in each state. In a few instances along the western edge of the BTPD range in New Mexico, we removed mapped colonies that were likely to be Gunnison’s prairie dogs rather than BTPDs, based on consultation with the New Mexico Department of Game and Fish and the New Mexico Natural Heritage Program.

3. Results

Among the three models used to build the ensemble, the GLMM was

more restrictive in identifying suitable prairie dog habitat compared to the RF and BRT models. But, the GLMM performed better at modeling suitability relative to soils across the BTPD range compared to the RF and BRT, while RF and BRT modeled suitability relative to climate better than GLMM. Climate variables were important predictors across all models, followed by topography and landcover ([Fig. 2](#)). For the final selected GLMM, the variables of greatest importance were topographic ruggedness, growing degree days, land cover type, soil texture (% clay and % sand), soil organic matter and soil pH (see Table S4 for coefficients). Variables of greatest importance for both the RF and BRT were summer-fall precipitation, growing degree days, winter-spring precipitation, landcover, and topographic ruggedness ([Fig. 2](#)). Across all models, predicted habitat suitability was maximized at intermediate values for growing degree days (i.e., intermediate levels of net primary productivity), increased with more winter-spring precipitation, and declined with more summer-fall precipitation. Habitat suitability was strongly positive for grassland, strongly negative for cropland, developed land, forests and water, and weakly negative for developed open space and wetlands. BTPD habitat suitability was positively associated with increased soil clay content, organic matter content and pH, and negatively associated with topographic ruggedness and soil sand content.

When we compared performance metrics of all four models (GLMM, RF, BRT, ensemble), the RF model performed slightly better than the ensemble, followed by BRT and GLMM (Table S3; [Fig. S1](#)). However, we selected the ensemble model to build our HSM because not only did it perform similarly well to the RF, but the ensemble HSM also reduced the impact of individual model biases. Indeed, ensemble HSMs often perform better than single HSMs because they can average out uncertainties and biases inherent in different model algorithms ([Hao et al., 2019](#)). Our final ensemble model exhibited high predictive accuracy, with an AUC of 0.96 and error rate of 13 % at a Sensitivity (ability to correctly identify prairie dog habitat) of 95 %, Specificity (ability to correctly classify non-prairie dog habitat) of 80 %, TSS of 0.75, kappa of 0.75, and PCC of 0.87 ([Fig. 3](#)). We also evaluated the model when Sensitivity was equal to Specificity and when Specificity was 95 % and found similar model performance (Table S5; [Figs. S2 and S3](#)). Our post-hoc analysis showed that 93 % of all ground-truthed and ground-mapped colonies were located in medium to high suitability habitat ([Table 2](#); [Fig. 4](#)).

Based on the total area of colonies in each state estimated from [McDonald et al.’s \(2015\)](#) analysis of NAIP imagery, 96 % of medium or high suitability habitat for the prairie dog ecosystem was unoccupied by prairie dogs within their U.S. range, and a similar amount of quality habitat was unoccupied within each state (95–99.8 %; [Table 3](#)). The most suitable habitat for the BTPD ecosystem under the current climate extends largely from northern and eastern New Mexico and the panhandle of Texas and Oklahoma through eastern Colorado, Wyoming, and Montana ([Fig. 3](#)). Under current conditions, the region containing the most extensive and contiguous patches of suitable habitat for BTPDs occurs in the nine counties of southeastern Colorado (Baca, Las Animas, Huerfano, Pueblo, Crowley, Otero, Bent, Prowers and Kiowa), which encompass 4.2 million ha (10.4 million ac) within the historic BTPD range. Within this region, we identified 2.6 million ha of moderate or high-quality BTPD habitat, primarily on gently undulating shortgrass plains. These plains are occasionally dissected by unsuitable or low-quality habitat associated with rugged canyonlands along the Purgatoire River and floodplains or cropland along the Arkansas River. The region is bounded on the south by mesas and canyonlands along the New Mexico/Oklahoma borders, and on the east by rowcrop agriculture near the Kansas border. Of the medium to high-quality habitat occurring in this region, 150,840 ha or 5.75 % is on the Comanche National Grassland and 78,802 ha or 3.0 % is on lands managed by the Department of Defense for military training. A second region of large and contiguous patches of suitable BTPD habitat persists in six counties of northeast Wyoming (Natrona, Converse, Niobrara, Johnson, Campbell and

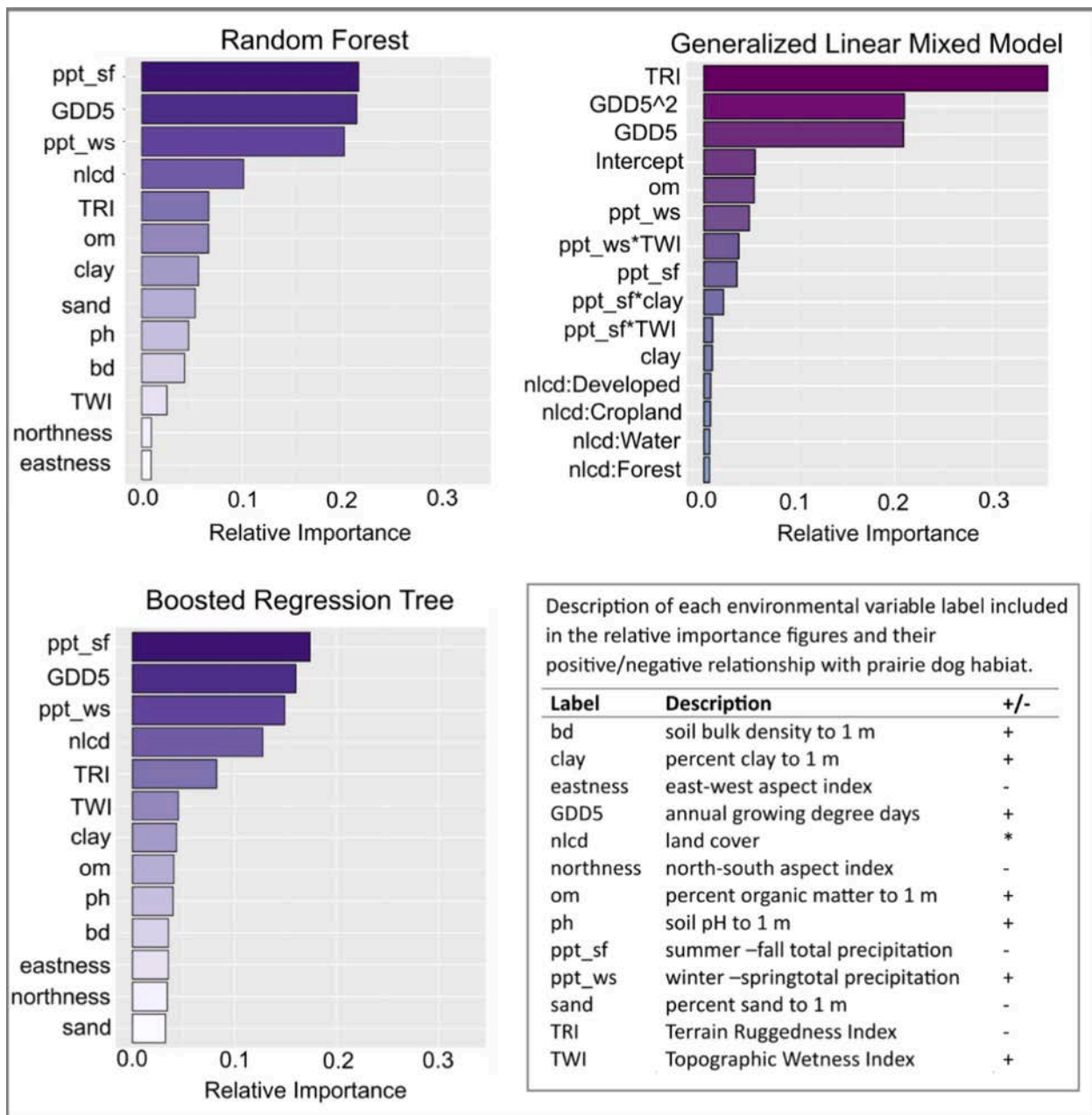


Fig. 2. Variable importance plots for the Random Forest, Generalized Linear Mixed Model, and Boosted Regression Tree. All values have been normalized so that the sum of all variable importance measures for a model = 1. See Table S2 for complete details of each variable. *Note that Land cover was a categorical variable, with grassland cover having a positive relationship with prairie dog habitat and others (cropland, developed, wetland, wetland, forest) having a negative relationship. Additionally, in the GLMM ppt_ws*TWI and ppt_sf*clay had a negative relationship with prairie dog habitat; whereas ppt_sf*TWI had a positive relationship; see Table S4 for details.

Weston), which encompass 5.7 million ha (14.2 million ac) within the historic BTPD range. Within this region of Wyoming, we identified 2.4 million ha of moderate or high-quality BTPD habitat, with the largest expanse occurring on broad, flat plains immediately west of the Black Hills in Weston County. Of the medium to high-quality habitat occurring in this region, 139,953 ha or 5.9 % is on the Thunder Basin National Grassland.

Other notably extensive and contiguous regions of BTPD habitat occur in South Dakota associated with the Buffalo Gap National Grassland, Badlands National Park, and the Pine Ridge, Cheyenne and Standing Rock Indian Reservations, and in northeast Colorado surrounding the Pawnee National Grassland, and in Montana in the portions of Yellowstone, Treasure, and Rosebud counties north of the

Yellowstone River. Suitable habitat also extends into the westernmost counties of Kansas and Nebraska, and into northeastern New Mexico (Fig. 3). Small patches of suitable habitat occur through the southwest in Arizona, southern New Mexico, and southwest Texas. The eastern part of the original prairie dog range is largely unsuitable due to the extensive conversion of grassland to cropland, and the southern portion of their geographic range is limited largely by climate suitability. Low suitability across most of Nebraska is due to excessively sandy soils.

Projecting suitable habitat into the future under both future scenarios (warm and wet; hot and dry) shows how suitable habitat shifts northward (Fig. 5). Under the warm and wet scenario, eastern Colorado remains a stronghold, and suitable habitat expands across Wyoming, Montana, western North Dakota, South Dakota, western Nebraska,

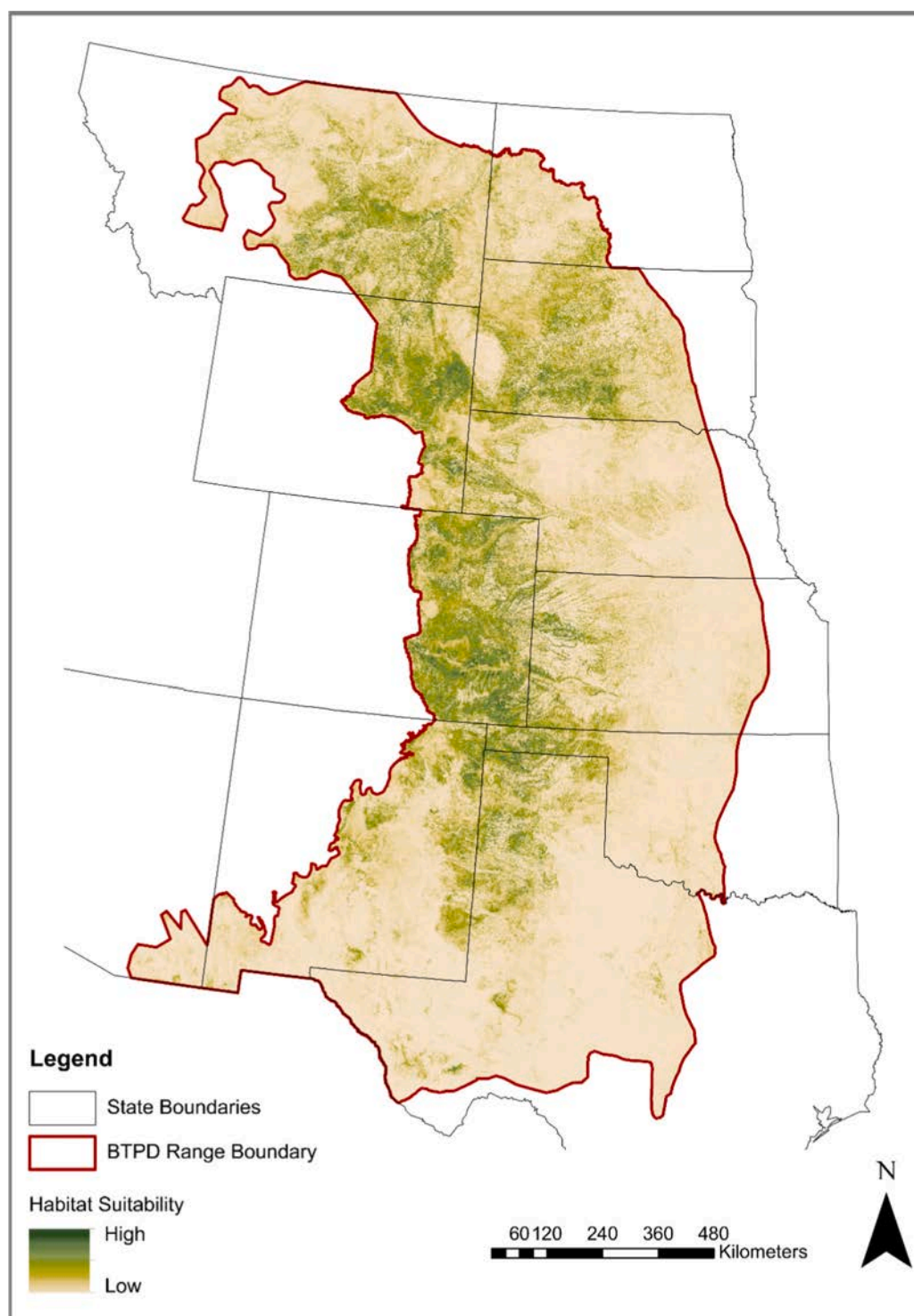


FIG. 3. Black-tailed prairie dog (BTPD) ensemble habitat suitability model, under current climate. Dark green shows areas of highest habitat suitability for BTPDs, and beige shows areas of lowest suitability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Kansas, and central Texas. Suitable habitat under this scenario retracts across the Southwest, with reductions especially in southern and eastern New Mexico with the northeastern part of New Mexico remaining as highly suitable habitat. Suitability also declines somewhat across the Texas-Oklahoma panhandle region. Under the more extreme hot and dry future scenario, suitable habitat substantially declines across the Southwest through Texas, Oklahoma, and Kansas. Central and north-eastern New Mexico and eastern Colorado remain favorable habitat but become the southern edge of suitable range, with the heart of suitable

habitat projected to occur across Wyoming, Montana, and the Dakotas. We did not model the future scenarios beyond the known historical range within the United States, but it is likely that suitable habitat could expand beyond the historical range in North Dakota, Montana, and Canada with the projected northward and eastward range shift.

4. Discussion

Our research shows there are large areas of suitable habitat available

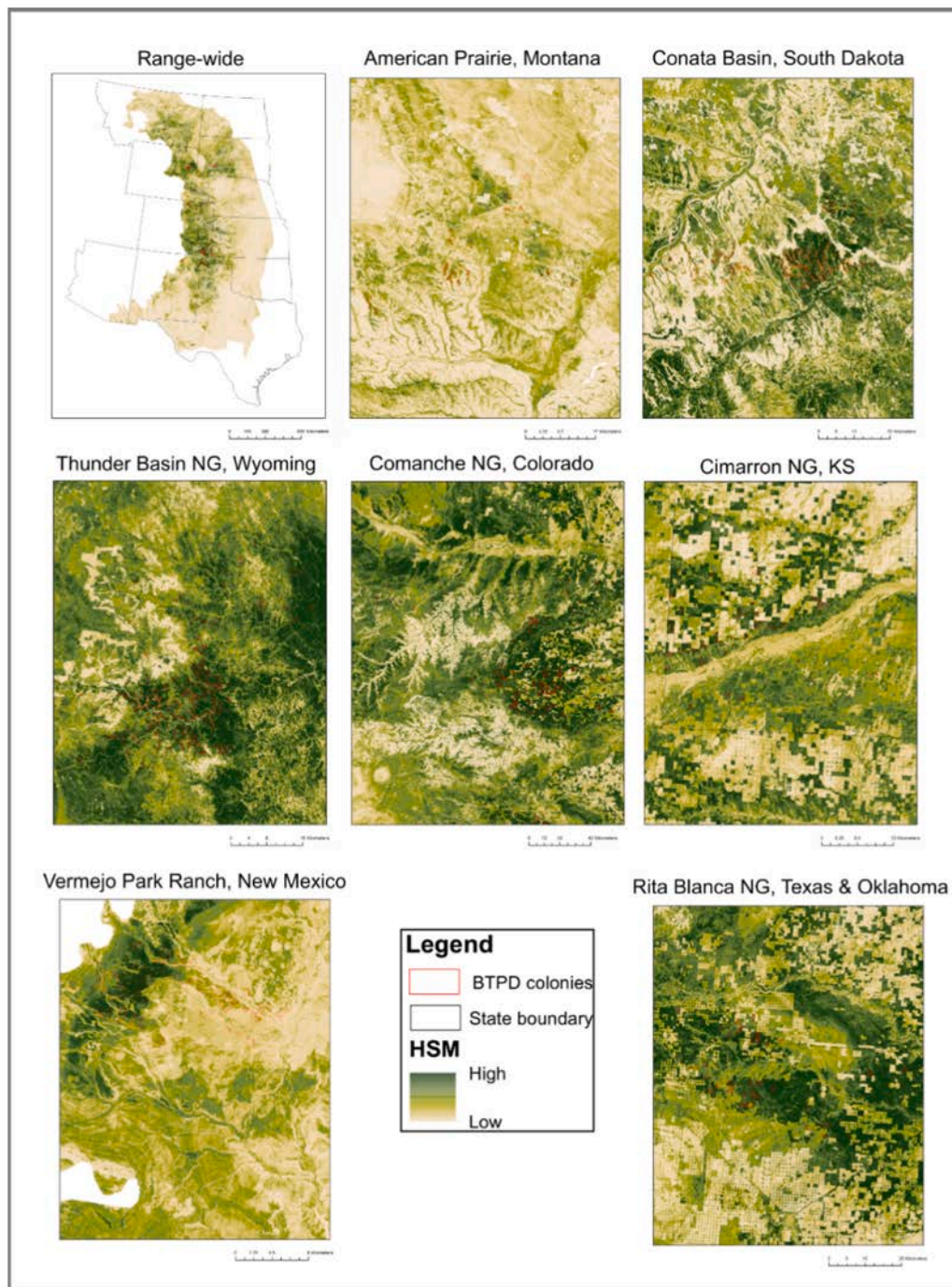


Fig. 4. Ground-truthed and ground-mapped black-tailed prairie dog (BTPD) colonies across Private Conservation Lands, the state of Colorado, and National Grasslands (NG), overlapped with BTPD ensemble habitat suitability model under current climate.

for the BTPD ecosystem, across their U.S. range and within each state. We identify 20.8 million hectares of remaining suitable grassland habitat. However, only 1.9 million hectares (9 %) are currently occupied by BTPDs. These results demonstrate the large amount of conservation potential for the prairie dog ecosystem. Such findings are especially encouraging for associated species that depend on BTPDs and their colonies for habitat, and for those species that require large colonies to support their populations (Augustine and Baker, 2013; Augustine and Skagen, 2014; Davidson et al., 2012; Duchardt et al., 2020; Livieri et al., 2022; U.S. Fish and Wildlife Service, 2013). Further, our HSM can help inform conservation planning and efforts to promote coexistence. For example, the impacts BTPDs can have on livestock producers (Crow

et al., 2022; Vermeire et al., 2004) and the susceptibility of BTPD populations to plague (Cully et al., 2010; Davidson et al., 2022; Eads and Biggins, 2015) will continue to be major factors affecting conservation efforts for BTPDs. Mitigating impacts on livestock producers will require careful consideration of the spatial distribution of colonies on and adjacent to livestock operations, and how management can effectively maintain colony complexes in desired locations while preventing expansion into undesired areas. Our HSM can assist in planning efforts not only by ensuring that locations targeted for BTPD conservation are in optimal habitat, but also in identifying transition zones between high and low habitat suitability where expansion may be more effectively and naturally prevented, to reduce the need for lethal control. Our maps can

Table 3

Number of hectares of black-tailed prairie dog (BTPD) habitat that is of low, medium, high, and medium + high suitability within each state and across the BTPD range within the United States. Table includes estimated number of hectares occupied by BTPD colonies within each state based on WEST data (McDonald et al., 2015); the occupied area was corrected for false negatives (but not false positives) across all states except Wyoming (see Part 2 of McDonald 2015 report, Wyoming).

State name	Area of low habitat suitability (ha)	Area of medium habitat suitability (ha)	Area of high habitat suitability (ha)	Area of medium + high habitat suitability (ha)	Area of medium + high habitat suitability occupied by BTPDs (ha)	Percent of medium + high habitat suitability occupied by BTPDs (%)
Arizona	13,750	5789	108	5897	14	0.2 %
Colorado	1,338,636	1,558,562	4,216,600	5,775,162	215,486	3.7 %
Kansas	631,120	420,207	760,199	1,180,406	62,662	5.3 %
Montana	1,763,366	1,345,433	1,588,702	2,934,135	74,516	2.5 %
Nebraska	692,534	441,174	389,552	830,726	36,117	4.3 %
New Mexico	1,169,982	863,150	728,047	1,591,197	50,242	3.2 %
North Dakota	340,733	180,275	63,826	244,101	6,300	2.6 %
Oklahoma	280,290	212,791	480,503	693,294	32,884	4.7 %
South Dakota	1,711,314	1,277,664	1,470,485	2,748,149	90,747	3.3 %
Texas	1,018,266	804,629	1,064,014	1,868,643	96,709	5.2 %
Wyoming	1,064,272	1,021,180	1,961,438	2,982,618	11,6845	3.9 %
Entire U.S. Range	10,024,502	8,130,936	12,723,491	20,854,427	78,2521	3.8 %

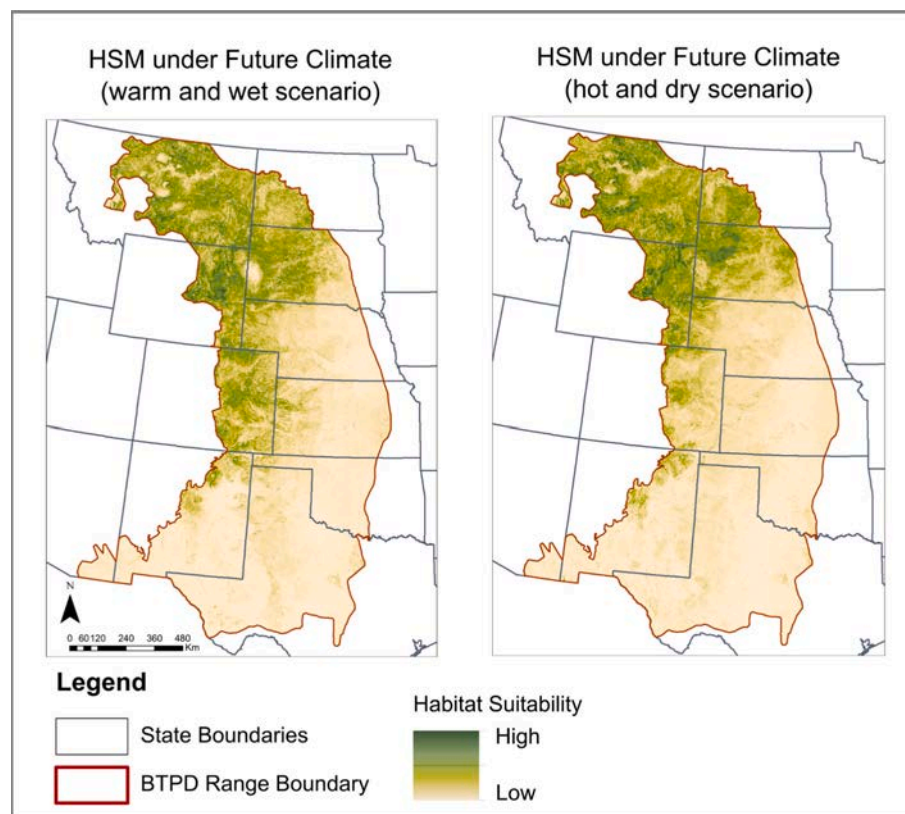


Fig. 5. Black-tailed prairie dog (BTPD) ensemble habitat suitability model (HSM) projected under future climate scenarios. Dark green shows areas of highest habitat suitability for BTPDs, and beige shows areas of lowest suitability. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

also be used to assess whether landscapes targeted for conservation efforts are large enough to support conservation goals for associated species such as BFFs and mountain plovers, which rely on extensive colony complexes (Augustine and Skagen, 2014; Dinsmore and Knopf, 2005; Duchardt et al., 2020). Additionally, the maps can support analyses of potential connectivity among colonies across landscapes, which often affects the likelihood and scale of plague epizootics (Barrile et al., 2023; Collinge et al., 2005; Davidson et al., 2022; Johnson et al., 2011). Another utility of our model could be informing which landowners might be best to participate in payment programs for BFF recovery (NRCS, 2022), by showing how their lands relate to the broader

landscape and may help to achieve range-wide conservation goals.

Suitable habitat for the BTPD ecosystem shows a dramatic shift northward under both future climate scenarios in our analysis, which is consistent with climate projections for the Great Plains and consequent species' range shifts across the region and globally (Bradford et al., 2020; Chen et al., 2011; Roberts et al., 2019). Harsh winters are known to negatively impact prairie dog reproduction (Grassel et al., 2016; Stephens et al., 2018); milder winter conditions in the northern regions under a warming climate could have a positive impact on prairie dog populations. Given the northward trend, and projected expansion of C4 grasses across the northern plains (Klemm et al., 2020), we suspect

suitable habitat will eventually extend beyond the current northern range boundary. Understanding this northward expansion would be worthy of future research. Meanwhile, there already have been significant losses in large prairie dog colony complexes in the southern portion of the BTPD range, not only due to plague, but also to increasing intensity and frequency of drought under climate change (Ceballos et al., 2010; Davidson et al., 2018; Davidson et al., 2014; Facka et al., 2010; Hale et al., 2013; Hayes et al., 2016), and our models indicate that recovery of these populations may be limited by climate change. Drought can suppress reproduction and population growth rates causing colony contractions and local extinctions (Davidson et al., 2014; Facka et al., 2010; Grassel et al., 2016; Hale et al., 2013; Hayes et al., 2016; Hoogland, 1995; Stephens et al., 2018). Nevertheless, our analysis highlights regions in the southern part of the range, such as northeastern New Mexico, that may remain suitable well into the future and be worthy of conservation investment, in addition to areas farther north (especially in Wyoming, Montana, and South Dakota).

Although we highlight a northward shift in suitable habitat for the BTPD ecosystem, we do not consider how climate change might interact with plague. When dry conditions are followed by wet weather with mild temperatures, the consequent increases in prairie dog densities, flea loads, and above-ground activity can coincide with conditions favoring fleas and plague transmission (Eads and Biggins, 2017). This suggests that the frequency of plague epizootics might increase where these conditions occur under a warming climate (Eads and Hoogland, 2017), which may become more typical across the northern region of their projected range (Fig. 5). Alternatively, Snäll et al. (2009) modeled future plague and black-tailed prairie dog dynamics under different climate change scenarios and found that plague may in fact decrease in the future, especially under those scenarios that project the greatest warming. They suggest the underlying mechanism reducing plague events is the effect of high temperatures on fleas and plague transmission. Understanding the role of climate in driving plague epizootics and how climate change might alter plague dynamics across the prairie dog range remains an important area of research (Barrile et al., 2023).

Our HSM highlighted climate, topography, and landcover type being the most important variables predicting suitable habitat for the BTPD ecosystem, with climate (growing degree days and precipitation) being the most important overall. Previous maps of BTPD habitat suitability developed for the southern Great Plains were based upon climate and topographic variables but did not evaluate the role of land use and cover (Augustine et al., 2012). Whereas recent work by Olimb et al. (2022) conducted comparable analyses, using climate, topography, and landcover as predictors of BTPD habitat in three Native nations of Montana. Our new models for the entire BTPD range identified similar effects of topography and climate, and additionally incorporated effects of land use. Our results reflect BTPD preference for deep, clayey-loam soils (with low percentage of sand) that facilitates burrowing and mound building, and their strong habitat association with grasslands in broad, flat plains where visibility is maximized (Augustine et al., 2012; Hoogland, 1995). The positive relationship we found with winter-spring precipitation reflects forage resources available during the key period of offspring production in the spring. Summer-fall precipitation also is important for BTPDs, particularly for enabling overwinter survival, but a large amount can cause tall vegetation that can impede colony growth (Bruggeman and Licht, 2020; Grassel et al., 2016), and also can potentially increase the presence of plague (Biggins et al., 2021).

Our model was trained on McDonald et al.'s (2015) dataset, which was (and to date still is) the only population survey available across the BTPD range. The dataset was ideal for creating a range-wide habitat suitability model because it was a systematic survey and it provided both presence and absence data. However, the data do have potential biases that are important to keep in mind when interpreting our model. McDonald et al. (2015) included a correction factor to account for the possibility that observers would miss small colonies (false negatives), but they did not account for potential sources of error that could lead to

their values being overestimates of colony area (false positives). McDonald et al. (2015) found a 15 to 30 % false positive rate for a subsample of their dataset (state of Wyoming), and a follow-up study that used the same methodology found a 26 % overall false positive rate (state of Colorado in 2016) (Howlin and Mitchell, 2016). Although state biologists helped us remove false positives from our dataset, there were still likely false positives that remained, meaning that our model may harbor some over-estimates of suitable habitat. Moreover, our model does not consider prairie dog population densities, only estimated area of occurrences. Population densities of prairie dogs are rarely gathered when conducting large-scale population surveys, because of the considerable logistical effort entailed. Nevertheless, such data are valuable for informing management, as relatively high population densities reflect good habitat quality and are important for sustaining populations of associated species, especially predators like black-footed ferrets (Ceballos et al., 2010; Livieri et al., 2022). Finally, plague has dramatically influenced prairie dog population dynamics across much of their geographic range (Cully et al., 2010; Augustine et al., 2008a; Davidson et al., 2022), and the data we used to train our model is based on colony occurrences across landscapes where plague is now endemic. This should be kept in mind when interpreting our HSMs, although it is unlikely that the presence of plague has altered what our model identifies as suitable habitat. In any given year and location, some colony complexes are at a low point induced by a recent plague epizootic, while others are undergoing expansion/recovery following plague, and still others are at a high point in colony area. Our modeling approach averages across all of this variation in colony extent by using a survey of colonies across the entire range of the species, enabling the model to identify overall patterns of soils, climate, topography, and vegetation that are associated with BTPD colonies.

The development of our HSM was a collaborative process with local experts and land managers. The reviews we received from experts, managers, and the WAFWA PDCT were integral to improving the accuracy and applicability of our model. Through the process we were able to learn about and correct erroneous data points, model deficiencies, as well as how our model could be made most useful to managers. Increasingly, scientists and managers are working together to co-create such decision support tools (Schwartz et al., 2018; Sofaer et al., 2019). Insights from the experts and managers we collaborated with greatly improved the quality of our model and its on-the-ground utility for wildlife management.

Our aim was to produce a model that could identify for management agencies and NGOs the most biophysically suitable areas to focus on for BTPD ecosystem conservation. With conservation dollars limited, our maps (at 30 m² resolution) provide insights for strategic conservation planning, with a lens into the effects of climate change. They enable entities engaging in conservation actions such as restoration, conservation, management, and land protection to evaluate the distribution of suitable habitat on a given property, as well as within the broader surrounding landscape. Central to any conservation strategy is understanding the connectivity of suitable habitat, landownership, and how different areas fit into the broader landscape (Augustine et al., 2021; Rudnick et al., 2012). Our maps show how northeast New Mexico, southeast Colorado, northeast Wyoming, and western South Dakota harbor some of the largest remaining high-suitability grassland habitat for the BTPD ecosystem today, and that many of these areas remain strongholds into the future. Plague is common throughout these areas, so plague mitigation is likely to be an important management consideration where conservation efforts are focused. From a range-wide perspective, these regions may be some of the best to focus on for purchasing land and conservation easements to support the BTPD ecosystem and BFF recovery. In southeast Colorado, for example, there have been major efforts by NGOs to focus on private lands conservation, primarily through conservation easements and land acquisition for conservancies (Colorado Natural Heritage Program and the Geospatial Centroid, 2022). In addition, Colorado State Land Board has

consolidated their holdings to create several large, contiguous properties that contain extensive BTPD habitat in southeast Colorado (Colorado Natural Heritage Program and the Geospatial Centroid, 2022).

Understanding the ecologically most suitable habitats for wildlife conservation is at the core of any conservation decision making, which our maps illuminate for the BTPD ecosystem. A critical next step in conservation planning for the BTPD ecosystem is to identify priority areas that not only consider this ecological landscape, but also the political, social, and threat landscapes (Ban et al., 2013; Miller et al., 2007; Niemiec et al., 2021; Pressey et al., 2007). This is especially important for contentious species like BTPDs where much of the suitable habitat occurs on private land, and for landscapes like the Central Grasslands that are highly fragmented with complex land ownership and jurisdictional boundaries (Augustine et al., 2021). As initiatives like the Central Grasslands Roadmap and America the Beautiful are implemented for North America's grasslands (Haaland et al., 2021), and others look to address the loss of temperate grasslands globally (Bardgett et al., 2021; Carbutt et al., 2017; Henwood, 2010), it will be key to identify landscapes that are not only ecologically suitable for wildlife conservation, but also have the social and political support to facilitate success. Conservation planning efforts such as these are urgently needed to address the global challenge of temperate grassland decline.

Credit authorship contribution statement

Ana Davidson: Conceptualization, methodology, writing – original draft, editing and review, visualization, supervision, project administration.

Michelle Fink: Formal analysis, writing – editing and reviewing.

Michael Menefee: Conceptualization, visualization, writing – reviewing.

Lindsey Sterling-Krank: Conceptualization, visualization, project administration, funding acquisition, writing – review.

Bill Van Pelt: Funding acquisition, visualization, writing – editing and reviewing.

David Augustine: Conceptualization, methodology, writing – editing and reviewing, visualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

BTPD habitat suitability maps can be downloaded here: <https://cnhp.colostate.edu/projects/hotr/#Downloads1>.

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Appendix A. Supplementary data

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ARTICLE

Disease and weather induce rapid shifts in a rangeland ecosystem mediated by a keystone species (*Cynomys ludovicianus*)

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Abstract

Habitat loss and changing climate have direct impacts on native species but can also interact with disease pathogens to influence wildlife communities. In the North American Great Plains, black-tailed prairie dogs (*Cynomys ludovicianus*) are a keystone species that create important grassland habitat for numerous species and serve as prey for predators, but lethal control driven by agricultural conflict has severely reduced their abundance. Novel disease dynamics caused by epizootic plague (*Yersinia pestis*) within prairie dog colonies have further reduced prairie dog abundances, in turn destabilizing associated wildlife communities. We capitalized on a natural experiment, collecting data on prairie dog distributions, vegetation structure, avian abundance, and mesocarnivore and ungulate occupancy before (2015–2017) and after (2018–2019) a plague event in northeastern Wyoming, USA. Plague decimated black-tailed prairie dog populations in what was then the largest extant colony complex, reducing colony cover in the focal area from more than 10,000 ha to less than 50 ha. We documented dramatic declines in mesocarnivore occupancy and raptor abundance post-plague, with probability of occupancy or abundance approaching zero in species that rely on prairie dogs for a high proportion of their diet (e.g., ferruginous hawk [*Buteo regalis*], American badger [*Taxidea taxus*], and swift fox [*Vulpes velox*]). Following the plague outbreak, abnormally high precipitation in 2018 hastened vegetation recovery from prairie dog disturbance on colonies in which constant herbivory had formerly maintained shortgrass structure necessary for certain colony-associates. As a result, we observed large shifts in avian communities on former prairie dog colonies, including near-disappearance of mountain plovers (*Charadrius montanus*) and increases in mid-grass associated songbirds (e.g., lark bunting [*Calamospiza melanocorys*]). Our research highlights how precipitation can interact with disease-induced loss of a keystone species to induce drastic and rapid shifts in wildlife communities. Although grassland taxa have co-evolved with high spatiotemporal variation, fragmentation of the remaining

North American rangelands paired with higher-than-historical variability in climate and disease dynamics are likely to destabilize these systems in the future.

KEYWORDS

disturbance, grassland birds, Great Plains, mesocarnivore, mountain plover, prairie dog, ungulate

INTRODUCTION

Ecological theory was built on the concept of systems at equilibrium either under short or long timescales (Holling, 1973; Wilson & MacArthur, 1967). However, many ecological systems are better described under a nonequilibrium model (Briske et al., 2017; Rapacciuolo & Blois, 2019), especially those ecosystems that co-evolved with frequent disturbance. These systems are by nature more difficult to characterize and predict, but rapid change in the Anthropocene (e.g., climate change; Gaüzère et al., 2018; disease, Holdo et al., 2009) threatens to further destabilize all ecological systems, leading to novel outcomes. Destabilization could have dramatic, undesirable consequences for imperiled systems expected to simultaneously support human use and retain ecological function, such as rangelands.

Rangelands (typically grasslands, shrublands, or other aridlands) are poorly described by single-equilibrium models and are shaped by highly variable disturbance and climate regimes (Briske et al., 2017). Although rangelands have historically occupied nearly half of the planet's terrestrial surface, nearly all of these lands have been converted to some form of human use (Sterling & Ducharme, 2008). Within North America, 40% of the Great Plains have been converted to rowcrop agriculture (Augustine et al., 2019), and the pace of cropland conversion remains rapid (Gage et al., 2016; Wright & Wimberly, 2013). Most remaining grasslands and shrublands in North America are managed as dual-purpose rangelands, providing forage for livestock and habitat for wildlife.

Although research supports the compatibility of managing rangelands for both livestock and biodiversity conservation (Augustine & Derner, 2021; Fuhlendorf et al., 2012; Riginos et al., 2012), the balance is delicate, and made increasingly complex on rangelands occupied by burrowing rodents such as prairie dogs (*Cynomys* spp.). As with many burrowing mammals (Davidson et al., 2012), black-tailed prairie dogs (*Cynomys ludovicianus*; from this point forward “prairie dog”) play an integral role as keystone species within the North American Great Plains. Through herbivory, clipping, and

burrowing, prairie dogs generate habitat for associated wildlife species including burrowing owls (*Athene cunicularia*) that nest in prairie dog burrows and mountain plovers (*Charadrius montanus*) that select for the short, sparse vegetation they engineer (Duchardt et al., 2020). Prairie dogs also serve as a food source for predators, including raptors, foxes (*Vulpes* sp.), coyotes (*Canis latrans*), American badgers (*Taxidea taxus*), and the endangered black-footed ferret (*Mustela nigripes*; Hoogland, 2013; Lomolino & Smith, 2004).

Despite their keystone role (Kotliar et al., 1999), prairie dogs are considered a nuisance or noxious species in some states in the USA because of their capacity to compete with livestock for forage, and they are lethally controlled throughout their range (Augustine & Derner, 2021; Derner et al., 2006; Miller et al., 2007; Wyoming Weed and Pest Council, 2019). Due to the combined effects of habitat loss and control efforts that began in the 19th century, prairie dogs currently occupy a small fraction of their historical range (Knowles et al., 2002; Luce, 2003). Additionally, prairie dogs have been decimated by epizootic outbreaks of sylvatic plague (*Yersinia pestis*). This nonnative pathogen was introduced to North America in the early 1900s and often resulted in >99% mortality in localized populations (Cully et al., 2006). Plague has been present throughout much of the prairie dog's range for the past one to three decades (Cully Jr. et al., 2010). The combined pressures of disease, habitat loss and control efforts that have severely reduced prairie dog populations have resulted in cascading declines in associated wildlife species (Ceballos et al., 2010; Davidson et al., 2012; Dobson & Lyles, 2000; Hoogland, 2013). Despite observed range-wide declines in associated species and detection of community shifts following long-term changes in prairie dog abundance (e.g., Ceballos et al., 2010), few studies have captured species-specific responses to plague events (e.g., Augustine et al., 2008; Seery & Matiatos, 2000), and assessments of community-level responses are even more rare. As such, the direct and indirect effects of plague events on associated vertebrate communities are still poorly understood (Eads & Biggins, 2015).

Drastic fluctuations in local prairie dog abundances across time due to plague (“boom-and-bust” cycles [Davidson et al., 2022]) are likely to impact wildlife

communities by reducing the availability of both prey and habitat. However, in considering the impacts of plague at the community level, it is important to recall that many rangeland wildlife species possess innate coping strategies for habitat variability. Periodic disturbance and unpredictable climate are the defining characteristics of rangelands (Samson & Knopf, 1994), and spatial and temporal variability has driven a suite of adaptations in species that inhabit these systems. For example, bison (*Bison bison*) and other ungulates track (Merkle et al., 2016), and sometimes engineer (Geremia et al., 2019) variable patterns of green-up following disturbance, and migrant songbirds can dramatically shift their breeding ranges in response to extreme precipitation years (e.g., Bateman et al., 2015). However, climate projections for the North American Great Plains consistently predict greater variation in precipitation with increased heavy precipitation events (Conant et al., 2018), which may present a novel degree of variability beyond those experienced historically. Although rangeland fauna co-evolved with, and may be better able to respond positively to variability, than wildlife in more stable or equilibrium ecosystems, the degree of variability predicted under climate change is unprecedented and may interact with other novel drivers such as disease (e.g., Biggins et al., 2021).

Compounding the challenges of climate change and novel disease interactions is a continued decrease in habitat availability. Variability in suitable habitat was historically buffered by broad-scale habitat availability, such that animals could alter their distribution to obtain needed resources in a given season. This is no longer the case as rangelands, and particularly grasslands, continue to be fragmented with less habitat remaining each year (Augustine et al., 2019). Quantifying the magnitude and speed at which species associated with prairie dogs respond to these novel drivers would enable the creation of models for holistic prairie dog management on the remaining grassland habitat, but this information has been previously unavailable.

We capitalized on a natural experiment in which we tracked responses in vegetation, avian communities, and the occupancy of mesocarnivores and ungulates, before and after a plague event in a prairie dog colony complex at a grassland-shrubland ecotone. Following a severe plague outbreak combined with above-average precipitation years, we were able to examine the combined impacts introduced by disease, disturbance, and extremes in precipitation that have contributed to transforming vertebrate communities in the northern Great Plains. We hypothesized that widespread plague would yield taller and denser vegetation on colonies (H₁. Vegetation structure; Figure 1), which would lead to decreased habitat suitability for shortgrass songbirds but increased suitability for mid-grass obligates (H₂.

Habitat structure; Figure 1). Although taller and denser vegetation would yield greater forage availability, we hypothesized that decreased forage quality (due to the loss of herbivory and clipping by prairie dogs) would reduce the use by ungulates (H₃. Forage quality; Figure 1). Prairie dogs maintain forage in an early phenological state (Connell et al., 2019; Whicker & Detling, 1988) and can trigger a shift from graminoids to forbs (Duchardt et al., 2021). Decline in the major prey resource (prairie dogs) was hypothesized to lead to declines in mesocarnivore occupancy and use in this landscape (H₄. Trophic effects; Figure 1). We predicted that population responses would be most dramatic and swift for the carnivores in our study system that relied on prairie dogs for a large proportion of their diet (e.g., ferruginous hawks [*Buteo regalis*], American badger, and swift fox [*Vulpes velox*]; Kagel et al., 2020; Nicholson et al., 2006; Seery & Matiatos, 2000), with the magnitude of their declines increasing with their dietary reliance on prairie dogs. We anticipated bird communities, which respond more to vegetation structure, would differ most at 2 years post-plague. This is because in other systems in which plague has occurred, responses in vegetation structure and associated species have typically taken multiple years, probably due to the slow recovery of vegetation structure (Augustine et al., 2008, but please refer to Seery & Matiatos, 2000).

METHODS

Study area

We collected data between 2015–2019 in the Thunder Basin Ecoregion of northeastern Wyoming, USA (Appendix S1: Figure S1). Thunder Basin is located at the ecotone between the Great Plains and sagebrush (*Artemisia* spp.) steppe, with mean annual precipitation ranging between 25 and 35 cm, generally falling during spring and summer (Porensky et al., 2018). This rangeland system is a mosaic of vegetation communities including sagebrush, shortgrass prairie, mixed-grass prairie, ponderosa pine (*Pinus ponderosa*) woodlands and plains cottonwood-dominated (*Populus deltoides* ssp. *monilifera*) riparian areas. Our research focused on a mosaic of sagebrush–grasslands, grasslands, and prairie dog colonies. In sites without prairie dogs, shrub species included Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*) and other sagebrush species, greasewood (*Sarcobatus vermiculatus*) and broom snakeweed (*Gutierrezia sarothrae*). Common graminoids included blue grama (*Bouteloua gracilis*), needle-and-thread (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), and threadleaf sedge (*Carex filifolia*). Prairie dog colonies were dominated by western wheatgrass, plains prickly

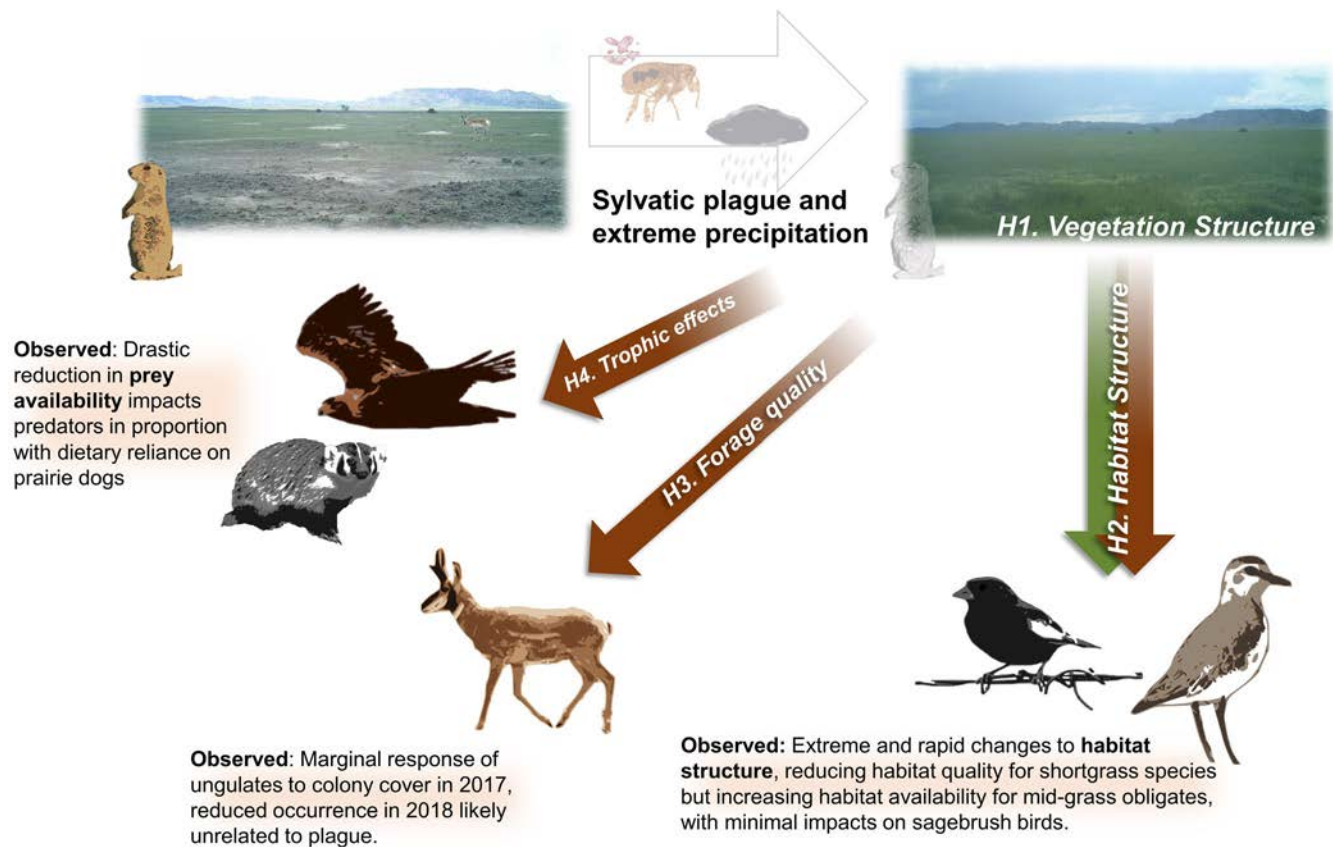


FIGURE 1 Conceptual figure describing the impacts of disease and climate on vegetation structure and associated species within the Thunder Basin Ecoregion, Wyoming, USA. Top panels show the vegetation structure in late May 2017 (left; pre-plague) and in 2018 (right; post-plague). Hypotheses of interest are noted in white text, along with predicted positive or negative effects (green or brown, respectively). We also note observed trends and how these aligned with hypotheses. Original photographs for creation of graphics are from C. Duchardt, J. Hennig, or the public domain.

pear (*Opuntia polyacantha*), and short-lived forb species (e.g., wooly plantain [*Plantago patagonica*], desert madwort [*Alyssum desertorum*], common pepperweed [*Lepidium densiflorum*]). Typical of most extant prairie dog complexes, the Thunder Basin Ecoregion has experienced multiple cycles of colony growth followed by outbreaks of sylvatic plague (2000 and 2007; Cully Jr. et al., 2010), with the most extreme event in the last 20 years occurring at the end of the growing season in 2017 (Davidson et al., 2022).

Study design

Prairie dog colony mapping

Prairie dog colony mapping occurred within the study area annually between 2015 and 2019. Mapping was conducted by multiple stakeholders including the U.S. Forest Service and Thunder Basin Grassland Prairie Ecosystem Association (TBGPEA). Mapping was conducted either on foot or in an all-terrain vehicle

(ATV) using a global positioning systems (GPS) device to map outer boundaries of colonies, similar to Cully Jr. et al. (2010). Boundaries consisted of outer active burrows, with activity denoted by vegetation clipping, recent digging, or fresh scat. Following a plague event in the summer and fall 2017, mapping efforts were complicated by extreme contraction in active colonies. In response, we used a two-phase approach to mapping in 2018 (Davidson et al., 2022), with the first phase consisting of surveys conducted in April–July of point grids spaced at 600 m intervals to detect signs of prairie dog occupancy. In autumn, phase two consisted of revisiting areas with activity and mapping active burrows. Mapping in 2019 consisted of revisiting previously identified occupied areas and mapping in those areas. Please refer to Davidson et al. (2022) for additional methodological details. We did not directly quantify prairie dog density in the study area over time, but did observe burrow densities of 150/ha and confirmed active (via scat or active digging) burrow densities of 68/ha in 2017 (Duchardt et al., 2021).

Avian and vegetation sampling

We conducted pre- and post-plague sampling at locations corresponding with avian point-count transects established in 2015 (Duchardt et al., 2019). One set of transects was randomly placed with the constraint that transects fell entirely within prairie dog colonies (“colony transects”), a second set was located randomly with the requirement that transects crossed the edge of a prairie dog colony with four points located outside the colony and one to four within the colony, depending on colony size (“edge transects”), and a third set was located nonrandomly in areas without prairie dogs and characterized by extensive sagebrush–grassland habitat (“sagebrush–grassland transects”). All transects contained between five and eight points spaced 250 m apart. Only a subset of these transects (five undisturbed sagebrush–grassland, eight colony, 23 edge; Appendix S1: Figure S1) were surveyed in all years between 2015 and 2019; subsequently, we only used these data for this analysis ($N = 263$ point-count locations).

We conducted avian surveys between sunrise and 10:00 AM on days with low wind and no rain (Pavlacky et al., 2017) from mid-May to mid-June, 2015–2019. By traveling to many points via ATV we ensured more effective detection of mountain plovers, which display more cryptic behavior in response to observers on foot (Dinsmore et al., 2002). Between mid-June and late-July each year, we measured maximum vegetation height and visual obstruction (a metric incorporating both vegetation height and density) using a Robel pole (Robel et al., 1970). We collected these measurements every 5 m along 30-m transects originating at the point-count location and running perpendicular to the axis of the point-count transect.

Mesocarnivore and ungulate sampling

We used previously established camera traps (please refer to Connell et al., 2018) and supplemented these with additional camera locations to begin characterizing the mammalian communities at these sites. We established 12 camera traps (Browning BTC-5HD, 20 s delay, two shot) in 2016 as part of a study to detect wildlife use of sites on historical fire scars, prairie dog colonies, and undisturbed areas (Connell et al., 2018). In 2017, we added 17 camera traps (Bushnell Trophy Camera 119636TCP) at a subset of the avian point-count locations described in section *Avian and vegetation sampling*. We selected locations for camera placement as follows: all point-count locations were characterized by duration of prairie dog occupancy (0–15 years), and we randomly selected point locations along a gradient of occupancy duration

(Appendix S1: Figure S1). These cameras were deployed from mid-May 2017 through April 2019. All cameras were placed ~1 m high with an unobstructed viewshed away from fences.

We reviewed all photographs to determine the presence of any animal species and recorded the number of each taxon present per photograph. We trained each individual involved in photo processing in species identification, and all data used in analyses were reviewed by individuals with >10 years field experience working with North American Great Plains and sagebrush wildlife (C. Duchardt and N. Dufek [please refer to “*Acknowledgments*”]). To align with the timing of breeding bird surveys and vegetation data, we extracted and analyzed camera trap data from mid-May to mid-August in 2017 and 2018 for analysis.

Precipitation data

We obtained precipitation data for each year from the NOAA divisional time series data for Wyoming Climate Division 7, the Cheyenne Niobrara drainage (NOAA, 2022). This division includes the entire study area and was centered at the convergence of Weston, Converse, Campbell, and Niobrara counties. We extracted data on cumulative annual precipitation for each year between 2015 and 2019.

Analytical framework

Avian and vegetation responses

We summed detections of each bird species on and off active colonies annually, correcting for number of survey points per transect (i.e., divided by number of points). Some target species had few detections (e.g., burrowing owl); therefore, we did not adjust for detectability and instead used number of detections as a proxy for abundance (but please refer to Duchardt et al., 2018, 2020 for detectability-adjusted abundances prior to plague in this system). To help mitigate detectability issues, we used a post-hoc detection radius of 200 m for all songbirds and shorebirds; after this distance, we observed detectability dropping off markedly in other data collected in this system. Because most raptors were detected >200 m, we used an unlimited radius for raptor detections. The majority of passerine and shorebird detections were aural, while raptors were typically detected in flight; therefore, differences in vegetation structure were likely to have had little impact on detectability.

We used distance-based redundancy analysis (dbRDA; Legendre & Anderson, 1999) using the “vegan” package in R (Oksanen et al., 2020) to examine avian community structure and change on and off prairie dog colonies following the plague outbreak. This technique employs RDA based on Bray–Curtis distance, providing a more rigorous test of covariate importance than other nonmetric approaches (e.g., NMDS; Kruskal, 1964) while still being robust to non-normal data (a common feature in data based on avian point counts). Prior to conducting the ordination, we applied a Wisconsin square-root transformation to relativize the data and reduce the influence of dominant species relative to less abundant species (van der Maarel, 1979). We summarized point data at the transect level for “colony” and “sagebrush” transects. We split edge transects each year into “inside” or “outside” colony points according to each year’s colony distribution. We tracked avian community change over time at both the transect level and in areas historically colonized versus uncolonized by prairie dogs. To assess the potential roles of plague and precipitation in the system, we included the environmental variables of annual precipitation and percent prairie dog colony cover within 200 m of the transect. We also included a categorical variable that represented sagebrush dominated versus other (colony and edge) because we assumed some variation in bird communities was driven by shrub cover. We then used a permutational ANOVA in *vegan* (`anova.cca, by = ‘term’`) to test for the significance of each of these variables (Legendre & Legendre, 1998).

We averaged readings of visual obstruction and maximum vegetation height at the point level annually. We then used the *glm* function in the *stats* package in base R to model the responses of maximum vegetation height and visual obstruction at the point level to annual precipitation and percentage prairie dog colony cover within 30 m of the point (the length of our vegetation transect). We considered models that included each of these factors individually, as well as both the additive and interactive combination of the two factors. We used Akaike’s information criterion corrected for small samples (AIC_c ; Burnham & Anderson, 2002) to compare each set of models with a null model.

Mesocarnivore and ungulate occupancy

We estimated single season occupancy of five mesocarnivores (swift fox, red fox [*V. vulpes*], coyote, American badger, bobcat [*Lynx rufus*]) and three ungulates (elk [*Cervus canadensis*], mule deer [*Odocoileus hemionus*], pronghorn [*Antilocapra americana*]) in the summers of 2017 and 2018. We present detections of cattle (*Bos taurus*) as a control

because, although cattle grazing behavior may be affected by prairie dog activity (e.g., Sierra-Corona et al., 2015), cattle movement among pastures was human driven and therefore not expected to be impacted by plague. We fitted single season occupancy models (MacKenzie et al., 2017) to weekly camera trap detections using the *unmarked* R package (Fiske & Chandler, 2011). To minimize temporal autocorrelation, we recorded presences per species at each camera trap station at 1-week intervals from mid-May through mid-August in 2017 and 2018 (similar to Davidson et al., 2018). Because the average distance between cameras was >2 km, we did not model spatial autocorrelation in detection probability. We predicted that the proportion of prairie dog colony cover would be a significant driver of site occupancy, so we calculated the proportion of a 2 km radius buffer around each camera trap that was occupied by prairie dogs. We used this buffer size as it approximates average home range sizes in swift fox (Kamler et al., 2003; Pechacek et al., 2000), and because a larger radius would lead to increased overlap among some cameras. We evaluated three models per species to assess whether the proportion of the surrounding area occupied by prairie dogs was an informative predictor of mesocarnivore and ungulate occupancy in 2017. These included an intercept-only model, a linear effect of proportion of colony on occupancy, and a quadratic effect of proportion of colony on occupancy. We included a quadratic effect because we had previously observed nonlinear responses of songbirds to aspects of colony cover in this system (Duchardt et al., 2019). We did not include any covariates in the detection portion of the model because we were mainly interested in how the presence of prairie dogs influenced occupancy. We only used the proportion of colony cover covariate in the 2017 models because prairie dogs were functionally absent in 2018 (Appendix S1: Figure S1). Consequently, we only ran an intercept-only model to estimate occupancy in 2018. We used AIC_c to rank models and report beta coefficients and standard errors of detection and occupancy from the top model. To understand the influence of plague on regional-scale occupancy rates of mesocarnivores and ungulates, we compared mean occupancy between 2017 (pre-plague) to 2018 (post-plague). We did this by predicting mean site occupancy from intercept-only models, and determining whether 95% confidence intervals overlapped between 2017 and 2018 estimates.

RESULTS

Prairie dog colony cover in the core area increased from 2015 to 2017 (Table 1). Maximum colony coverage reached 10,391 ha on public lands in 2017. The entire complex, including colonies on private lands, exceeded 16,000 ha in 2017, but these areas were not surveyed in

TABLE 1 Responses of prairie dog colony cover, vegetation structure, and multiple wildlife taxa to changing climate and disease dynamics from 2015 to 2019 in the Thunder Basin Ecoregion, Wyoming, USA. Mesocarnivore and ungulate data were collected from camera traps deployed 2017–2018.

	2015 ^a	2016 ^a	2017 ^a	2018 ^a	2019 ^a	
	Prairie dog core area (ha) ^a					
Wildlife and vegetation trends	5616	6505	10,391	47	265	Conservation status
Passerines and shorebirds ^b						
Mountain plover	0.18	0.11	0.16	0.01	0.04	IUCN-NT, FSS, SGCN
Lark bunting	0.49	0.26	0.50	3.11	3.57	
Grasshopper sparrow	0.03	0.00	0.02	0.22	0.61	FSS, SGCN
Brewer's sparrow	0.72	0.60	0.46	0.33	0.43	FSS, SGCN
Horned lark	1.24	1.31	1.11	1.17	1.12	
Killdeer	0.10	0.07	0.08	0.07	0.05	
Lark sparrow	0.17	0.13	0.08	0.11	0.14	
Loggerhead shrike	0.02	0.05	0.03	0.03	0.02	IUCN-NT, FSS
Sage thrasher	0.03	0.02	0.02	0.00	0.01	SGCN
Vesper sparrow	0.11	0.15	0.10	0.04	0.09	
Western meadowlark	1.40	1.33	1.72	1.56	1.72	
Raptors and owls ^c						
Ferruginous hawk	0.00	0.02	0.05	0.00	0.00	FSS, SGCN
Golden eagle	0.04	0.03	0.09	0.02	0.01	SGCN
Red-tailed hawk	0.02	0.02	0.03	0.00	0.01	
Burrowing owl	0.00	0.01	0.03	0.02	0.00	FSS, SGCN
American kestrel	0.02	0.05	0.04	0.02	0.01	
Northern harrier	0.00	0.05	0.01	0.00	0.01	FSS
Mammalian carnivores ^d						
Swift fox	...	...	0.25	0.07	...	FSS, SGCN
Badger	...	...	0.11	0.00	...	
Red fox	...	...	0.02	0.01	...	
Coyote	...	...	0.23	0.09	...	
Bobcat	...	...	0.03	0.00	...	
Raccoon	...	...	0.01	0.00	...	
Striped skunk	...	...	0.01	0.01	...	
Ungulates ^d						
Pronghorn	...	...	0.69	0.36	...	
Mule deer	...	...	0.13	0.01	...	
Elk	...	...	0.11	0.03	...	
Cattle	...	...	0.12	0.15	...	
Vegetation ^e						
Δ Visual obstruction inside/outside colony	4.70	3.61	3.63	2.59	1.45	
Δ Vegetation height inside/outside colony	17.91	10.90	9.56	5.70	3.19	

Abbreviations: FSS, Forest Service Sensitive Species (US Forest Service, 2018); IUCN-NT, International Union for the Conservation of Nature - Near-threatened (IUCN, 2021); SGCN, Wyoming Game and Fish Department - Species of Greatest Conservation Need (WGFD, 2010).

^aTotal hectares mapped in core area of study excluding private lands, as these were not mapped 2015–2016. Does not represent total prairie dog acres across the Thunder Basin study area.

^bNumber observed/number points surveyed. Detections were restricted to 200 m radius.

^cNumber observed/number points surveyed. Detections were unlimited radius.

^dNumber of site-weeks in which a species was detected in each year divided by the total number of unique site-weeks when cameras were active in that year (2017 = 363, 2018 = 265).

^eAverage reading (visual obstruction reading or maximum height) at sites occupied by prairie dogs subtracted from the average reading at unoccupied points in a given year. Because colonies expanded 2015–2017, but were functionally absent in 2018 and 2019, we used prairie dog occupancy status at the beginning of the study (2015) and tracked this across years.

all years and are not discussed further. Plague was first detected in one localized area in mid-summer of 2017 (pers. observ. Dave Pellatz, Courtney Duchardt; Davidson et al., 2022); but by the following spring it had affected most of the region, leaving only 47 ha of colony in our focal study area in summer 2018. Prairie dogs occurred at low densities in areas where they persisted following the plague outbreak, typically in clusters of four or five individuals separated by >100 m. Consequently, prairie dog disturbance was functionally absent in 2018, except for one small complex (~400 ha) in the southeastern portion of the grassland, ~7 km from the nearest sampling location included in our focal study area. Concomitant with this reduction in prairie dog disturbance were climatic extremes observed in 2018 (Appendix S1: Figure S1). While 2017 was a relatively average year in terms of both moisture and temperature, 2018 represented the second wettest summer in these counties in half a century (NOAA, 2022); total precipitation from May through July was 13.7 cm in 2017 and 33.8 cm in 2018.

Avian and vegetation responses

We observed 80 bird species during the 5-year period of study, including owls, passerines, raptors, shorebirds, and waterfowl. Across years and sites, the most common species observed were western meadowlark (*Sturnella neglecta*), horned lark (*Eremophila alpestris*) and lark bunting

(*Calamospiza melanocorys*; Table 1). Passerines associated with mid-grass structure, including western meadowlark, grasshopper sparrow (*Ammodramus savannarum*), and lark bunting, all reached their greatest abundances in the final 2 years of the study, following the plague event (Table 1). Conversely, mountain plover, which prefers early seral stage vegetation, declined to their lowest observed abundances in the year immediately following the plague event (effort-adjusted abundance was 16 times greater in 2017 vs. 2018; Table 1). Burrowing owls, which are dependent on burrow structures, were still observed in the first year following plague but their abundance decreased in 2019. Raptors that rely heavily on prairie dogs as prey also declined following plague (i.e., ferruginous hawk and golden eagle [*Aquila chrysaetos*]; Figure 2; Table 1) with no detections of ferruginous hawks after 2017. Red-tailed hawks (*B. jamaicensis*) showed modest but nonsignificant (based on 95% CIs) declines, whereas northern harrier (*Circus hudsonius*) and American kestrel (*Falco sparverius*) observations did not differ substantially in the latter part of the study period (Figure 2). Similarly, Brewer's sparrow (*Spizella breweri*) numbers were fairly constant across the study period, whereas the other sagebrush obligate passerine, sage thrasher (*Oreoscoptes montanus*), was relatively rare across all transects (Table 1).

We conducted a distance-based redundancy analysis based on community data at the transect scale focusing on 20 species of shortgrass, mid-grass, and sagebrush

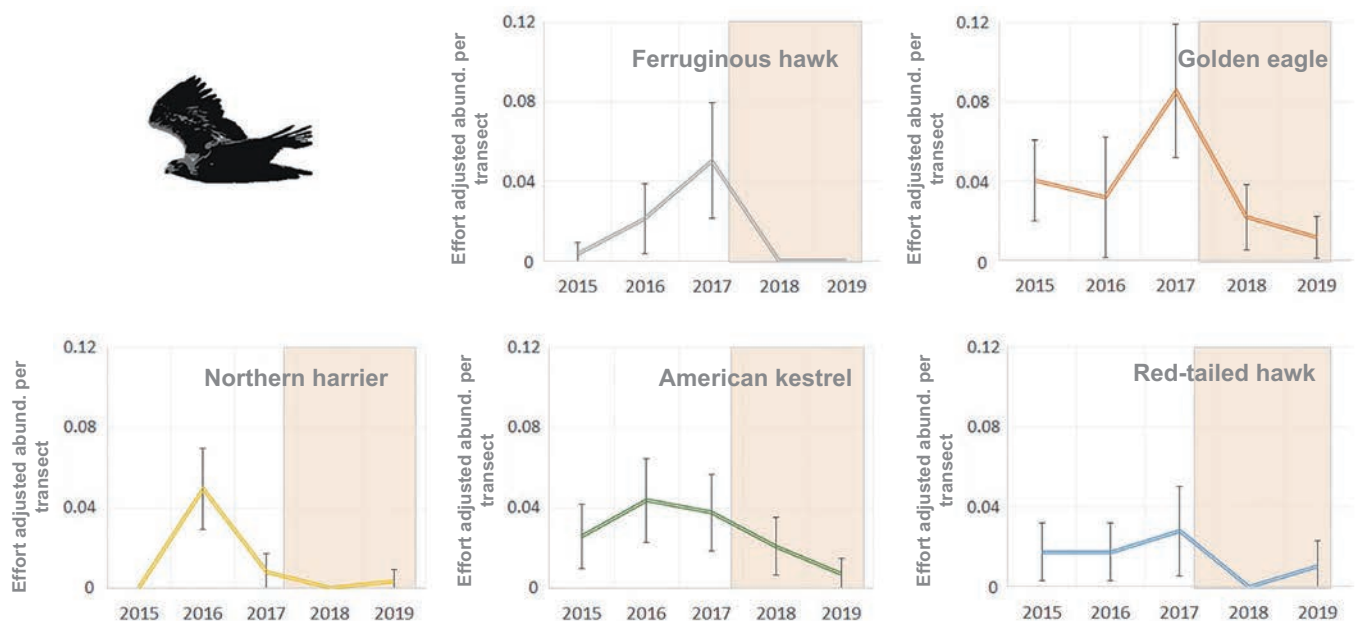


FIGURE 2 Number of observations of five raptor species adjusted for number of points surveyed, with 95% confidence intervals, between 2015–2019 in Thunder Basin Ecoregion, Wyoming, USA. Orange polygons indicate the responses after the plague event in the summer of 2017.

passerines and shorebirds. We also included burrowing owls in this ordination because of their association with colony habitat but did not include raptors because the scale of their habitat use extended beyond individual transects. Distance-based redundancy analysis yielded an adjusted R^2 of 0.20. Percentage prairie dog cover had the strongest relationship with bird community data ($F_{1,291} = 31.8$, $p < 0.001$), followed by annual precipitation ($F_{1,291} = 16.5$, $p < 0.001$) and whether transects were dominated by sagebrush ($F_{1,291} = 5.2$, $p < 0.001$) (Figure 3a). Shortgrass associates (mountain plover [MOPL], horned lark [HOLA], and to some extent burrowing owl [BUOW]) received low scores on both axes, and were associated with increasing prairie dog cover. Species either strongly or moderately associated with sagebrush (e.g., Brewer's sparrow [BRSP] and vesper sparrow [VESP]) were more abundant on sagebrush transects, whereas lark bunting (LARB) and grasshopper sparrows (GRSP) increased with increasing annual precipitation (Figure 3a).

Post-plague, centroids for avian communities in undisturbed sagebrush–grasslands (Figure 3a, green and yellow) that had previously few to no prairie dogs previously shifted mainly upon an axis of increased precipitation, while bird communities on colony core centroids (Figure 3a, red and purple) shifted along axes of both disturbance and precipitation. To better visualize site-level trajectories across the study period, we mapped vectors for both colony and sagebrush–grassland transects across the study period (Figure 3b). The magnitude of change on former colonies (measured as vector length in Figure 3b) was even more apparent at the site level, as distance in ordination space of bird communities on a given site before plague compared with afterwards was greater than distances between centroids measured at the treatment scale (Figure 3a), but the direction of change followed the same general trend as observed in centroids.

For vegetation structure, model comparison using AIC_c indicated strong support (ΔAIC_c 293.41 from the null) for an additive effect of precipitation ($\beta_{\text{precip}} = 0.26$, $SE = 0.05$) and colony cover ($\beta_{\text{colony}} = -0.04$, $SE = 0.003$) on visual obstruction, and an interactive (ΔAIC_c 859 from the null, $\beta_{\text{int}} = -0.005$, $SE = 0.002$) effect of precipitation ($\beta_{\text{precip}} = 1.39$, $SE = 0.11$) and colony cover ($\beta_{\text{colony}} = -0.06$, $SE = 0.03$) on maximum vegetation height (Appendix S1: Tables S2 and S3).

Visual obstruction on colonies during 2015–2017 ($2.49 \text{ cm} \pm 95\% \text{ CI } 0.25$) was significantly lower than readings off-colonies ($6.42 \text{ cm} \pm 0.61$). Visual obstruction on colonies occupied by prairie dogs 2015–2017 increased post-plague to $5.88 \text{ cm} (\pm 0.6)$ and $6.49 (\pm 0.73)$ in 2018 and 2019, respectively. Increases in visual obstruction on areas occupied inconsistently (either unoccupied for the entire study or having prairie dogs 1–2 years) were less

extreme ($2018 = 8.47 \pm 1.05 \text{ cm}$, $2019 = 8.06 \pm 1.15 \text{ cm}$), and were not different from formerly colonized areas in 2019. We also observed similar trends in changes of maximum vegetation height over time (Table 1).

Mesocarnivore and ungulate occupancy

We examined more than 216,335 camera trap photographs between 2017 and 2018 (Figure 4). Pronghorn were the most frequently detected native mammal at the weekly scale and were observed on all sites. Estimated detection probability for ungulates varied widely, from 0.71 for pronghorn in 2017 to 0.12 for mule deer in 2018. Detection probabilities for mesocarnivores were lower than for ungulates, with an average of 0.22 and a maximum of 0.38 (coyote in 2017). Five species (American badger, swift fox, coyote, elk, and cattle) were observed on at least half of the sites in one or both years. Striped skunk (*Mephitis mephitis*) was the least widespread species and was observed at only three sites, with only six observations total. Because skunk observations were low, we did not include them in our occupancy models.

Prairie dog observations declined rapidly in July and August 2017 (pers. observ., Dave Pellatz, Courtney Duchardt; Figure 5), with lagged declines in badgers and swift fox by January 2018 (Figure 5). In contrast, we found no clear patterns of decline for ungulate species following plague-induced collapse of prairie dogs (Appendix S1: Figure S2). We found that the proportion of prairie dog colony cover within a 2-km radius of camera traps (p_{col}) was included in the top-ranked occupancy models for four mesocarnivores in 2017 (Table 2; Appendix S1: Figure S3). Colony cover had the greatest influence on badger occupancy ($\beta = 11.9$, $SE = 4.9$, $p = 0.01$), followed by swift fox ($\beta = 6.8$, $SE = 3.0$, $p = 0.03$) and bobcat ($\beta = 4.1$, $SE = 2.1$, $p = 0.05$). Colony cover was not included in the top-ranked model for red fox occupancy (Table 2). For both badgers and swift fox, probability of occupancy reached 0.75 at 25% colony cover, with predicted occupancy at 1.00 when 75% of the area within 2 km was occupied by prairie dog colonies (Appendix S1: Figure S3). Coyote occupancy also tended to increase with percentage colony cover, but this was not significant at the $\alpha = 0.05$ level ($\beta = 21.2$, $SE = 15.9$, $p = 0.18$). Red fox occupancy was unaffected by percentage colony cover. Percentage colony cover was included in the top-ranked model of pronghorn occupancy, but this effect was not significant ($\beta = 96.7$, $SE = 133.9$, $p = 0.47$) and pronghorn occupancy was predicted to be 100% even at low (~15%) colony cover. We observed no effect of percentage colony cover on

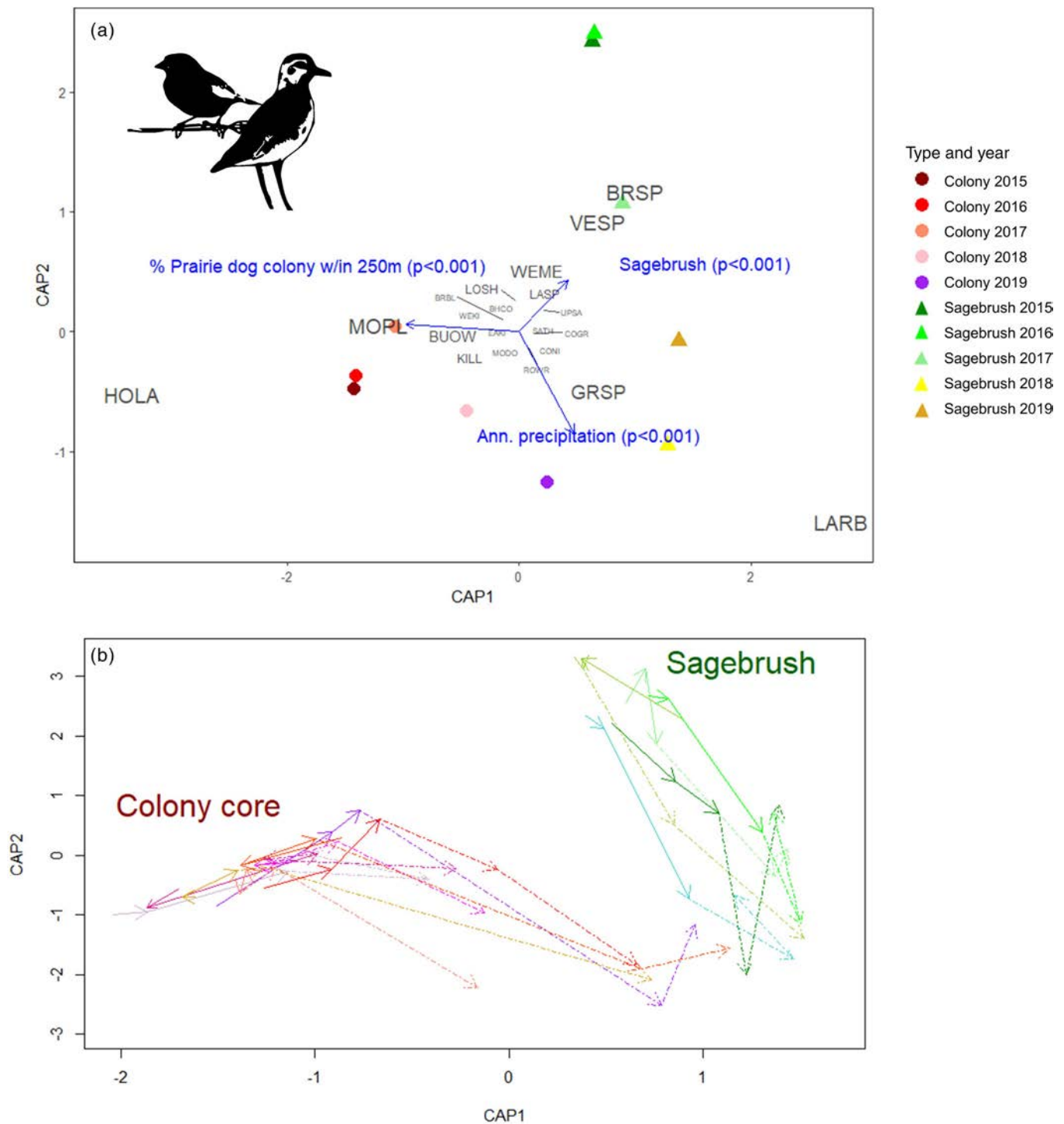


FIGURE 3 Results of distance-based redundancy analysis in the Thunder Basin Ecoregion, Wyoming, USA generated from all transects in 2015–2019. Points in panel (a) represent centroids for colony core and sagebrush transects in all years, whereas species acronyms represent density centers for each species. Vectors in panel (a) (blue) represent environmental covariates. Vectors in panel (b) indicate direction and degree of community change in individual colony core (red/purple) and sagebrush (blue/green) transects over time, with the origin of vectors in 2015 and the endpoint in 2019. BHCO, Brown-headed cowbird; BRBL, Brewer's blackbird; BRSP, Brewer's sparrow; BUOW, burrowing owl; COGR, common grackle; CONI, Common nighthawk; GRSP, grasshopper sparrows; HOLA, horned lark; LARB, lark bunting; LASP, lark sparrow; LOSH, loggerhead shrike; MODO, mourning dove; MOPL, mountain plover; ROWR, rock wren; SATH, sage thrasher; UPSA, upland sandpiper; VESP, vesper sparrow; WEME, western meadowlark.

cattle or elk occupancy, whereas a quadratic effect was included in the best model for mule deer, indicating a peak in occupancy at 20% colony cover and declining at

higher coverage (but note that both terms in the model were nonsignificant (colony, $p = 0.16$; colony², $p = 0.12$); Table 2).



FIGURE 4 Example of camera trap images captured in the Thunder Basin Ecoregion, Wyoming, USA, between 2017 and 2018. Images, from left to right on the top row: American badger, coyote carrying pronghorn head, pronghorn. Bottom row: bobcat, swift fox, and cattle and prairie dogs.

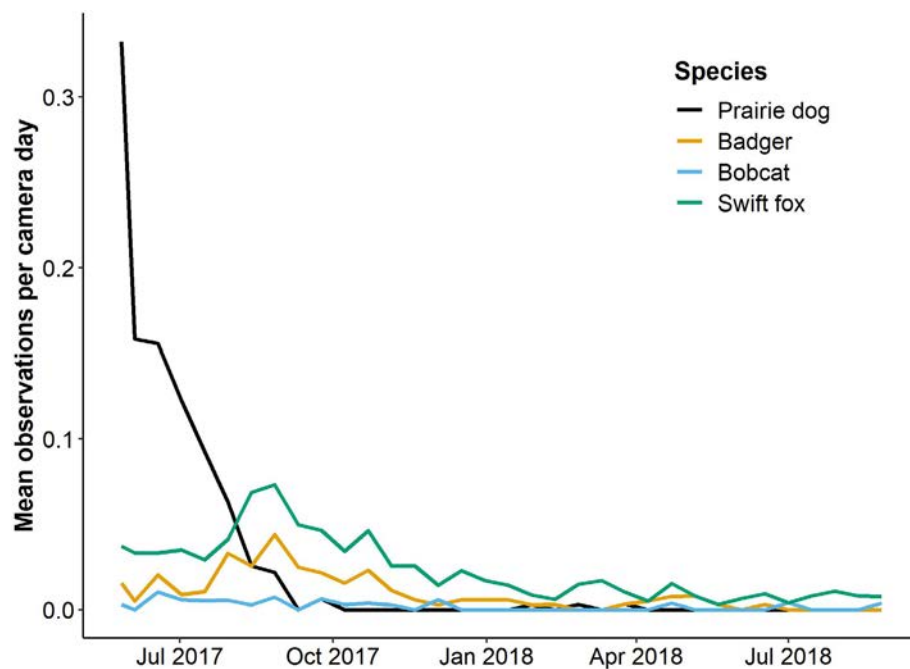


FIGURE 5 Mean daily observations of prairie dogs and associated mesocarnivores averaged over 2 week intervals, May 2017 through August 2018, Thunder Basin Ecoregion, Wyoming, USA.

When we examined regional-scale occupancy models of mammals pre- versus post-plague (i.e., 2017 vs. 2018), we found that low numbers of observations in 2018 led to some issues in prediction for mesocarnivore species. Bobcats were uncommon throughout the study area (12 detected in 2017, probability of occupancy 0.15, $SE = 0.07$), and none were detected in 2018, leading to model nonconvergence in that year. Badgers were

detected relatively frequently pre-plague (40 in 2017, probability of occupancy 0.5, $SE = 0.1$), but declined to only a single detection in 2018; this model converged, but generated estimates with confidence intervals overlapping both zero and one. For these two species, we only reported estimates generated from 2017 data (Figure 6a), but note that occupancy in 2018 was essentially zero. For species that we could model occupancy in

TABLE 2 Akaike's information criterion corrected for small sample size (AIC_c) rankings per species for modelling occupancy as a function the proportion of prairie dog colony within 2 km of a camera, Thunder Basin Ecoregion, Wyoming, USA, 2017–2018.

Model	AIC_c	ΔAIC_c
Mesocarnivores		
American badger		
Colony	217.5	0.0
Null	235.4	17.9
Colony ²	... ^a	... ^a
Bobcat		
Colony	82.5	0.0
Null	84.9	2.4
Colony ²	...	...
Coyote		
Colony	360.2	0.0
Colony ²	363.0	2.8
Null	370.1	9.9
Red fox		
Null	63.6	0.0
Colony	65.2	1.6
Colony ²	66.8	3.2
Swift fox		
Colony	342.2	0.0
Null	350.6	8.4
Colony ²	... ^a	... ^a
Ungulates		
Cattle		
Null	198.8	0.0
Colony	201.3	2.5
Colony ²	203.5	4.7
Elk		
Null	243.8	0.0
Colony	246.3	2.5
Colony ²	248.7	4.9
Mule deer		
Colony ²	208.9	0.0
Colony	211.1	2.2
Null	212.7	3.8
Pronghorn		
Colony	439.2	0.0
Null	440.8	1.6
Colony ²	441.8	2.6

Note: Quadratic model of colony cover is shown as "Colony²".

^aModel did not converge.

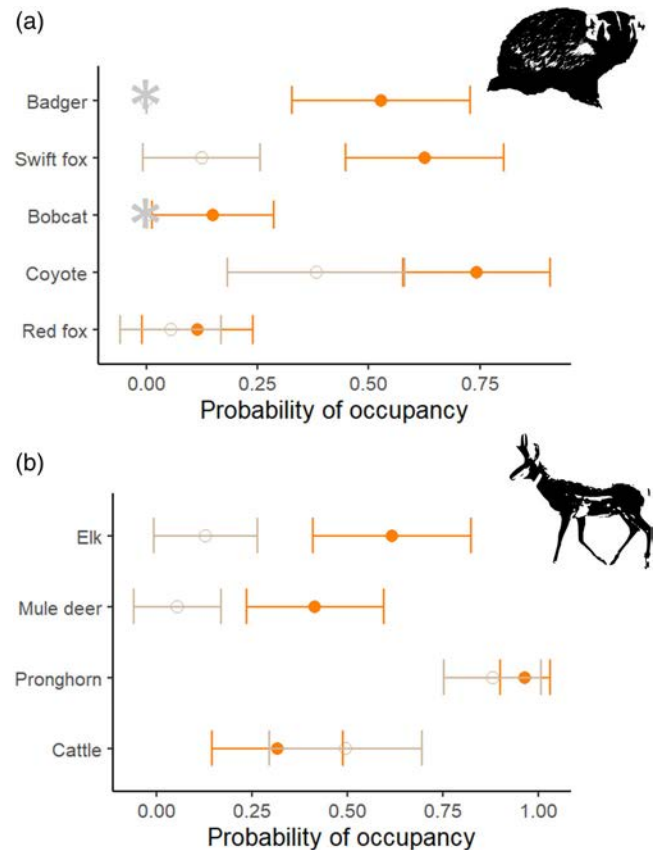


FIGURE 6 Mean probability of occupancy for five mesocarnivores (a) and four ungulates (b) before and after a sylvatic plague outbreak, mid-May to mid-August in 2017 (orange, filled) and 2018 (tan, unfilled), Thunder Basin Ecoregion, Wyoming, USA. Asterisks indicate model nonconvergence because of low badger ($n = 1$) and bobcat ($n = 0$) detections.

both years, swift foxes declined substantially after plague ($Occu_{2017} = 0.63$, $SE = 0.09$, $Occu_{2018} = 0.01$, $SE = 0.007$) and coyote numbers were marginally lower after plague ($Occu_{2017} = 0.74$, $SE = 0.08$, $Occu_{2018} = 0.38$, $SE = 0.1$). Occupancy rates of cattle and pronghorn did not change significantly among years, whereas occupancy rates of elk ($Occu_{2017} = 0.62$, $SE = 0.11$, $Occu_{2018} = 0.13$, $SE = 0.07$) and mule deer ($Occu_{2017} = 0.41$, $SE = 0.91$, $Occu_{2018} = 0.055$, $SE = 0.058$) declined following the plague event (Figure 6b).

DISCUSSION

Following the outbreak of sylvatic plague in late 2017, we observed rapid changes in the Thunder Basin Ecoregion that supported three hypotheses of our system-level conceptual model (Figure 1). Due to the concomitant loss

of prairie dogs and extremely high precipitation, mean height and total biomass of herbaceous vegetation was greater during the final 2 years of our study (H_1). We observed changes in passerine and shorebird community structure (H_2) and decreased occupancy in multiple predator species, with the magnitude of change linked to species-specific degree of dietary reliance on prairie dogs as a food resource (H_4). We found minimal support for H_3 , which posited that ungulates would respond negatively to plague because vegetation was no longer maintained at an earlier phenological stage providing higher forage quality (please refer to Connell et al., 2019).

Incorporating prairie dog disturbance and precipitation into ordinations of rangeland bird communities helped to disentangle the effects of these two drivers on bird community structure (Figure 3a). The loss of prairie dogs mainly affected shortgrass obligates, with marked declines of mountain plovers (16-fold reduction), horned larks, and burrowing owls. Breeding mountain plovers and horned larks are reliant on disturbed habitat with high levels of bare soil exposure, features in this landscape that are found almost exclusively on prairie dog colonies (Duchardt et al., 2018, 2020). Burrowing owl density was relatively low throughout the study area, but our data indicate that this species declined 2 years after the plague event, likely because of lagged burrow collapses, which occur 1–2 years after prairie dog removal (please refer to Alverson & Dinsmore, 2014 for more on burrowing owls and plague). In addition, increased precipitation led to a community shift toward greater numbers of lark buntings and grasshopper sparrows in 2018 and 2019. Interestingly, these wet years in the northern Great Plains corresponded with drought in the southern Great Plains, where these species also breed. This probably compounded the importance of our study area for ground-nesting birds associated with mid-height grasses, as our study area may have provided habitat for individuals unable to breed in the more southerly part of their range. Bolstering this hypothesis, we recorded the first occurrence of Cassin's sparrows (*Peucaea cassinii*) in Weston County, Wyoming in 2018, a species generally restricted to the southern Great Plains but known to be somewhat nomadic in habitat use.

Passerines and shorebirds responded to changes in habitat structure influenced by plague and precipitation, but predators were more directly influenced by loss of prairie dogs as a prey resource. The two raptor species most reliant on prairie dogs as a food resource, ferruginous hawk and golden eagle (Katzner et al., 2020; Ng et al., 2020), increased during the prairie dog “boom” but declined rapidly once this resource was removed. Although it can sometimes be difficult to disentangle landscape-level responses from regional ones, neither breeding bird survey

data at the scale of Wyoming between 2015 and 2019 (Pardieck et al., 2020) or visual assessment of eBird data (eBird, 2021; eBird.org) indicated higher than average abundances of either of these species at the regional scale in 2017 or a population decline in 2018, supporting the role of prairie dogs in the response we observed. Similarly, the lack of “boom-and-bust” response in raptors that rely less on prairie dogs (e.g., red-tailed hawk, a generalist predator) or do not use prairie dogs as a food resource (e.g., American kestrel, which consumes mainly invertebrates as well as reptiles, birds, and small mammals, and northern harrier, which relies on mammals or birds generally smaller than prairie dogs) indicates that the years following plague were not marked by the reduction of other prey resources.

We also documented substantial declines in occupancy rates of mammalian predators after the plague epizootic, and species were affected in direct proportion to their dietary reliance on prairie dogs. In addition to the black-footed ferret, American badgers have the greatest dietary reliance on prairie dogs (e.g., Kagel et al., 2020) and habitat specialization often manifests where the two species overlap (Grassel & Rachlow, 2018). On a landscape scale, badger occupancy in Thunder Basin was most strongly affected by proximity to prairie dog colonies prior to plague and declined to a near-zero level after plague. Across their range, swift fox reliance on prairie dog colonies for prey or denning habitat appears to vary considerably (e.g., Kintigh & Andersen, 2005; Nicholson et al., 2006; Shaughnessy & Cifelli, 2004), but we found that swift fox occurrence was both positively associated with proximity to colonies pre-plague and declined substantially following the plague epizootic. These results highlight the importance of prairie dogs for supporting the swift fox population in this landscape. Interestingly, we observed frequent diurnal behavior in both predator species, similar to Kagel et al. (2020), which highlights that studies using nocturnally-biased survey techniques may miss the importance of prairie dog resources, especially for swift foxes because this species is often surveyed using spotlighting. We found that coyote occurrence was influenced by prairie dog abundance, but to a lesser degree than badgers and swift fox, showing that both increased occurrence with increasing proximity to prairie dog colonies pre-plague, and a modest decline following the plague epizootic. Finally, bobcats used prairie dog colonies within this grassland at low rates when prairie dogs were abundant, and then occurrence rate declined to zero following the plague epizootic, adding to our knowledge of the relationship between these two species that has rarely been described in the literature (e.g., Licht, 2010). We hypothesize that these declines were due, at least in part, to emigration from the study

area due to decreased food availability, but we were not able to directly assess mortality or decreased fecundity related to these changes in food availability.

Mule deer and elk displayed landscape-scale declines following plague, consistent with findings in South Dakota (Whicker & Detling, 1988). These species may use prairie dog colonies because of maintenance of forage in a nutritious, early phenological state (Connell et al., 2019) and the relatively high abundance of forbs on prairie dog sites (Duchardt et al., 2021). However, modeling of responses of ungulates to colony cover in 2017 did not clearly support this hypothesis, as elk showed no response to colony cover and mule deer only had a high probability of occupancy of areas with up to 30% colony cover, after which probability of occupancy declined (Table 2; Appendix S1: Figure S3). Furthermore, detection probabilities of mule deer in this study were fairly low. Mule deer declines in 2018 may have instead been driven by macro-scale factors affecting the population of this migratory species, and we note that the estimated mule deer population throughout northeastern Wyoming was reported to be well above the 5-year average in 2017 and declined by ~12% in 2018 (WGFD, 2017; WGFD, 2018; reported for the Cheyenne River herd). We observed no landscape-scale difference in pronghorn occupancy between years, and only a weak positive relationship between colony cover at the 2-km scale and probability of pronghorn occupancy in 2017. Although other researchers have indicated that ungulate species utilize prairie dog colonies for grazing (e.g., Krueger, 1986; Whicker & Detling, 1988), it is still unclear the degree to which ungulates may utilize prairie dog colonies across their range, and how spatiotemporal dynamics of prairie dog disturbance may influence ungulate populations.

Our conceptual model focused on disease as a driver of wildlife community structure independent of climate, but climatic variability can also influence the probability of plague epizootics (Eads & Biggins, 2017). There have been three major plague outbreaks in Thunder Basin in the past 20 years, with each occurring in a relatively average precipitation year following a dry one (Davidson et al., 2022). While this pattern does not hold true in every landscape (Savage et al., 2011; Stapp et al., 2004), other studies have also linked plague epizootics with transitions from dry to wet years (Eads & Biggins, 2017). The hypothesis explaining this mechanism is that dry conditions may suppress fleas, the main pathogen host, and *Y. pestis* (Eads & Biggins, 2017), but wet years can lead to both increases in prairie dog abundance and concurrent increases in flea-loads and aboveground activity. We also note that while we did not directly measure prairie dog abundance/density in this study, concurrent work in this system reported many areas of very high prairie dog burrow density in 2017

(Duchardt et al., 2021). Future efforts in this system include increased focus on prairie dog density as a driver of community response and we encourage other researchers and managers to also incorporate this metric into their work, in addition to monitoring colony size.

Conservation implications

As with other burrowing rodents in rangeland ecosystems worldwide (Davidson et al., 2012), we found that prairie dogs play a critical role in structuring associated vegetation and wildlife communities in this system. Our research highlights drastic and rapid community shifts following the functional loss of prairie dogs in the landscape due to an epizootic outbreak of sylvatic plague. Boom-and-bust disease cycles such as the one we describe in our study are a major conservation challenge. Direct threats from disease and unreliable food resources make these systems untenable for black-footed ferret reintroductions (Matchett et al., 2010). Furthermore, unreliable prey resources destabilize predator communities (MacArthur, 1955; Petchey, 2000), and the lack of consistent habitat availability may negatively impact avian species with high site fidelity, such as mountain plovers and burrowing owls (Crowley et al., 2019; Gaul, 1973; Klute et al., 2003; Pierce et al., 2017; Skrade & Dinsmore, 2010). This may lead to increased time spent moving through the landscape or prospecting (Ponchon et al., 2013) and delayed breeding, or to the selection of suboptimal habitat and reduced reproductive output (Battin, 2004), all of which could be compounded with the fact that much of the remaining landscape is highly fragmented by agriculture, energy extraction, and other human land uses.

Given the strained relationship between agricultural production and burrowing rodent conservation objectives (e.g., Miller et al., 2007), it may be surprising that these cyclical die-offs are also challenging from a livestock management perspective. Uncertainty is directly at odds with agricultural production and huge efforts have been made to improve our ability to predict rangeland productivity to allow stocking rate adjustments in a timely fashion (e.g., Hartman et al., 2020; Raynor et al., 2020). Although reduced prairie dog numbers yield increased vegetation biomass, the unpredictability of these cycles make capitalizing on additional forage difficult for agricultural producers. Essentially, the undesirability and unpredictability of these cycles is potentially the one thing that most, if not all, stakeholders can agree on. Future work could simultaneously focus on predicting these cycles and identifying the management tools to mitigate them. Insecticides to control fleas (Eads et al., 2021; Eads & Biggins, 2019) have generally been successful in stabilizing

and maintaining colonies, but less consideration has been given to strategic spatial application of these tools to maximize long-term effectiveness, or how the influence of colony configuration on epizootic plague spread could inform active management of colony complex configuration (Collinge et al., 2005; Cully Jr. et al., 2010; Johnson et al., 2011).

Although extreme precipitation following the plague outbreak could be viewed as “noise” interfering with the interpretation of prairie dog effects in this landscape, these extremes are likely to increase in the future and continue to interact with prairie dog colony dynamics (Reeves et al., 2020), making them a necessary consideration in understanding these ecological processes. We acknowledge that our study was only able to measure responses to the interaction of plague and high precipitation; we are extremely curious about how responses may have differed had 2018 been a dry year, and we see this as an avenue for future research. Future work could also focus on incorporating these drivers into a multi-equilibrium model (also known as “ball-in-cup” or “basin of attraction” model; Briske et al., 2017) to help managers to better understand the levels of variability that are likely to push communities past thresholds into alternative stable states and focus management on avoidance of undesirable thresholds.

These climatic extremes also highlight the importance of this landscape for nomadic, mid-grass bird species, especially in years when drought affects other parts of their range. This gives rise to another challenge: how should managers address the trade-offs in rangeland management for nomadic versus philopatric breeders? Some grasslands may only provide habitat for certain species in 1 of 10 years (e.g., Green et al., 2019), yet that 1 year is exactly when the peripheral habitat is most essential. The answer is not straightforward, but we believe it is one that should be tackled not by individual rangeland managers but instead via collaborative adaptive management at a regional scale, with emphasis on the creation of a consistent, real-time communication network among spatially disparate managers, stakeholders, and researchers working in rangeland ecosystems.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Duchardt, 2022) are available on Dryad at <https://doi.org/10.5061/dryad.pzgmsbcpx>. These include all field-collected data except prairie dog colony locations and boundaries, as these data are curated by the United States Forest Service and Thunder Basin Grasslands Prairie Ecosystem Association. Data available on Dryad also do not include associated spatial data because these pertain to species of conservation concern. Full data (including spatial location) are available to qualified researchers from the Department of Natural Resource Ecology and Management at Oklahoma State University.

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SUPPORTING INFORMATION

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A NEW METHOD FOR SELECTION OF UMBRELLA SPECIES FOR CONSERVATION PLANNING

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Abstract. Umbrella species, species whose protection serves to protect many co-occurring species, have been proposed as a shortcut for conservation planning. Potential criteria for selection of umbrella species include rarity, sensitivity to human disturbance, and mean percentage of co-occurring species. Using butterflies in montane canyons in the Great Basin (USA) as a case study, we examined correlations among those three selection methods. We also developed a new index that specifically ranks species according to their potential to serve as umbrellas for their taxonomic group. Different methods for prioritizing species generally produced divergent rankings. Although rare butterflies tended to co-occur with more species than widespread butterflies, rare species may be poor umbrellas because their distributions are too highly restricted and often cannot be influenced by managers. Umbrella species are useful in meeting certain conservation challenges, particularly prioritization of habitat remnants for conservation or other land uses. Our work demonstrates that a subset of a fauna may serve as an effective umbrella for a larger ecological community, and therefore play an important role in contemporary management planning.

Key words: butterflies; conservation planning; disturbance sensitivity; ecosystem management; Great Basin (USA); indicator species; life-history characteristics of umbrella species; rarity; specialization vs. rarity; species ranking methods; umbrella species, identification.

INTRODUCTION

Rarely blessed with either time or funding to carry out the breadth of science to guide land management, conservation biologists and resource managers are forced to look for shortcuts to inform land-use decisions (Stohlgren et al. 1995, Oliver and Beattie 1996, Longino and Colwell 1997, Niemi et al. 1997, Simberloff 1998). “Umbrella” species, which we define as species whose conservation confers a protective umbrella to numerous co-occurring species, offer an appealing shortcut. The use of umbrella species is attractive because their employ promises to maximize information return from minimal financial commitments to research and monitoring. To date, however, empirical evidence that umbrella species are a valid conservation tool rather than simply an intriguing theoretical construct has been lacking. In this paper, we first evaluate existing criteria for identification of umbrella species. We then present a new method for selection of umbrella species that explicitly considers the management issues and resource constraints faced by practitioners. By using butterflies in montane canyons in the Great Basin (USA) as a case study for these analyses, we also contribute to an ongoing debate about the ability of a single species or a subset of a greater fauna to convey information necessary to manage a larger ecological community (Simberloff 1998).

Use of umbrella species is most appropriate in landscapes where managers must prioritize habitat remnants for conservation, or any given land use, on the basis of species richness. Ranking and protecting geographic areas according to either their total species richness or their richness of species of concern is the most direct approach to minimizing species losses across a landscape (Dufrêne and Legendre 1997, Freitag et al. 1997, Carroll and Pearson 1998, Heikkinen 1998, Tardif and DesGranges 1998, Troumbis and Dimitrakopoulos 1998). The disadvantage of this method is that it requires extensive biotic surveys, which in turn may require substantial investment of resources (Longino and Colwell 1997, Mac Nally 1997). Identification of umbrella species could reduce the sampling effort necessary to prioritize areas for protection or other land uses, because it usually is faster and cheaper to sample a subset of a taxonomic group than to survey all members of the group (Scott 1998). Umbrella species have limited application in landscapes where practitioners are interested in shortcuts to assess ecosystem integrity for purposes of land management. In these latter situations, “indicator” species whose viability is tied to the status of specific habitats or ecosystem processes are more appropriate shortcuts than umbrella species. Umbrella species may prove not to be the species most sensitive to habitat conditions (Thomas 1995, Fagan and Kareiva 1997).

Although we recognize that comprehensive survey data often are not available to conservation planners

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(Stohlgren et al. 1995), we took advantage of an extensive, previously compiled data set to test the merits of different methods for selecting umbrella species. Two of the most common criteria used to select umbrella species are rarity and sensitivity to human disturbance (e.g., Niemi et al. 1997, Rodríguez et al. 1998). Rare or sensitive species certainly are worthy of protection on their own merits. However, these selection or ranking methods may not be effective ways to choose umbrella species. For example, species that are rare or sensitive to disturbance may not co-occur with many other species (Thomas 1995, Fagan and Kareiva 1997, Freitag et al. 1997), even with other rare species (Swengel and Swengel 1997, Tardif and DesGranges 1998). Moreover, rarity may not reflect the influence of environmental factors that managers realistically can control. Some species are rare because their resources have been degraded by human activities, but others are rare simply because their resources inherently are patchily distributed (Cody 1986).

In response to these dilemmas, we developed a new index that measures the potential of each species in a regional biota to serve as an umbrella for other species in that community. This study is the first of which we are aware that attempts to select umbrellas within a taxonomic group. We propose that to serve as an effective umbrella species in a managed landscape, a species should be neither extremely rare (e.g., occupy <5% of the area to be managed) nor ubiquitous, and should be moderately sensitive to human disturbance (that is, generally unable to exploit landscapes heavily modified by humans; Blair 1996, Blair and Launer 1997). An intermediate degree of rarity is important because relatively rare species may not be distributed across enough of the landscape to ensure the viability of populations of many other species. Disturbance sensitivity should enable umbrella species to protect sympatric species that also are sensitive to similar disturbances. We suggest that an additional necessary criterion for selecting umbrella species is percentage of co-occurring species. In other words, where an umbrella species occurs, a relatively large percentage of its close taxonomic relatives also should be present. This is a pertinent consideration for two reasons. First, species rarely are protected throughout their entire range. Second, mean species co-occurrence is not always correlated with ubiquity. To illustrate, imagine that species A inhabits some fraction of a landscape and that the fraction is relatively species-rich. Hypothetical species B is more widespread than species A, but its range includes both relatively species-rich and relatively depauperate localities. Under these circumstances, protecting less than the whole of the range of species A may prove more effective than protecting a segment of the range of species B.

We used data on butterfly communities in two central Great Basin mountain ranges to evaluate previous methods for selecting umbrella species, develop our

new umbrella index, and test whether a subset of a fauna might serve as an umbrella for a greater fauna. Butterflies satisfy many of the pragmatic criteria for umbrella species, and frequently have been proposed to play that role (e.g., Pyle et al. 1981, Erhardt 1985, Ehrlich and Murphy 1987, Eyre and Rushton 1989, Morris et al. 1989, Viejo et al. 1989, Hafernik 1992, Pearson and Cassola 1992, Kremen et al. 1993, Prendergast et al. 1993, Kremen 1994, Nelson and Andersen 1994, Holl 1995, Thomas 1995, Blair and Launer 1997, Dufrêne and Legendre 1997). They are well understood biologically (Scott 1986, Shapiro 1996), easy to study (Ehrlich and Davidson 1960, Pollard 1977, New 1991, Kremen 1992, Pollard and Yates 1993, Harding et al. 1995), have relatively short generation times (thus may exhibit rapid responses to management), and the presence of some butterflies is thought to convey information on other taxa or ecosystem attributes of concern.

Regional communities of birds, vascular plants, or other focal taxa would be equally appropriate candidates for the analytical exercises presented here using butterflies as a model system. Because species richness of invertebrates, vertebrates, and plants is variably correlated at spatial and temporal scales that concern managers (Erhardt 1985, Thomas and Mallorie 1985, Dobkin and Wilcox 1986, Murphy and Wilcox 1986, Wilcox et al. 1986, Ehrlich and Murphy 1987, Hafernik 1992, Kremen 1992, Prendergast et al. 1993, Launer and Murphy 1994, Holl 1995, Thomas 1995, Shapiro 1996), single taxonomic groups may not always function as effective cross-taxonomic umbrellas. However, previous research has not tested whether certain species could serve as umbrellas for other members of their taxon. Although this is a fairly focused question, there are several reasons why it is relevant to ecosystem management. First, managers often have a mandate to minimize species losses among all organismal groups. Second, some taxa are relatively easy to study and monitor; butterflies are among the most amenable invertebrates. Third, a few groups of plants and animals (again including butterflies) are thought to be particularly sensitive to anthropogenic disturbances and able to provide early warning of ecological change (Noss 1990, Kremen et al. 1993, New et al. 1995, Hamer et al. 1997).

Study system

The Great Basin of western North America includes more than 400 000 km² of internal drainage extending from the Sierra Nevada on the west to the Rocky Mountains on the east. Mean annual precipitation is roughly 30–45 cm (Grayson 1993). The region is dominated by more than 200 parallel, north–south oriented mountain ranges that are separated by wide desert valleys (Grayson 1993). The elevation of the valley bottoms generally is between 1200 and 1800 m. In most mountain ranges, vegetation shifts with increasing elevation

from sagebrush (*Artemisia tridentata* ssp.), to piñon-juniper (*Pinus monophylla*, *Juniperus osteosperma*) woodland, to low brush (*Artemisia tridentata* vaseyana), and finally to limber pine (*Pinus flexilis*). A depauperate alpine flora caps the summits of taller ranges (Grayson 1993).

More than 75% of the Great Basin is federally owned and managed; state and local resource agencies also play roles in managing ecosystems in the Great Basin. The U.S. Forest Service manages many of the largest and most biologically diverse mountain ranges in the Great Basin. Strategic plans generally are developed for individual mountain ranges. Because most ranges have been incised deeply by canyons, and those canyons are comparatively accessible, land uses within mountain ranges commonly are delineated at the level of individual or several adjacent canyons. Permanent streams often flow in the canyon bottoms. Particularly in arid regions, riparian areas are notably species-rich and sensitive to human disturbance (Kauffman and Krueger 1984, U.S. GAO 1988, Armour et al. 1991, Thomas 1991, Dawson 1992, Chaney et al. 1993). Properly functioning riparian ecosystems also provide critical ecosystem services. For example, they filter sediment and nutrients, and sustain streamflow during the relatively dry summer months (Knight 1994). As a result, riparian corridors and riparian-obligate species are of special concern to resource agencies in the Great Basin. Therefore, we predominantly have focused on butterflies in riparian canyons. Our analyses were based on species presence-absence data collected during 1994–1998 from 19 canyons in the Toiyabe Range and 10 canyons in the adjacent Toquima Range (Lander and Nye counties, Nevada). More than 80% of these canyons have seeps, springs, or permanent streams.

METHODS

Detailed descriptions of study locations and field methods are in Fleishman et al. (1997, 1998, 1999). Briefly, we inventoried butterflies in each canyon roughly every 2 wk throughout the majority of the flight season (late May–early September). During each of these visits, we walked the length of the canyon at a constant pace and recorded the presence of all butterfly species seen. Sampling effort was roughly equal per unit area (Fleishman et al. 1998). Walking transects are a standard technique for surveying butterfly communities (Shapiro 1975, Pollard 1977, Thomas and Mallorie 1985, Swengel 1990, Kremen 1992, Pollard and Yates 1993, Harding et al. 1995). When necessary, individual butterflies were caught and either identified on site or held for later identification. Voucher specimens were deposited at the University of Nevada, Reno and at the Nevada State Museum and Historical Society, Las Vegas (Nevada, USA). Nomenclature largely follows that of Austin (1998). Migratory species were excluded from our analyses (Fleishman et al. 1997, 1999).

Because presence-absence data provide little information on viability, a species' value as a conservation tool might be increased if not only its presence but also its variation in abundance paralleled that of sympatric species (Simberloff 1998; B. Noon, *personal communication*). Nonetheless, two practical considerations led us to restrict our analyses to presence-absence data. First, butterfly abundance varies temporally both within and between years. Some butterfly species are present throughout the flight season, but others are present only relatively early or late in the season. Moreover, most species have staggered emergence patterns. In addition, butterfly abundance often fluctuates markedly within and between years in response to variation in temperature and precipitation (Shapiro 1975, Pollard 1977, Kremen 1992, Pollard and Yates 1993, DeVries et al. 1997, Crisp et al. 1998, Shaffer et al. 1998, Pollard et al. 1998). Second, inexperienced observers, such as agency biologists with broad training, may have insufficient knowledge or time to collect unbiased data on butterfly abundances (Droege et al. 1998, Link and Sauer 1998).

We ranked butterfly species according to three criteria: rarity, sensitivity to human disturbance, and mean percentage of co-occurring species. Rarity rankings were based on a method outlined by Baz (1991) and were calculated separately for the Toiyabe and Toquima ranges. Within each mountain range, we first calculated the proportional occurrence (P_j) of each butterfly species j across the n study canyons by summing the number of canyons in which the species was present and dividing by n . The rarity of each species, Q_j , was then calculated as $1 - P_j$. A Q_j of 0 indicates ubiquity; rarity increases as Q_j approaches 1.

We ranked species according to their sensitivity to human disturbance with an index modified from Nelson and Andersen (1994). Species vary in their life histories, and some life-history traits are thought to increase a species' vulnerability to human activities. We based our disturbance-sensitivity index (DSI) on three life-history parameters—mobility, larval host-plant specificity, and riparian dependence—that may contribute to the likelihood that a butterfly species will decline as a result of human activities. Mobility was estimated from a variety of sources, including field observations on the distance from their larval host plants at which individual butterflies were seen, mark-recapture studies, notes and observations of experienced lepidopterists, field guides, and natural histories (e.g., Scott 1975, Shapiro et al. 1979, Scott 1986). Because the resident butterfly fauna of the Toquima Range is a subset of the resident butterfly fauna of the Toiyabe Range (Fleishman et al. 1997, 1999), DSI was not calculated separately for the two ranges. Using data presented in Fleishman et al. (1997), we assigned every butterfly species an integer value from 1 (low sensitivity) to 4 (high sensitivity) for each of the three parameters (Table 1), summed the three values, then divided the sum

TABLE 1. Definitions of the three life-history traits (parameters) included in the disturbance-sensitivity index (DSI). The adults of some species of butterflies feed from mud puddles (see Boggs and Jackson [1991] for an overview), which are more common in riparian canyons than in dry canyons or uplands.

Trait	Score†	Definition
Mobility	1	>10 km
	2	1000's of m
	3	100's of m
	4	10's of m
Potential larval host-plant specificity	1	more than one family
	2	several genera in one family
	3	several species in one genus
	4	one species
Riparian dependence	1	no use
	2	facultative, individuals occasionally recorded at mud puddles
	3	facultative, individuals frequently recorded at mud puddles
	4	obligate

† 1 = low sensitivity, 4 = high sensitivity.

by the maximum calculated for any butterfly species. DSI thus was quantified on a relative scale from 0 (low sensitivity) to 1 (high sensitivity). Our DSI readily could be modified and adapted for other taxonomic groups with different life histories and sensitivities on other landscapes.

We also ranked butterflies according to their mean percentage of co-occurring species (PCS). Ranks for the Toiyabe and Toquima ranges were calculated separately. To calculate PCS, we averaged the number ($n - 1$) of butterfly species in each canyon from which the target species was recorded, then divided the average by the maximum possible number of co-occurring butterfly species in the mountain range ($n_{\text{butterfly species in the range}} - 1$). PCS therefore was quantified on a scale from 0 (tends to occur with few other species) to 1 (tends to occur with many other species).

We used Spearman rank correlation to test whether individual butterfly species received similar Q_j and PCS rankings in both the Toiyabe and Toquima ranges. We also tested whether pairwise correlations between species rankings based upon Q_j , DSI, and PCS were statistically significant.

We developed a new index to rank the potential of a species to serve as an umbrella (a species whose protection will confer substantial protection to co-occurring species) for other species in the community. For each species, the umbrella index (UI) is calculated as the sum of its medium-rarity ($1 - |0.5 - Q_j|$), disturbance sensitivity (DSI), and mean percentage of co-occurring species (PCS). We defined potential umbrella species as those with a UI greater than the mean plus 1 SD for that mountain range. We used Spearman rank correlation and the Jaccard index (Magurran 1988) to measure the influence of each component of UI on rankings and identities of potential umbrella species. The Jaccard index was calculated as $C_j = j/(a + b - j)$, where j = the number of species common to both lists, a = the number of species on the three-variable list of umbrella species, and b = the number of species on the two-variable list of umbrella species. $C_j = 0$

when no species are shared and $C_j = 1$ when species composition is identical. As a preliminary test of the efficacy of this new umbrella index, we calculated how many sympatric species would be protected if all or a random half of the range of the umbrella species was protected in the Toiyabe Range.

RESULTS

The riparian association (obligate or non-obligate), rarity (Q_j), disturbance sensitivity (DSI), and mean percentage of co-occurring species (PCS) of each resident butterfly species recorded from the Toiyabe ($N = 69$ species) and Toquima ($N = 56$ species) ranges is presented in Table 2. We defined species as riparian obligates if their larval host plants in the Toiyabe and Toquima ranges grow largely or exclusively in mesic habitats. Q_j ranged from 0.00 to 0.95 for butterfly species in the Toiyabe Range and from 0.00 to 0.90 for butterfly species in the Toquima Range. Rarity rankings for individual species were highly correlated between the Toiyabe and Toquima ranges ($df = 1, 55$; $r_s = 0.603$; $P < 0.0001$). Minimum and maximum DSI scores were 0.53 and 1.00, respectively. PCS varied relatively little as compared to the other variables included in the umbrella index. PCS fell between 0.56 and 0.86 for butterfly species recorded from the Toiyabe Range and between 0.64 and 0.93 for species in the Toquima Range. PCS rankings for individual species were not significantly correlated between the Toiyabe and Toquima ranges ($df = 1, 55$; $r_s = 0.228$; $P = 0.090$).

A matrix that compares butterfly species rankings according to Q_j , DSI, and PCS is presented in Table 3; results are shown separately for the Toiyabe and Toquima ranges. Correlations between Q_j and DSI rankings were not statistically significant. In other words, relatively rare species were no more or less sensitive to human disturbance than relatively widespread species. In both mountain ranges there was a significant positive correlation between Q_j and PCS rankings: relatively rare butterflies co-occurred with a greater number of species than did relatively widespread butterflies.

This reflects the fact that butterflies in Great Basin mountain ranges often have nested distributions (Fleishman 1997); i.e., butterfly species present in relatively depauperate locations are statistically proper subsets of the butterfly species present in richer locations (for reviews of nestedness across taxa, see Patterson and Atmar [1986], Patterson [1987], Wright and Reeves [1992]). Correlations between DSI and PCS rankings were not statistically significant in either mountain range. Thus, species that are highly sensitive to disturbance were no more or less likely to co-occur with a large number of species than were species that are less sensitive to disturbance.

Using our umbrella index (UI), we evaluated the potential of each butterfly species to serve as an umbrella for other butterfly species. These rankings, calculated separately for the Toiyabe and Toquima ranges, are presented in Table 4. Two species, *Hesperia uncas* and *Satyrrium sylvinum*, appeared to be potential umbrellas ($UI > \text{mean} + 1 \text{ SD}$) in both mountain ranges. Fourteen additional species in the Toiyabe Range (*Erynnis icelus*, *Harknclenus titus*, *Icaricia shasta*, *Loranthomitora spinetorum*, *Lycaena arota*, *L. helloides*, *L. nivalis*, *L. rubidus*, *Mitoura siva*, *Papilio bairdii*, *P. indra*, *Speyeria egleis*, *S. nokomis*, and *Thessalia leanira*) and five other species in the Toquima Range (*Euphilotes enoptes*, *Glaucoopsyche lygdamus*, *Nymphalis antiopa*, *N. milberti*, and *Phyciodes pulchella*) were identified as potential umbrella species. Rankings for individual species based upon UI were significantly correlated between mountain ranges ($r_s = 0.481$, $P < 0.005$).

The quantitative importance of each component of the umbrella index in terms of its influence on species selection varied. In no case would eliminating any one of the three components from the index result in a significant change in the UI rankings of butterfly species in either mountain range ($P < 0.0001$ for all pairwise comparisons). However, the identities of the potential umbrella species would change to some extent. Omitting medium-rarity from the UI would remove eight species from and add five species to the list of Toiyabe Range umbrellas; two species would be removed from the list of Toquima Range umbrellas, and six species would be added (C_j [Jaccard index] = 0.38 for both mountain ranges). If DSI was eliminated from the UI, seven species would be removed from and four species added to the list of Toiyabe Range umbrellas ($C_j = 0.47$), while four species would be removed from and three species added to the Toquima Range list ($C_j = 0.30$). Omitting PCS from the UI would have less of an effect than removing either medium-rarity or DSI: only three species would be removed from and one added to the Toiyabe Range list ($C_j = 0.76$); although four species would be added to the list of Toquima Range umbrellas, none would be removed ($C_j = 0.64$).

Preliminary tests of the effectiveness of our umbrella index were promising. Individual inter-range umbrella

species were present in 7–14 of the canyons we inventoried in the Toiyabe Range (50–74%) and in 4–5 of the canyons we inventoried in the Toquima Range (40–50%). At least one of the two umbrella species was present in 14 (79%) of the Toiyabe Range canyons and 6 (60%) of the Toquima Range canyons. In the Toiyabe Range, protecting all canyons in which one or both umbrella species was present would protect at least a portion of the distribution of no fewer than 66 of the other butterfly species recorded from the mountain range (97%). In the Toquima Range, protecting all canyons in which one or both umbrella species was present would protect at least a portion of the distribution of all other butterfly species recorded from the mountain range. As noted, species rarely are protected throughout their entire distributional range. Accordingly, we tested how many sympatric species would be protected if roughly half of the range of each umbrella species, selected at random, was protected in the Toiyabe Range. Protecting roughly half of the canyons occupied by *Hesperia uncas* and *Satyrrium sylvinum* would protect some portion of the range of, respectively, 90% and 96% of the other butterfly species present in the Toiyabe Range. Protecting a random half of the canyons occupied by *H. uncas* in the Toiyabe Range would require an area of ~190 ha; about 540 ha would be needed to protect a random half of the canyons occupied by *S. sylvinum*. These estimated areas correspond to roughly 14% (*H. uncas*) and 39% (*S. sylvinum*) of the total area of the canyons that we inventoried.

DISCUSSION

Our results demonstrate that different methods for prioritizing species for management planning purposes can produce divergent rankings. The only significant correlation among the three pairs of rankings we tested was between rarity and mean percentage of co-occurring species; this follows from the fact that butterflies in the Toiyabe and Toquima ranges have nested distributions (Fleishman 1997). Surprisingly, we did not find evidence of a link between disturbance sensitivity (loosely analogous to ecological specialization) and rarity. Although conventional wisdom—backed by some empirical data (e.g., Thomas and Mallorie 1985, Quinn et al. 1997)—maintains that geographically restricted species have more specific habitat needs than more widespread species (Brown 1984, Hodgson 1993), this was not the case in our study system. This outcome may suggest that human impacts in the Toiyabe and Toquima ranges are not severe enough to affect the viability of at least some vulnerable butterfly species. However, it is equally possible that butterfly species with extreme sensitivity to anthropogenic habitat modification had been extirpated prior to our field inventories. Given that conservation of sympatric species arguably is the primary consideration in selecting umbrella species, the relatively minor influence of PCS

TABLE 2. Riparian association (obligate or non-obligate), rarity (Q_j), disturbance sensitivity (DSI), and mean percentage of co-occurring species (PCS) of each butterfly species recorded from the Toiyabe and Toquima ranges (Nevada, USA).

Species	Riparian obligate?	Q _j		DSI	PCS†	
		Toiyabe	Toquima		Toiyabe	Toquima
Family HesperIIDae						
<i>Erynnis icelus</i>	x	0.79	...	0.87	0.85	...
<i>Erynnis persius</i>		0.21	0.30	0.60	0.74	0.67
<i>Pholisora catullus</i>		0.74	...	0.73	0.84	...
<i>Hesperia uncas</i>		0.63	0.60	0.80	0.69	0.81
<i>Hesperia juba</i>		0.00	0.00	0.67	0.69	0.64
<i>Hesperia comma</i>		0.00	0.00	0.73	0.69	0.64
<i>Ochlodes sylvanoides</i>		0.00	0.20	0.73	0.69	0.69
Family Papilionidae						
<i>Papilio bairdii</i>		0.47	...	0.73	0.79	...
<i>Papilio zelicaon</i>		0.11	0.80	0.60	0.70	0.88
<i>Papilio indra</i>		0.58	...	0.73	0.76	...
<i>Papilio rutulus</i>	x	0.05	0.20	0.80	0.70	0.68
<i>Papilio multicaudatus</i>	x	0.11	0.60	0.73	0.71	0.75
Family Pieridae						
<i>Neophasia menapia</i>		0.26	0.20	0.80	0.76	0.64
<i>Pontia beckerii</i>		0.05	0.00	0.60	0.72	0.64
<i>Pontia sisymbrii</i>		0.16	0.60	0.67	0.73	0.81
<i>Euchloe ausonides</i>		0.11	0.50	0.53	0.72	0.74
<i>Euchloe hyantis</i>		0.63	0.70	0.53	0.78	0.74
<i>Anthocharis sara</i>		0.32	0.40	0.67	0.75	0.74
<i>Colias philodice</i>	x	0.16	0.70	0.73	0.72	0.83
<i>Colias alexandra</i>		0.00	0.00	0.67	0.69	0.64
Family Lycaenidae						
<i>Lycaena arota</i>		0.53	0.60	0.67	0.78	0.70
<i>Lycaena rubidus</i>	x	0.32	0.70	0.87	0.73	0.72
<i>Lycaena heteronea</i>		0.16	0.30	0.73	0.72	0.72
<i>Lycaena helloides</i>	x	0.32	0.70	0.87	0.75	0.68
<i>Lycaena nivalis</i>	x	0.84	...	0.87	0.86	...
<i>Harkenclenus titus</i>	x	0.74	0.90	0.80	0.83	0.93
<i>Satyrrium behrii</i>		0.16	0.00	0.60	0.73	0.64
<i>Satyrrium californicum</i>		0.21	0.40	0.53	0.74	0.74
<i>Satyrrium sylvinum</i>	x	0.26	0.40	1.00	0.73	0.69
<i>Callophrys affinis</i>		0.37	0.20	0.67	0.73	0.69
<i>Callophrys comstocki</i>		0.84	...	0.67	0.77	...
<i>Loranthomitoura spinetorum</i>		0.58	0.70	0.67	0.78	0.69
<i>Mitoura siva</i>		0.21	0.20	0.93	0.73	0.64
<i>Incisalia augustinus</i>		0.89	...	0.67	0.82	...
<i>Incisalia fotis</i>		0.84	...	0.67	0.78	...
<i>Incisalia eryphon</i>		0.11	0.00	0.87	0.71	0.64
<i>Everes amyntula</i>		0.16	0.30	0.73	0.72	0.69
<i>Celastrina ladon</i>		0.16	0.40	0.60	0.73	0.75
<i>Euphilotes battoides</i>		0.89	...	0.80	0.75	...
<i>Euphilotes enoptes</i>		0.00	0.40	0.80	0.69	0.73
<i>Glaucopsyche piasus</i>		0.05	0.20	0.73	0.70	0.69
<i>Glaucopsyche lygdamus</i>		0.26	0.50	0.73	0.75	0.76
<i>Lycaeides melissa</i>		0.00	0.00	0.67	0.69	0.64
<i>Plebejus saepiolus</i>	x	0.11	0.30	0.87	0.72	0.71
<i>Icaricia icarioides</i>		0.00	0.00	0.80	0.69	0.64
<i>Icaricia shasta</i>		0.53	0.30	0.73	0.78	0.72
<i>Icaricia acmon</i>		0.37	0.80	0.67	0.77	0.75
<i>Icaricia lupini</i>		0.05	0.00	0.80	0.72	0.64
<i>Apodemia mormo</i>		0.32	0.20	0.67	0.76	0.66
Family Nymphalidae						
<i>Speyeria nokomis</i>	x	0.63	...	0.87	0.79	...
<i>Speyeria coronis</i>		0.37	0.70	0.67	0.69	0.74
<i>Speyeria zerene</i>		0.00	0.30	0.67	0.69	0.72
<i>Speyeria callippe</i>		0.05	0.30	0.67	0.72	0.67
<i>Speyeria egleis</i>		0.37	...	0.73	0.75	...
<i>Thessalia leanira</i>		0.53	...	0.67	0.76	...
<i>Chlosyne acastus</i>		0.05	0.20	0.67	0.70	0.69
<i>Phyciodes pulchella</i>	x	0.16	0.50	0.80	0.70	0.79
<i>Phyciodes mylitta</i>		0.16	0.50	0.67	0.71	0.71
<i>Euphydryas anicia</i>		0.11	0.00	0.60	0.72	0.64
<i>Euphydryas editha</i>		0.42	0.10	0.67	0.74	0.65

TABLE 2. Continued.

Species	Riparian obligate?	Q_j		DSI	PCS†	
		Toiyabe	Toquima		Toiyabe	Toquima
<i>Polygonia satyrus</i>	x	0.84	...	0.80	0.85	...
<i>Polygonia zephyrus</i>		0.32	0.40	0.60	0.77	0.74
<i>Nymphalis antiopa</i>	x	0.05	0.40	0.87	0.72	0.74
<i>Nymphalis milberti</i>	x	0.16	0.60	0.80	0.73	0.75
<i>Limenitis weidemeyerii</i>		0.11	0.00	0.67	0.73	0.64
<i>Coenonympha tullia</i>		0.05	0.00	0.67	0.69	0.64
<i>Cercyonis sthenele</i>		0.00	0.00	0.67	0.69	0.64
<i>Cercyonis oetus</i>		0.00	0.10	0.67	0.69	0.65
<i>Neominois ridingsii</i>		0.95	0.40	0.73	0.56	0.72

† See *Methods* for how PCS is calculated.

(percentage of co-occurring species) on the composition of lists of potential umbrella species also was somewhat unexpected. The latter result again emphasizes that different ranking methods often may target different species as focal for conservation planning.

Our results further suggest that several common methods of ranking species for protection are not optimal for identifying potential umbrella species. A species that occupies roughly 5% of a given landscape, regardless of the richness of those areas, will not be an effective umbrella for planning purposes at the scale of that landscape. Moreover, geographic restriction often cannot be attributed to human impacts. For example, the larval host plant (*Ceanothus* sp.) of one of the rarest butterfly species in the Toiyabe Range, *Incisalia augustinus*, occurs in only a few isolated locations across the central Great Basin. Although patches with *Ceanothus* might be included in a matrix of protected areas, managers realistically can take little action to increase the distribution of *I. augustinus*.

An important message that follows from our analyses is that potential umbrella species do not fit a single biological profile. For example, the larval host plants of the two potential inter-range umbrella species include both grasses (used by *Hesperia uncas*) and deciduous trees (*Satyrrium sylvinum*). Baseline abundances of the two species also differ—local populations of *H. uncas* tend to be smaller than those of *S. sylvinum* (Fleishman et al. 1997). Thus, at least among butter-

flies, there is no apparent way of selecting umbrella species solely on the basis of life-history data. Interestingly, our potential umbrella species tended to be relatively sedentary; both typically exhibit vagilities on the order of 10's of meters (Fleishman et al. 1997). This is fortuitous for management, because the presence of the umbrella species in a habitat patch likely will signify that they are resident and breeding in the patch rather than just visiting the patch for nectar or to locate mates.

Of course, umbrella species will not be useful in addressing all conservation challenges. To illustrate this point, we present three situations that frequently confront practitioners. The first conservation scenario is delineation of reserve boundaries within a larger managed landscape—for example, determining where to locate a wilderness or natural area in an ecosystem managed under a multiple-use mandate. Umbrella species will be of moderate relevance in this situation. When a single reserve is being delineated, it often may be appropriate to maximize either the number of rare species that will be protected within the reserve or the number of species whose viabilities might suffer from human activities outside the reserve. But, as we have shown, taxa with the greatest number of sympatric species may be neither rare nor highly sensitive to disturbance. The demand for shortcuts for assessing species richness during the reserve-delineation process varies. Inventory efficiency inevitably is a consideration in conservation activities. However, especially in temperate regions, reserve delineation arguably is less subject to sampling constraints than other conservation processes. Particularly when federal and state agencies are responsible for biological surveys, it is more likely that comprehensive inventories will be initiated when a reserve is being delineated than after the boundaries of the reserve have been drawn.

A second and distinct conservation challenge arises when managers are faced with an array of habitat remnants that they must survey and subsequently prioritize for land uses including protection. Rapid assessment techniques, including umbrella species, are most relevant in this context. Nonetheless, conservation biol-

TABLE 3. Spearman rank correlations of butterfly species rankings according to rarity (Q_j), disturbance sensitivity (DSI), and mean percentage of co-occurring species (PCS).

Statistic	Toiyabe Range ($N = 69$ species)		Toquima Range ($N = 56$ species)	
	Q_j	DSI	Q_j	DSI
DSI				
df	1, 68	...	1, 55	...
r_s	0.126	...	0.072	...
P	0.303	...	0.559	...
PCS				
df	1, 68	1, 68	1, 55	1, 55
r_s	0.778	0.060	0.868	0.012
P	<0.0001	0.627	<0.0001	0.932

TABLE 4. Butterfly species ranked in descending order of their potential to serve as umbrella species for the Toiyabe and Toquima ranges (Nevada, USA). In each mountain range, species with an umbrella index (UI) greater than the mean plus 1 SD were identified as potential umbrella species.

Toiyabe Range			Toquima Range		
Species	Riparian obligate?	UI	Species	Riparian obligate?	UI
<i>Speyeria nokomis</i>	x	2.52	<i>Phyciodes pulchella</i>	x	2.59
<i>Papilio bairdii</i>		2.50	<i>Satyrrium sylvinum</i>	x	2.59
<i>Satyrrium sylvinum</i>	x	2.49	<i>Nymphalis antiopa</i>	x	2.51
<i>Icaricia shasta</i>		2.49	<i>Hesperia uncas</i>		2.51
<i>Lycaena helloides</i>	x	2.43	<i>Glaucopsyche lygdamus</i>		2.50
<i>Lycaena arota</i>		2.42	<i>Nymphalis milberti</i>	x	2.45
<i>Erynnis icelus</i>	x	2.42	<i>Euphilotes enoptes</i>		2.43
<i>Papilio indra</i>		2.41	<i>Lycaena rubidus</i>	x	2.39
<i>Lycaena rubidus</i>	x	2.41	<i>Papilio multicaudatus</i>	x	2.38
<i>Thessalia leanira</i>		2.40	<i>Plebejus saepiolus</i>	x	2.38
<i>Harknclenus titus</i>	x	2.39	<i>Phyciodes mylitta</i>		2.38
<i>Lycaena nivalis</i>	x	2.38	<i>Pontia sisymbrii</i>		2.37
<i>Mitoura siva</i>		2.38	<i>Colias philodice</i>	x	2.36
<i>Loranthomitoura spinetorum</i>		2.37	<i>Lycaena helloides</i>	x	2.35
<i>Hesperia uncas</i>		2.36	<i>Neominois ridingsii</i>		2.35
<i>Speyeria egleis</i>		2.35	<i>Harknclenus titus</i>	x	2.33
<i>Pholisora catullus</i>		2.34	<i>Anthocharis sara</i>		2.31
<i>Euphydryas editha</i>		2.33	<i>Euchloe ausonides</i>		2.28
<i>Neophasia menapia</i>		2.32	<i>Mitoura siva</i>		2.27
<i>Polygonia satyrus</i>	x	2.31	<i>Lycaena arota</i>		2.27
<i>Icaricia acmon</i>		2.31	<i>Lycaena heteronea</i>		2.25
<i>Callophrys affinis</i>		2.26	<i>Icaricia shasta</i>		2.25
<i>Glaucopsyche lygdamus</i>		2.25	<i>Celastrina ladon</i>		2.25
<i>Apodemia mormo</i>		2.24	<i>Polygonia zephyrus</i>		2.24
<i>Anthocharis sara</i>		2.24	<i>Everes amyntula</i>		2.23
<i>Speyeria coronis</i>		2.23	<i>Speyeria coronis</i>		2.21
<i>Plebejus saepiolus</i>	x	2.19	<i>Speyeria zerene</i>		2.18
<i>Nymphalis milberti</i>	x	2.19	<i>Papilio rutulus</i>		2.18
<i>Polygonia zephyrus</i>		2.18	<i>Satyrrium californicum</i>		2.18
<i>Incisalia eryphon</i>		2.18	<i>Papilio zelicaon</i>		2.18
<i>Euchloe hyantis</i>		2.18	<i>Loranthomitoura spinetorum</i>		2.16
<i>Phyciodes pulchella</i>	x	2.16	<i>Neophasia menapia</i>		2.14
<i>Euphilotes battoides</i>		2.16	<i>Speyeria callippe</i>		2.14
<i>Nymphalis antiopa</i>	x	2.13	<i>Ochlodes sylvanoides</i>		2.13
<i>Everes amyntula</i>		2.11	<i>Glaucopsyche piasus</i>		2.13
<i>Incisalia fotis</i>		2.11	<i>Icaricia acmon</i>		2.11
<i>Colias philodice</i>	x	2.11	<i>Euchloe hyantis</i>		2.07
<i>Lycaena heteronea</i>		2.11	<i>Erynnis persius</i>		2.07
<i>Callophrys comstocki</i>		2.10	<i>Callophrys affinis</i>		2.06
<i>Incisalia augustinus</i>		2.10	<i>Chlosyne acastus</i>		2.06
<i>Icaricia lupini</i>		2.07	<i>Apodemia mormo</i>		2.03
<i>Erynnis persius</i>		2.05	<i>Incisalia eryphon</i>		2.00
<i>Pontia sisymbrii</i>		2.05	<i>Icaricia icarioides</i>		1.94
<i>Papilio rutulus</i>	x	2.05	<i>Icaricia lupini</i>		1.94
<i>Papilio multicaudatus</i>	x	2.04	<i>Euphydryas editha</i>		1.92
<i>Phyciodes mylitta</i>		2.03	<i>Cercyonis oetus</i>		1.92
<i>Limenitis weidemeyerii</i>		2.00	<i>Hesperia comma</i>		1.87
<i>Euphilotes enoptes</i>		1.99	<i>Hesperia juba</i>		1.80
<i>Icaricia icarioides</i>		1.99	<i>Colias alexandra</i>		1.80
<i>Satyrrium behrii</i>		1.99	<i>Lycaeides melissa</i>		1.80
<i>Celastrina ladon</i>		1.99	<i>Limenitis weidemeyerii</i>		1.80
<i>Glaucopsyche piasus</i>		1.98	<i>Coenonympha tullia</i>		1.80
<i>Satyrrium californicum</i>		1.98	<i>Cercyonis sthenele</i>		1.80
<i>Speyeria callippe</i>		1.93	<i>Pontia beckerii</i>		1.74
<i>Hesperia comma</i>		1.93	<i>Satyrrium behrii</i>		1.74
<i>Ochlodes sylvanoides</i>		1.93	<i>Euphydryas anicia</i>		1.74
<i>Euphydryas anicia</i>		1.92			
<i>Chlosyne acastus</i>		1.92			
<i>Coenonympha tullia</i>		1.91			
<i>Papilio zelicaon</i>		1.91			
<i>Pontia beckerii</i>		1.87			
<i>Hesperia juba</i>		1.86			
<i>Colias alexandra</i>		1.86			
<i>Lycaeides melissa</i>		1.86			
<i>Speyeria zerene</i>		1.86			
<i>Cercyonis sthenele</i>		1.86			
<i>Cercyonis oetus</i>		1.86			
<i>Euchloe ausonides</i>		1.86			
<i>Neominois ridingsii</i>		1.85			

Note: For Toiyabe Range, mean = 2.14, 1 SD = 0.30, mean + 1 SD = 2.34; for Toquima Range, mean = 2.16, 1 SD = 0.24, mean + 1 SD = 2.40.

ogists and managers need to evaluate honestly whether focusing surveys on a minimal subset of a fauna truly will prove cheaper and more straightforward logistically than surveying a substantially larger, more taxonomically diverse representation of an entire fauna. The answer to this question inevitably will vary with geographic context.

Management of reserves, unique habitats, or vital ecosystem processes presents a third type of conservation challenge. In these situations, practitioners must assess whether their actions successfully minimize losses of native species and maximize habitat integrity (Slocombe 1998). Understandably, there is enthusiastic support for developing scientifically defensible short-cuts, including surrogate measurements of biological diversity or ecosystem integrity, that can be used in these contexts. Time and money may limit the ability of managers to conduct biotic surveys in areas that already have been excluded from most extractive human uses. Managers instead may need to devote their resources toward ensuring that ongoing human activities do not have adverse effects on ecosystem structure, composition, and function in areas outside reserves. Moreover, streamlined inventories may enable managers to respond promptly to biological data, adapting their treatment of the landscape sufficiently quickly to alleviate some threats to species or ecosystem viability. Umbrella species may not be the best shortcut for assessing the status of unique habitats or ecosystem processes, however. Instead, we recommend that conservation biologists and managers target "indicator" species whose viability is better tied to the integrity of those habitats or processes. Thoughtful consideration of the biology and life history of potential indicators may be more useful than distributional studies in the identification of such species.

Our research implies that limited suites of species may serve as effective umbrellas for regional faunal assemblages when practitioners must prioritize areas for conservation in a managed landscape. Because environmental stochasticity affects the geographic distribution and abundance of many organisms, with asynchronous effects on different taxa, we recommend that a suite of umbrella species rather than a single species be employed in conservation management. Our study also emphasizes that the contention that any species or group of species can serve as a reliable surrogate measure of diversity, management efficacy, or ecosystem integrity must be treated as a hypothesis to be rigorously tested: it cannot be assumed that proposed umbrella or indicator species do indeed signal what they are supposed to (Landres et al. 1988, Swengel and Swengel 1997, Brussard et al. 1998, Carroll and Pearson 1998). There are few ready short cuts, and no single panacea, for management planning at the landscape scale. Careful analysis, however, can identify scientifically reliable umbrella species and species groups with

considerable potential as tools for large-scale conservation planning.

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Review

Second chance for the plains bison

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ABSTRACT

Before European settlement the plains bison (*Bison bison bison*) numbered in the tens of millions across most of the temperate region of North America. Within the span of a few decades during the mid- to late-1800s its numbers were reduced by hunting and other factors to a few hundred. The plight of the plains bison led to one of the first major movements in North America to save an endangered species. A few individuals and the American Bison Society rescued the remaining animals. Attempts to hybridize cattle and bison when bison numbers were low resulted in extensive cattle gene introgression in bison. Today, though approximately 500,000 plains bison exist in North America, few are free of cattle gene introgression, 96% are subject to anthropogenic selection for commodity production, and only 4% are in herds managed primarily for conservation purposes. Small herd size, artificial selection, cattle-gene introgression, and other factors threaten the diversity and integrity of the bison genome. In addition, the bison is for all practical purposes ecologically extinct across its former range, with multiple consequences for grassland biodiversity. Urgent measures are needed to conserve the wild bison genome and to restore the ecological role of bison in grassland ecosystems. Socioeconomic trends in the Great Plains, combined with new information about bison conservation needs and new conservation initiatives by both the public and public sectors, have set the stage for significant progress in bison conservation over the next few years.

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1. Introduction

Perhaps no species is as emblematic of the Great Plains of North America as the American bison (*Bison bison*). The explorers Meriwether Lewis and William Clark often commented on the “immense” herds and more than once estimated 10,000–20,000 were within view while traversing the Great Plains from 1804–1806 (Ambrose Tubbs, 2003). The range of the plains bison (*B. bison bison*) before European settlement extended from nearly coast-to-coast in the US and from the Great Plains of southern Canada to northern Mexico (Hornaday, 1889).

The bison was also an early icon of the conservation movement in the US and Canada, being one of the first species that stirred citizens and governments in North America to intervene on behalf of a species that seemed destined for extinction (Coder, 1975; Lothian, 1981). Due largely to commercial and subsistence hunting, as well as probably exotic bovine diseases and forage competition with domestic stock (Flores, 1991), plains bison were reduced from tens of millions at the time of European colonization (Shaw, 1995) to a few hundred by the mid-1880s (Hornaday, 1889; Isenberg, 2000). The other sub-species of American bison, the wood bison (*B. bison athabasca*) which inhabited woodlands of northern Canada and Alaska, was reduced to perhaps 250 animals (Hornaday, 1889; Soper, 1941).

Pleas in the early 1800s to halt the destruction of bison in North America were largely ignored (Dary, 1989). Protective legislation in Canada and the United States was not enacted until much later when bison were near extinction. In Canada, the 1877 Buffalo Protection Act was the first attempt to legislate protection (Hewitt, 1921). However, this measure was ineffective because of a lack of enforcement. It was reinforced in 1894 when the Dominion Government passed a law protecting the surviving wood bison (Soper, 1941). By this time, plains bison had been extirpated from the wild in Canada. In the absence of protective legislation the plains bison disappeared from the wild in the United States except in Yellowstone National Park. The states of Idaho, Wyoming, and Montana implemented statutes to reduce the killing of game, including bison, between 1864 and 1872, but these were largely ineffective due to limited enforcement. The Act to Protect the Birds and Animals in Yellowstone National Park and to Punish Crimes in Said Park was signed by President Grover Cleveland in 1894, thereby halting the extirpation of the last free-ranging plains bison population in North America (Gates et al., 2005). In 1902, fewer than 25 bison remained in the re-

mote Pelican Valley in Yellowstone National Park (Meagher, 1973).

The independent actions of private citizens, taken long before national governments reacted, were responsible for saving the plains bison (Dary, 1989; Coder, 1975). Between 1873 and 1889 several individuals in areas ranging from Manitoba to Texas captured the last of the wild plains bison, except for the few remaining in Yellowstone National Park. Concerned about the fate of the bison, William Hornaday, Director of the New York Zoological Park, and other wildlife advocates formed the American Bison Society in 1905, which successfully lobbied for the creation of several public conservation herds in the United States (Isenberg, 2000). In Canada, the national parks system first became involved in plains bison conservation in 1897 when three animals were purchased from Charles Goodnight in Texas. However, the most significant early contribution by the Government of Canada was made in 1907 when it purchased the privately owned Pablo-Allard herd in Montana. The herd was shipped first to Elk Island National Park, then on to a new park in the grasslands of east-central Alberta (Lothian, 1981). With protection, numbers of both the plains and wood bison increased quickly and a close brush with extinction was averted (Hornaday, 1927; Boyd, 2003). Although the wood bison also faces conservation challenges today, it is not considered further here. (We also note that the European bison [*Bison bonasus*] faces similar conservation problems as well as opportunities for significant restoration (Olech and Perzanowski, 2002; Perzanowski et al., 2004), and that closer collaboration between North American and European bison conservation efforts may be fruitful.)

These early efforts to save the plains bison have rightfully been regarded as a conservation success story. With roughly 500,000 plains bison now in North America (Boyd, 2003), their future would seem secure. A new body of knowledge, however, exposes major problems that give urgency to a second effort a century later to conserve this icon of the Great Plains.

2. Current problems facing conservation of the plains bison

Species extinctions occur in two basic ways: (1) the last individuals of a species die, bringing the genetic lineage of that species to an end; (2) the genetic makeup of a species changes substantially over time, whether through natural evolutionary processes, anthropogenic selection, or hybridization, resulting in genomic extinction (Rhymer and Simberloff,

1996; Allendorf et al., 2001). A new species need not emerge before we can label this genetic transformation an “extinction.” For example, though domestic cattle (*Bos primigenius taurus*) belong to the same species as their extinct wild ancestor, the aurochs, it is not justifiable to claim that the Heck breed of cattle, the attempted re-creation of the aurochs, is a suitable substitute for aurochs conservation, despite having distinctly aurochs-like characteristics.

Bison barely escaped the first type of extinction in the late 1800s. Now, more than a century later, the plains bison is confronting the second form of extinction due to two major problems: (1) domestication and anthropogenic selection and (2) cattle gene introgression. In addition, we can now add ecological extinction to our concerns, a concept not generally considered by conservationists a century ago.

2.1. Anthropogenic selection and small herd size

There is a disconnect, if not antagonism, between bison conservation and intensive anthropogenic selection for domestication of bison. Domestication may not only be irreversibly altering the bison gene pool and its morphology, physiology and behavior (Price, 1999; O'Regan et al., 2005), but the large and growing number of commercial bison herds one sees while traveling around the continent may create complacency and weak support among the public for bison conservation.

A continent-wide survey in 2002 by Boyd (2003), conducted on behalf of the World Conservation Union's North American Bison Specialist Group (IUCN Bison Specialist Group), found that of the roughly 500,000 plains bison in North America,

fewer than 20,000 are in herds managed principally for conservation purposes. The rest (96%) are being bred for commodity-production purposes such as ease of handling and meat production. In fact, the number of bison in conservation herds has stayed relatively constant since it peaked in the 1930s, while the number of bison in private, commercial herds has exploded since around 1970, when the number of bison in commercial herds surpassed those in conservation herds for the first time (Fig. 1) (McHugh, 1972). Apart from the potential problems posed by domestication of such a large portion of the bison population of North America, conservation of the wild bison genome is further compromised by problems confronting conservation herds, such as small herd size, confinement to fenced areas, introgression of cattle genes, intensive management and culling practices, absence of major predators, and non-native diseases.

The largest conservation herds of plains bison within their original range are in Yellowstone National Park (4000–5000 animals) and Grand Teton National Park (approximately 800), referred to as the Greater Yellowstone Area. These herds are free-ranging within the boundaries of the parks and nearby areas. With the successful reintroduction of wolves in 1995, they are subject to the full suite of native predators and other natural selection factors. Both herds, however, are infected with *Brucella abortus*, a non-native pathogen that causes brucellosis, a disease that causes abortion in many ungulate species, though it appears to have limited direct effect on these bison populations (Meyer and Meagher, 1995; Berger and Cain, 1999). The primary problem with brucellosis is the management conflict it creates because of fears that domestic cattle will be infected by bison wandering outside

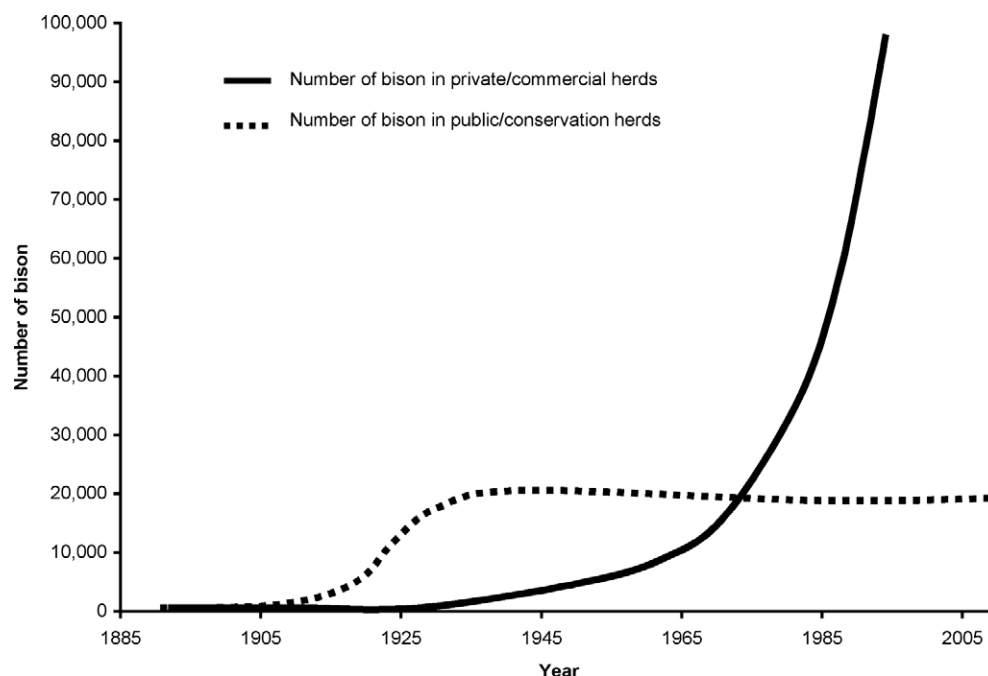


Fig. 1 – A comparison of bison numbers estimated to occur in public/conservation herds (sensu Boyd, 2003) and in private/commercial herds from 1883 to 2003; private/commercial animals totaled around 500,000 by 2003. (Sources: Hornaday, 1889; Seton, 1906; American Bison Society, 1908, 1911, 1914, 1918, 1923, 1930; Garretson, 1934, 1938; Dary, 1989; Callenbach, 1996; Boyd, 2003).

the park (Gates et al., 2005). Free-ranging, disease-free (i.e., free of non-native regulated diseases such as brucellosis) populations that are potentially influenced by natural regulating factors in the original range of plains bison accounted for, at the time of Boyd's (2003) survey, only 1289 bison (6.7% of the total conservation population). No herd among this latter group numbers more than 400 animals, which is probably well below the minimum number of animals needed to maintain the long-term genetic health of the herd (see below). Thus, no viable population that is free of regulated diseases such as brucellosis exists under natural conditions within the original range of the plains bison.

2.2. Introgression of cattle genes

Hybridization, with or without introgression, has caused the extinction of many plant and animal taxa, and is of growing concern in the conservation community (Rhymer and Simberloff, 1996; Allendorf et al., 2001). In the United States, considerable uncertainty exists concerning if and how the US Endangered Species Act should be applied to hybrids (Allendorf et al., 2004; Campton and Kaeding, 2005). The legacy of extensive efforts to create "cattalo" by cross-breeding bison and domestic cattle during the period when bison numbers were very low in the late 1800s and early 1900s (Garretson, 1938; Coder, 1975) is evident today by widespread domestic cattle gene introgression in both the mitochondrial (Polziehn et al., 1995; Ward et al., 1999) and nuclear (Halbert et al., 2005; Halbert and Derr, in press) genomes of bison herds across North America. While many public bison herds harbor evidence of domestic cattle nuclear gene introgression, the amount of introgression across the genome of each individual herd appears to be fairly low, with introgression rates ranging from 0.56% to 1.80% (Halbert et al., 2005; Halbert and Derr, in press).

All significant public herds of plains bison in the US and Canada have been tested and all but six show domestic cattle gene introgression. Of these six, sufficient numbers of individuals have been examined from only two herds to allow statistical confidence (>95%) in the lack of detection of domestic cattle introgression (i.e., low probability of type II error): Wind Cave National Park in South Dakota and Yellowstone National Park (Halbert et al., 2005; Halbert and Derr, in press). Four other public herds show no evidence of cattle introgression but the sample size is too small for statistical inference: Henry Mountains State Park in Utah, Teton National Park in Wyoming, Sully's Hill National Game Preserve in North Dakota, and Elk Island National Park in Alberta (Polziehn et al., 1995; Ward et al., 1999; Halbert and Derr, in press).

Four of these six herds contain fewer than 400 animals and, as noted previously, the two larger herds of Yellowstone and Grand Teton National Parks carry brucellosis and face troubling management issues (Gates et al., 2005). The only known private herd (of more than 100 tested; J.N.D., unpublished data) that has a high probability of being free of cattle genes based on known history and number of animals examined is the Castle Rock herd on the Turner Enterprise's Vermajo Park Ranch in New Mexico. At best, therefore, less than 1.5% of the 500,000 plains bison in existence today can be classified as likely free of domestic cattle gene introgression.

Intentional translocations or unintentional immigration of cattle-gene-introgressed bison into bison herds of conservation importance is a threat, particularly for herds that are cattle-gene free. The Wind Cave herd is separated from the cattle-gene-introgressed herd of Custer State Park by a single fence, and Custer bison have recently crossed this divide into Wind Cave (S.C.F., C.H.F. and K.K., unpublished data). At least one private bison herd with cattle gene introgression (J.N.D. and C.H.F., unpublished data) and other herds that have not been tested for cattle gene introgression occur in the region around Yellowstone and Grand Teton National Parks, raising the possibility of cross-breeding with these valuable conservation herds. In spring 2006, a young male bison that escaped from a private herd was shot inside Yellowstone National Park's north boundary (R. Wallen, personal communication). As the popularity of private bison breeding increases without restrictions on bison that can inhabit lands near these conservation herds, the potential for interbreeding between conservation herds and cattle-gene-introgressed herds that are also undergoing selection for domestication will increase.

2.3. Ecological extinction

A primary mission of conservation should be to restore interactive species, species whose "virtual or effective absence leads to significant changes in some feature of its ecosystem(s)" (Soule et al., 2003, p. 1239). As an interactive species that was also highly abundant on the Great Plains, the plains bison was almost certainly a foundation species (Soule et al., 2003). Today, the plains bison is for all practical purposes ecologically extinct within its original range. Even in the few areas of the Great Plains where bison occur, they contribute less to food chains and landscape heterogeneity than they once did. Lost is the large influence of bison as a grazer that once roamed over large areas creating a mosaic of grazing intensities, as a major converter of grass to animal biomass that provided food for Native Americans, predators, scavengers and decomposers, as a key link in nutrient recycling, and as a maker of wallows and mini-wetlands, among other factors (Knapp et al., 1999; Truett et al., 2001). Heavily grazed areas also may have acted as fire breaks which further influenced habitat heterogeneity. Bison grazing has been shown to increase plant species diversity and structural heterogeneity in tall grass prairie (Hartnett et al., 1996). Bison were probably important in enabling the establishment of prairie dogs (*Cynomys* spp.), especially in the tallgrass prairie, by creating heavily grazed areas which are preferred by prairie dogs (Truett et al., 2001). As a keystone species, prairie dogs in turn affect multiple ecosystem processes and species, including bison (Kotliar et al., 2006). Although more research is needed to understand the relationship, one reason that grassland birds have experienced steeper declines than any other guild of birds in North America may be the loss of habitat heterogeneity that bison grazing patterns once created (Knopf, 1996).

Restoring the ecological role of bison is a prerequisite to large-scale and comprehensive restoration of biodiversity in the Great Plains and other grassland regions of North America that bison once inhabited. Although cattle, if managed to create heterogeneous grazing intensities (which is rarely done), are often proposed as surrogates for bison, the ecological

effects of the two species are substantially different. Research at Konza Prairie in Kansas and in Utah indicates that the abundance and richness of annual forbs and the spatial heterogeneity of biomass and cover are higher in sites with bison than in sites with cattle. Plumb and Dodd (1993) reported a difference in diet of the two species, with bison demonstrating a stronger preference for graminoids over forbs compared to cattle. Cattle do not create wallows and generally stay closer to bodies of water, which causes different grazing patterns and impacts on streams and riparian areas. Bison grazing, especially in combination with burning, has the potential for inducing a much more complex set of local interactions and spatial and temporal patterns of vegetation than cattle grazing (Steuter, 1997). Apart from the ecological differences between bison and cattle, perhaps the most important constraint is that cattle are invariably managed for commodity production. In addition to the truncation of the food web caused by removal of livestock for human consumption, large prairie dog populations are generally not tolerated by livestock producers, nor are large numbers of wolves (*Canis lupus*) and grizzly bears (*Ursus arctos*) (Freilich et al., 2003). Particularly in the Great Plains, large reserves with abundant bison will be needed if these ecologically important species are to be restored.

3. Restoration issues and potential

Unlike many endangered species restoration efforts, there are no significant biological challenges to building bison populations, as evidenced by the success of commercial bison breeders across North America and successful reintroductions of plains bison to the wild in Yellowstone National Park's northern range, the Henry Mountains of Utah, four areas in Alaska (Boyd, 2003), and wood bison in several locations in Canada (Gates et al., 2001). Millions of acres of bison habitat, particularly native grasslands of the Great Plains, remain largely intact. Rebuilding a population is biologically relatively simple: give a suitable founder herd lots of land to roam and grass to eat and watch their numbers double every 4 or 5 years (Fredin, 1984). The major challenge is primarily a socioeconomic one of securing sufficiently large areas of land.

The primary biological questions regarding bison restoration are genetic, including providing for natural selection. The amount of genetic diversity within and between historic populations of plains bison across pre-European North America is largely unknown; individuals were routinely traded among the founding herds thereby largely precluding any attempt today to reconstruct historic genetic patterns. If there was significant genetic variation across their range, we were lucky that the half dozen or so herds rescued in the late 1800s sampled a relatively broad cross-section of the North American distribution of the sub-species (Halbert, 2003). Though the bison went through a severe population bottleneck, this was short-lived as herds quickly grew in the early 1900s. The brevity of the bottleneck may have served to prevent significant genetic erosion as the nuclear genetic variation of bison today is generally much greater than other mammal species that have gone through population bottlenecks (McCleneghan et al., 1990; Stormont, 1993) and is simi-

lar to other wild ungulates (Wilson and Strobeck, 1999; Halbert, 2003).

Genetic differences exist among the conservation herds of plains bison in North America. Some herds, including those with cattle gene introgression, have a distinct genetic composition compared with other bison populations due to unique bison alleles and allelic distributions (Halbert, 2003). Development of a North American bison conservation strategy needs to address the resulting questions: Do these differences reflect local adaptations or simply represent the random effect of a small number of founders? Should we strive to create several populations replicating each of the herds without detectable domestic cattle introgression, such as those of Wind Cave and Yellowstone National Parks, as well as those cattle-gene-introgressed herds that have a unique genetic constitution and historical significance, such as the National Bison Range herd in Montana? Or, given limited resources and land, is the best strategy to found new herds that incorporate the genetic diversity of all these herds and manage all or most conservation herds as one metapopulation?

Given the option, we agree with Allendorf et al. (2001) that in cases where widespread introgression has occurred in a species, highest priority should be given to conserving populations that are genetically pure. However, some bison populations with low levels of domestic cattle introgression might also be valuable conservation targets due to their historical importance and unique genetic constitution, and because they can presumably fulfill the ecological role of bison. We say "presumably" because we do not know what effects, if any, cattle DNA may have on bison physiology, behavior and fitness. For example, given the distinct metabolisms of cattle and bison (e.g., bison, unlike cattle, greatly reduce their metabolic rate in winter [Rutley and Hudson, 2000]), the presence of a domestic cattle mitochondrial genome in bison might affect bison energetics, growth, and seasonal foraging behavior. The potential for selectively removing bison with cattle mitochondrial DNA from these important introgressed herds emerges as a possibility with new DNA screening methods under development. Domestic cattle nuclear fragments have been widely dispersed throughout the bison genome over a long enough period of time (hybrid swarm), however, that recapitulation of the parental bison nuclear germplasm through similar selective removal and breeding is highly cost- and labor-prohibitive at this point.

The goals of conserving the bison gene pool and ensuring the viability of bison populations pose questions about what herd sizes must be maintained and how these herds must be managed, both individually and collectively. Inbreeding depression appears to significantly increase the risk of extinction for small populations (Frankham, 2005), including many mammalian taxa at populations of less than a few thousand individuals (O'Grady et al., 2006). Population viability analysis for vertebrates has similarly suggested that adult population sizes of several thousand are needed for long-term persistence (Reed et al., 2003).

One important bison conservation herd has already exhibited problems of inbreeding depression. The Texas State Bison Herd, which has a distinct genetic composition and history, suffers from dangerously low levels of genetic diversity resulting from a small number of founders, chronically small

herd size, and inbreeding which has resulted in fertility and recruitment problems (Halbert et al., 2004).

Although the National Park Service, the United States Fish and Wildlife Service, and Parks Canada manage a large proportion of public herds and the most important conservation herds on the continent, none of the agencies has science-based quantitative management objectives for conserving the genetic diversity of bison, nor is there a policy for coordination of bison conservation among agency units. Recent computer models aimed at informing National Park Service decisions about this question suggest that an actual population size of about 400 animals is likely to achieve a goal of retaining 90% of currently existing herd heterozygosity if management closely follows simulated management actions and if assumptions on (poorly known) bison breeding behavior are approximately correct (Gross and Wang, 2005). Because management practices are seldom as precise as models and our knowledge of bison behavior is limited, a larger population may well be needed to meet this goal.

Gross and Wang (2005) estimate that to retain 90% of existing alleles over 200 years an actual population size of 1000 bison is required. However, to meet the need for bison to adapt to new areas where they are reintroduced and to adapt to large current (e.g., exotic diseases) and future (e.g., climate change) alterations in their habitats, as well as for the intrinsic value of conserving genetic diversity, a more prudent goal would be retention of at least 95% of allelic diversity over 200 years. Their analysis suggests a herd size of at least 2000 animals is required to meet this goal. As Gross and Wang (2005, p. 11) state: “High allelic diversity will virtually always be correlated with the occurrence of many alleles that have a low frequency in the population. These rare alleles are unlikely to contribute substantially to short-term population responses to selection, but they can be a very important limit to the response to selection over many generations. Allelic diversity is thus considered important for the long-term survival of a species, especially where there may be substantial environmental changes, range expansions, or (re)introduction into new sites.”

No federal or state conservation area that currently harbors bison in the Great Plains maintains even one half of a herd goal of 2000 animals. However, The Nature Conservancy's Tallgrass Prairie Preserve in Oklahoma harbors a herd of around 2000 animals (The Nature Conservancy, 2006). Within the original range of the plains bison, the only federal or state herd that currently meets the 2000 goal is in the Rocky Mountains of Yellowstone National Park. Managing the genetic diversity of these small herds is compounded by the fact that all of them, including the Yellowstone National Park herd, are currently subject to culling practices that may inadvertently affect genetic diversity.

Although the genetic questions are complex, probably the most difficult question to answer with any certainty is: How many bison over how large an area are needed to restore the ecological role of the bison on a meaningful scale for biodiversity conservation in the Great Plains? We can develop some reasonably sound estimates for how many thousands of bison over several hundred thousand hectares, combined with other native ungulates, would be needed to support viable populations of wolves and perhaps grizzly bears. But

questions of scale become much more difficult to answer as we try to envision how, for example, bison and prairie dogs, as two ecologically important species of the Great Plains, historically interacted to create a mosaic of grassland habitats. Our understanding of how habitat features and patch size were influenced by bison carcasses and grazing patterns, and how these in turn affect grassland bird distribution and nesting success, is still too rudimentary for the formulation of sound management recommendations (Truett et al., 2001).

The late bison biologist and conservationist Dale Lott proposed that “A Great Plains Park must be very large—at least 5000 square miles (1.3 million hectares)—and must include both upland and river bottom habitat” (Lott, 2002, p. 203). Only 1.5% of the Northern Great Plains Ecoregion is in parks, reserves and similar protected areas (Forrest et al., 2004), a figure probably representative of the Great Plains as a whole. No protected area in the Great Plains is close to 13,000 square kilometers in size. Nevertheless, roughly 50% of the Northern Great Plains ecoregion remains in largely native prairie, with 10 areas recently identified that have several hundred thousand to more than a million hectares of public lands in primarily native prairie, often interspersed with private land that also contains substantial intact prairie (Forrest et al., 2004). Thus, several areas in the Northern Great Plains alone appear to have suitable habitat for supporting populations of 10,000–30,000 or more bison. Ecosystem restoration at such a scale is challenging, given that much of the landscape is privately owned or managed for a multitude of other uses, some of which are incompatible with bison restoration.

4. The social context

Large-scale biodiversity restoration always involves various layers of social complexity. Clewell and Aronson (2006) discuss the five major motivations or rationales for the restoration of ecosystems (and their associated species). These include technocratic, biotic, heuristic, idealistic, and pragmatic rationales and often result in apparent social conflicts. Restoration of bison and their native ecosystems is no exception, as a diversity of socioeconomic factors, from local to regional to international scales, are involved. Some of these factors are largely unique to bison conservation because bison occupy a rather distinct spiritual, iconic, and legal status among wildlife of the Great Plains, if not more broadly across much of North America, and because they are particularly important culturally and economically for many Great Plains Indians (Wyckoff and Dalquest, 1997).

The cattle ranching culture and economy, occupying more than 95% of the Great Plains grasslands, is the successor to the bison economy of Native Americans that previously dominated the region. The potential for restoring bison at a meaningful ecological scale is therefore inextricably linked to the existing cattle industry. The Buffalo Commons concept for ‘re-bisoning’ the Great Plains proposed by geographers Frank and Deborah Popper in the 1980s (Popper and Popper, 1987) created a firestorm of protest among communities of the region that continues to taint discussions about present-day bison conservation. Nevertheless, the Popper's predictions have withstood the test of time as the economic tailspin and human population decline, with the exception of the Native

American population, continues unabated in the Great Plains (Forrest et al., 2004).

These conditions create both a socioeconomic need and an opportunity for large-scale conservation of bison and native grasslands. The economic revitalization of many rural communities may be possible through the development of a natural-amenity economy based on grassland reserves and abundant wildlife, whether done through privately or publicly funded initiatives. Abundant wildlife and wildlands brought the wealthy from the east coast and Europe on safari to the Great Plains in the 1800s, and the Rocky Mountain West provides many examples of the positive effect today that wildlife and wildlands have on the economic vitality of local communities (Rudzitis and Johansen, 1991; Rudzitis, 1999; Rasker and Hansen, 2000). The depopulation of rural areas, an ageing population of current ranch owners, and relatively low land prices in much of the Great Plains provide the conditions for large-scale changes in land ownership, in the subsequent management of those lands, and in the rural economy over the next decade. How these changes will unfold remains to be seen, but conservationists, Native American tribes, and ranching communities have perhaps an unparalleled opportunity over the next few years to restore ecological relationships, structure, and function at a regional scale in a manner that is sensitive to cultural history and heritage while providing economic opportunities.

Bison also fall into an unusual legal framework that greatly complicates conservation efforts. Unlike any other native animal species in North America, bison are commonly not classified or managed as “wildlife,” but rather, with some exceptions, as “livestock” by state and provincial agencies, although they are considered wildlife in federal refuges and parks (Forrest et al., 2004) and on some state and provincial lands (Gates et al., 2001; Boyd, 2003). This leaves one of North America’s most majestic and adaptable native grassland species, legally and in the public’s mind, straddling the fence between being wild and domestic (Cahalane, 1944).

This dual status complicates management, as indicated by recent events in Canada. In May 2004, Canada’s Committee on the Status of Endangered Wildlife in Canada (COSEWIC) recommended to list plains bison as a threatened species (COSEWIC, 2004). Following a review of public commentary, the Governor General in Council, on the recommendation of the Minister of the Environment, decided to not list the plains bison “because of potential economic implications for the Canadian bison industry” (Canada Gazette, 2005). Instead of listing, the federal government committed to “working with provincial governments, the bison industry and other stakeholders to develop an approach for the recovery of wild plains bison.”

Although bison conservation is not a priority for most states, Montana lists free-ranging herds as a species of concern with an S2 status: “imperiled because of rarity or because other factors demonstrably making it very vulnerable to extinction throughout its range” (Carlson, 2003), and the state’s recently released Comprehensive Fish and Wildlife Conservation Strategy lists bison as Tier 1—those species in greatest need of conservation—and proposes large-scale bison restoration (Montana Fish, Wildlife and Parks, 2005).

Native American Tribes have made available thousands of acres of land for bison restoration and thus there is consider-

able potential for tribes to play an important role in the ecological recovery of bison. Tribes often take a “hands-off” approach to bison management and allow, to the extent possible, natural processes to unfold. Because many of the tribal bison herds were started or reinforced with surplus bison from national parks and refuges, some herds may be free of domestic cattle introgression and most, if not all, are brucellosis-free.

The InterTribal Bison Cooperative provides technical assistance to many tribes involved in bison restoration and has created a network where tribes can share information on management practices. The Cooperative has a membership of 55 tribes that collectively have more than 8000 bison which, depending on the tribe, are managed for various marketing, spiritual and conservation purposes. According to its web site, the Cooperative is “committed to reestablishing buffalo herds on Indian lands in a manner that promotes cultural enhancement, spiritual revitalization, ecological restoration, and economic development” (InterTribal Bison Cooperative, 2006).

5. The way forward

Although the restoration of bison in North America faces a new set of social and ecological circumstances and challenges, we need to avoid repeating mistakes evident in the history of bison conservation. Bison need to be established as a free-ranging wildlife species with the appropriate social and ecological values. We should avoid the pitfall of conducting species conservation at the expense of ecological function.

Conservation of the plains bison urgently needs to move forward simultaneously on two fronts. First, the genetically important herds, both those that are apparently free of cattle genes and those that harbor unique parts of the total bison gene pool, need to be conserved. This means developing best management practices and applying them to existing herds. A precautionary approach dictates that we create viable satellite herds of each of the existing genetically important bison herds in North America. Second, we need to restore large herds numbering in the thousands on native grasslands where the ecological role of the bison can be fully expressed. There is ample need and opportunity here for both public and private lands to contribute to this effort.

Restoration efforts are moving forward on several fronts. The US National Park Service is now developing management guidelines to maintain the genetic health of federal herds. The IUCN Bison Specialist Group is currently completing a new status assessment and conducting a review to determine if the species should be red-listed as threatened or endangered. In addition, the IUCN Bison Specialist Group, World Wildlife Fund, Turner Endangered Species Fund, and Turner Enterprises hosted a meeting in May 2005 of bison researchers and managers from across North America to kick off the preparation of North American conservation strategy for the plains bison. The Wildlife Conservation Society is conducting a comprehensive review of the range-wide status of bison in follow-up to Boyd’s earlier work and is working in concert with the IUCN Bison Specialist Group. In 2005, the centennial year of the American Bison Society, the Wildlife Conservation Society also revitalized the principles of the historic American

Bison Society campaign to help bring about ecological recovery of American bison across its entire historic range.

Meanwhile, on-the-ground conservation efforts need to continue. As refuges and national parks now focus on developing a strategy for managing and expanding their important conservation herds, one significant constraint is the absence of public lands currently available for creating large, new public herds. In Canada, Grasslands National Park reintroduced bison from the Elk Island population in December 2005, and Banff National Park is investigating the feasibility of bison reintroduction in the Central Rockies ecosystem. Management plans for Waterton Lakes and Banff National Parks mention plains bison restoration, but no operational plans have been developed at this time. We know of no other formal federal or state/provincial initiatives at this time to establish new conservation herds of bison in the Canada, Mexico, or the United States.

At least three initiatives by the non-profit sector to create conservation herds of bison are underway: Nature Conservancy Canada's Old-Man-on-His-Back Preserve in Alberta with Elk Island animals; American Prairie Foundation and World Wildlife Fund in Montana with Wind Cave source stock; and The Nature Conservancy in South Dakota, also with animals from Wind Cave. Elsewhere in the private sector, Turner Enterprises has separated the apparently cattle-gene-free Castle Rock herd into three units to reduce risk and grow the herd (Joe Truett, personal communication).

Tribal initiatives are also underway. The Cheyenne River Sioux Tribe has started a 8900-hectare Tribal Wildlife Reserve with approximately 1100 bison (Cheyenne River Sioux Tribe, 2006). The Rosebud Sioux Tribe has officially endorsed "The Million Acre Project" developed by the Great Plains Restoration Council and centered on the Pine Ridge Indian Reservation in South Dakota, with plans to restore bison and a prairie ecosystem (Great Plains Restoration Council, 2006). Additionally, Native American Tribes may have the opportunity to manage or co-manage federal lands adjacent to or within reservation boundaries and create large contiguous blocks of federal and tribal land that may be suited for large-scale bison restoration. At least one tribe, the Lower Brule Sioux Tribe, has formalized the early stages of this vision in a strategic plan (Lower Brule Sioux Tribe. In review. 10-year strategic plan. Lower Brule Sioux Tribe Department of Wildlife, Fish and Recreation, Lower Brule, South Dakota).

The Great Plains is at an ecological and socioeconomic cross-roads. Change could be swift, massive, and far-reaching. The next decade—a very narrow window on the conservation time scale—will be our best chance to capitalize on a new era of land use that embraces wild bison on vast, intact grasslands, alongside sustainable agriculture and other suitable land uses, as an ecological and socioeconomic cornerstone for the region. As one of North America's most charismatic megafauna, bison hold great potential for sparking the public's imagination about, and support for, restoring the wildlife spectacle that once graced the Great Plains. Through public and private initiatives and partnerships, tens of thousands of largely wild and free-roaming bison could again populate these grassland ecosystems by the end of this century. Bringing back the wild bison is not only important for conserving the bison genome and restoring its ecological and economic

roles in North America's native grasslands. It also promises the intrinsic value of having countless numbers of bison and other wildlife on a vast, horizon-to-horizon prairie vista, and the power of that vista for uplifting the human spirit.

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

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

SAMUEL D. FUHLENDORF AND DAVID M. ENGLE

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 interspersed 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 palidicinctus*), 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

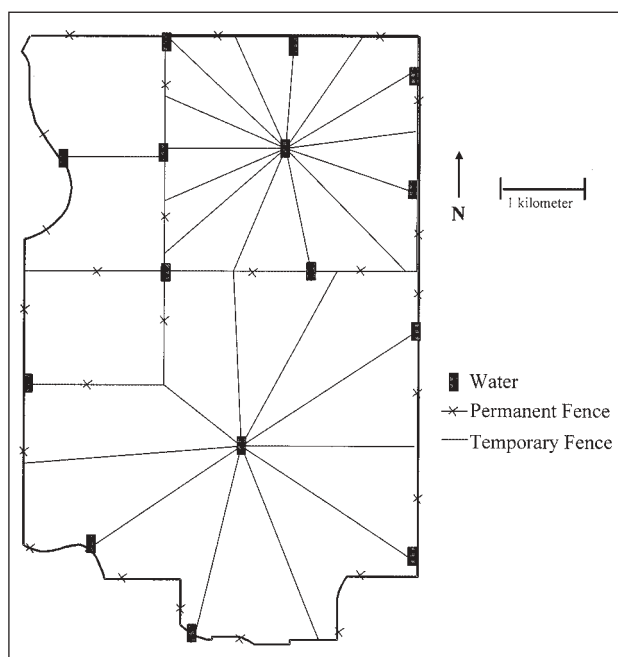


Figure 1. Landscape plan for rotational grazing. A cross-fencing scheme for a traditional grazing management plan implements a rapid rotational grazing system; the objective is to achieve a more uniform distribution of grazing across the landscape. This and similar traditional grazing management practices 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.

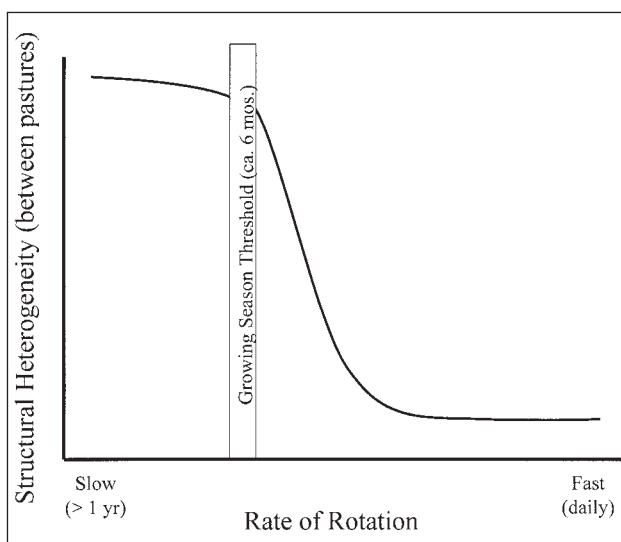


Figure 2. A conceptual model demonstrating the relationship between rate of grazing rotation and structural heterogeneity within rangeland landscapes. Rapid rotation of livestock through multiple pastures results in uniform utilization of forage and low levels of structural heterogeneity within the landscape. 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

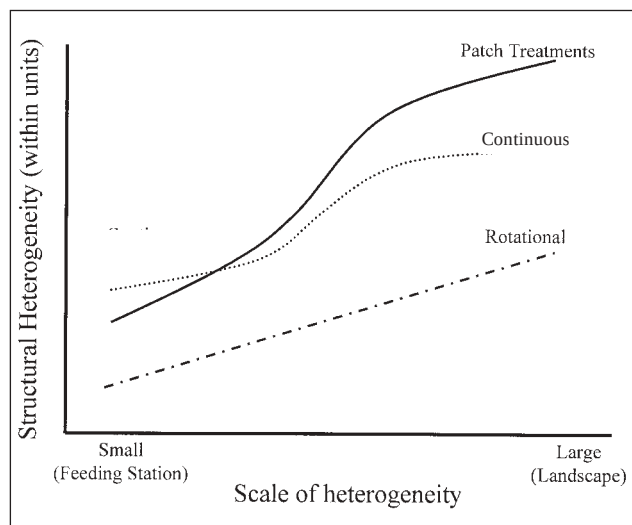


Figure 3. Structural heterogeneity within units in response to different grazing systems across several spatial scales (i.e., feeding station, patch, landscape) of herbivore site selection. Rotational grazing results in a relatively low level of structural heterogeneity across all of these spatial scales 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.

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.

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 granivorous (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.

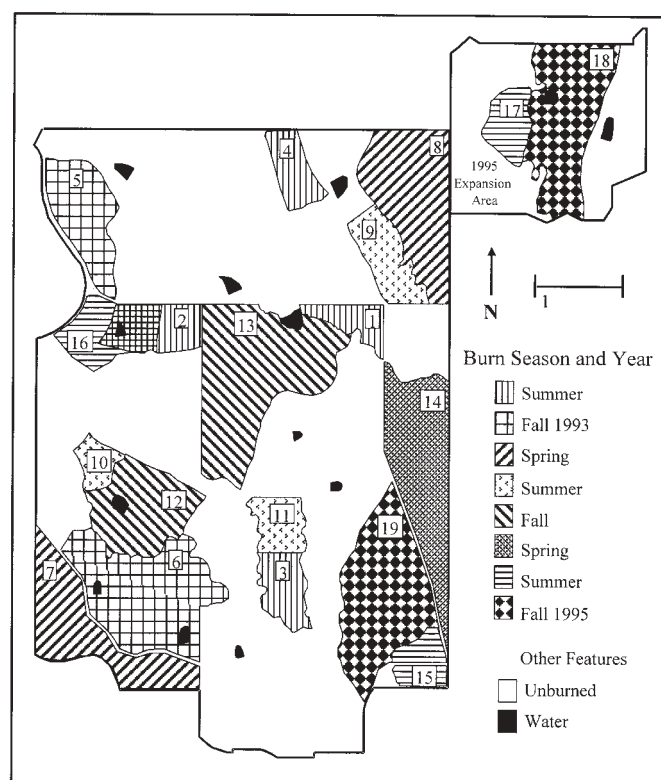


Figure 6. Chronology of patch burning within the bison enclosure on the Tallgrass Prairie Preserve, Oklahoma, 1993–1995. Numbers refer to the order in which burns were conducted. Bison within this area were allowed unrestricted selection of patches within the landscape. Figure from Coppedge and Shaw (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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A Hierarchical Perspective to Woody Plant Encroachment for Conservation of Prairie-Chickens



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ABSTRACT

Encroachment of Great Plains grasslands by fire-sensitive woody plants is a large-scale, regional process that fragments grassland landscapes. Using prairie grouse (*Tympanuchus* spp.) of conservation concern, we apply hierarchy theory to demonstrate how regional processes constrain lower-level processes and reduce the success of local management. For example, fire and grazing management may be locally important to conservation, but the application of fire and grazing disturbances rarely cause irreversible fragmentation of grasslands in the Great Plains. These disturbance processes cause short-term alterations in vegetation conditions that can be positive or negative, but from a long-term perspective fire maintains large tracts of continuous rangelands by limiting woody plant encroachment. Conservation efforts for prairie grouse should be focused on landscape processes that contribute to landscape fragmentation, such as increased dominance of trees or conversion to other land uses. In fact, reliance on local management (e.g., maintaining vegetation structure) to alter prairie grouse vital rates is less important to grouse population persistence given contemporary landscape level changes. Changing grass height, litter depth, or increasing the cover of forbs may impact a few remaining prairie-chickens, but it will not create useable space at a scale relevant to the historic conditions that existed before land conversion and fire suppression.

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Introduction

Many factors contribute to the fragmentation of rangelands, which is a primary cause of population declines in species endemic to these landscapes (Herkert 1994; Helzer and Jelinski 1999). Fragmentation describes the active conversion or separation of large tracts of a vegetation type or state into small isolated fragments that may have limited value for certain species (Pietz et al. 2009). Separation of habitat into smaller, more isolated units can lead to local extinction or regional declines because of limited dispersal among habitat patches (Herkert 1994). For populations of species such as grouse that rely on expansive landscapes, fragmentation can have dire consequences. Population declines of Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) and Greater Prairie-Chicken (*Tympanuchus cupido*) have been attributed to fragmentation from alteration of disturbance regimes (primarily fire) and the associated woody plant encroachment (Merrill et al. 1999; Wu et al. 2001; Fuhlendorf et al. 2002a; McNew et al. 2012).

One of the major challenges for conservation efforts of a myriad of species occurring on public and private lands is that the conditions that are critical for the support and restoration of a population often occur

at many spatial scales that may or may not correspond to management scales (Wiens 1989; Fuhlendorf and Smeins 1996). For example, many grouse species have specific life history requirements that are proximally required and variable for different activities such as nesting, brood rearing, lekking, or roosting (Fig. 1). This local heterogeneity may be critical to maintain populations, but from a broader spatial and temporal perspective, large suitable landscapes that are connected to other populations may be more important for species persistence (Fuhlendorf et al. 2002a; Johnson et al. 2003). In fact, the size of the landscapes necessary for even a given population to persist often can exceed parcel size, making local management largely irrelevant if the landscape matrix is not suitable for the species of concern. Further, conservation practices at the more local scale (e.g., for a given parcel or landholding) can be quite different from those focused on broader scales and either population or species persistence. For example, local conservation practices may focus on conditions related to successful nesting or brood rearing while broader scale perspectives may focus on landscape composition and pattern that prioritize connectivity between local populations. While reproduction and survival at the local scale are obviously necessary for population persistence, they are inherently constrained by higher-order processes and are therefore a secondary concern to landscape-scale conservation efforts. As resources for conservation are always limited, it is critical that we prioritize conservation actions that

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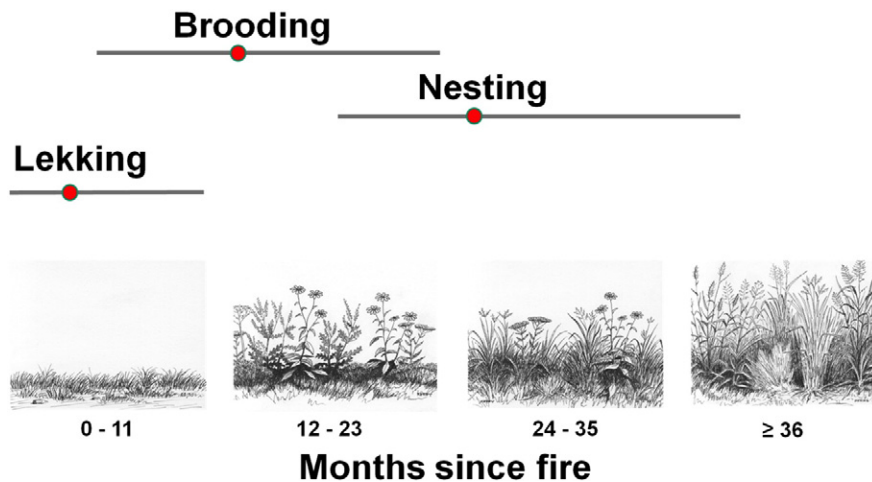


Figure 1. Median (red dot) and first and third quartile (lines) of sites selected by Greater Prairie-Chickens (*Tympanuchus cupido*) for lekking, nesting, and brood rearing, illustrating how different life history needs are met by various vegetation conditions. Data were collected at The Nature Conservancy's Tallgrass Prairie Preserve, OK, USA, 2010–2013. (Artwork courtesy of Gary Kirby.)

are most likely to be successful. It is the goal of this paper to provide a generalized framework to prioritize conservation from a landscape perspective for prairie grouse in the Great Plains.

How to Prioritize Conservation Practices on Rangelands

The range management discipline has focused traditionally on managing vegetation to sustain production of forage for the livestock industry (Holechek et al. 2004). Recently, an alternative approach that is based on conservation of pattern and processes on rangelands has been proposed (Fuhlendorf et al. 2012). This approach suggested the following principles: 1) maintain large continuous tracts of rangeland, 2) understand the importance of stocking rate while recognizing that no single rate is appropriate, 3) promote uneven distribution and understand heterogeneity, 4) promote shifting mosaics where disturbance patterns are variable in space and time, 5) recognize that all species are important to conservation, and 6) emphasize the importance of restoring disturbance regimes on large landscapes. In addition to the need for a new approach focused on conservation of rangelands, many other practices and actions on rangelands influence the ability of a landscape or region to support species of conservation concern.

A primary approach for prioritizing conservation is to use hierarchy theory, viewing habitat as a hierarchically nested organization of conditions and resources required by an organism, where all units are composed of subunits within larger subunits (Kolasa and Waltho 1998; Fuhlendorf et al. 2002a). This pattern results in a situation where broad-scale patterns constrain fine-scale processes and suggests that broad-scale conditions must be suitable before success (e.g., increased nest survival) can occur from finer-scale management actions. Through this framework, there is no justification for conducting local management if populations are constrained by higher-level fragmentation as the objectives will not be achievable until higher-order patterns and conditions are addressed relevant to the species of interest. Therefore, in fragmented landscapes, the major conservation focus should be on limiting additional fragmentation and attempting to identify the best places to reverse previous fragmentation. A first step in this process is to determine what constitutes fragmentation for the species of conservation concern.

When prioritizing factors that contribute to fragmentation, it would be most effective to first focus on factors that are at risk of crossing a threshold where reversal is unlikely (Fahrig 2001). This aims to limit additional and irreversible damage to landscapes and the species that require broad-scale continuity. For example, land cover/land use changes contribute to fragmentation, but if change is due to development from suburban conversion or cultivation, reversal of those

changes is unlikely. Avoiding these kinds of nonreversible changes should be the initial goal of conservation, particularly when they occur at large spatial scales (Fig. 2). Once the landscape is largely converted, then the priority should be addressing the most at-risk and easily restored landscape elements that will provide the greatest connectivity. When landscape connectivity is maintained and large rangeland landscapes are intact, finer-scaled and reversible management focused on factors that influence proximal vegetation structure suitable for certain life history activities have a reasonable expectation of success (Fitzgerald and Tanner, 1992).

A hierarchical approach requires recognition of factors that alter conservation by constraining the success of local management. Broadly, we can categorize these into constraining and fine-scaled (proximal) management factors. The argument through hierarchy theory is that conservation should first focus on limiting constraining factors and then focus on the fine-scaled management. This process of classification

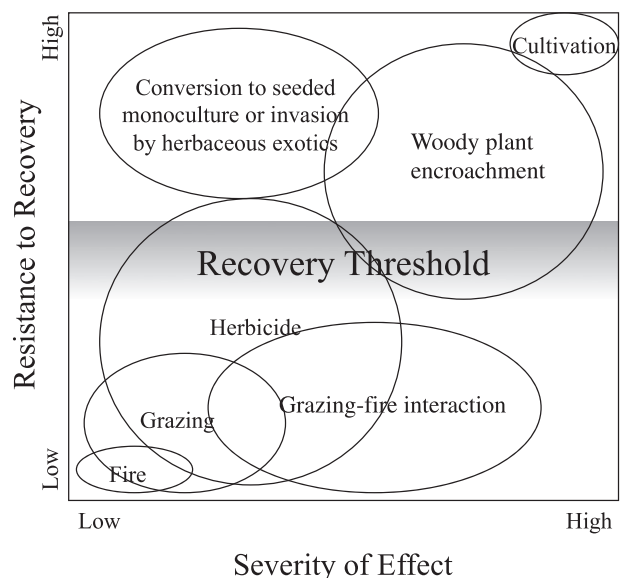


Figure 2. Descriptive matrix of categories of practices grouped by resistance to recovery and by severity of change. Size and shape of a sphere denote the relative severity of the change and influence of the disturbance practice on the resulting patch's resistance to recovery. The horizontal line marks a recovery threshold beyond which rangeland will not likely recover from the change. Rangelands subjected to change above the recovery threshold constrain the influence of local management practices.

will differ among species and regions, so it is important to develop specific case studies. For this paper, we focus on Lesser and Greater Prairie-Chickens in the Southern Great Plains, although the implications could be more broadly applied to many conservation issues on rangelands.

Fragmentation—The Constraining Factor for Grouse

Grouse species require large, relatively unfragmented landscapes that include local heterogeneity (Johnsgard 2002). Specifically, Greater Prairie-Chickens and Lesser Prairie-Chickens require expansive landscapes that resemble native vegetation and include local needs for activities such as nesting and brood rearing but also encompass year-round needs such as wintering, roosting, and lekking locations (Hovick et al., 2014a, 2014b; McNew et al. 2015). These patterns are not unique among prairie chickens. For example, similar findings have been reported for the Greater Sage-grouse (*Centrocercus urophasianus*) on rangelands of the western United States (Coates et al., 2015; Dahlgren et al. 2016). To promote the conservation of these grouse species, landscape-level models may be required to identify specific geographical areas with high potential to serve as core areas, while local-level models may be best for evaluating effects of site-specific management (i.e., local disturbances) within the landscape context (Coates et al., 2015). A key component for nesting ecology is fine-scale concealment at nest locations (Coates and Delehanty, 2010; Hovick et al. 2015a; McNew et al. 2015; Dinkins et al. 2016), but as we emphasize in this paper, filters at higher scales such as woody encroachment and land conversion need to be considered for population persistence (Fuhlendorf et al., 2002a, 2002b; Doherty et al., 2010). For purposes of this review, we keep our main focus on the Great Plains and the prairie grouse that occupy this region, but most of these principles apply to grouse found throughout rangelands, including sage grouse.

Historically, conversion of rangeland to cropland has caused the greatest alteration to the Great Plains (Samson and Knopf 1994). The widespread cultivation of grasslands is frequently cited as having permanently altered the Great Plains. This alteration represents the single greatest threat to sustainability of Great Plains grassland ecosystems and their fauna (e.g., Samson and Knopf 1994). Cultivation in particular has long-term consequences including soil erosion, increased decomposition, depletion of soil organic matter, and reduced site fertility (Tieszen et al. 1982; Aguilar et al. 1988; Burke et al. 1989). Because of these effects, recovery of native grasslands after cultivation, even with reseeding, is either slow or nonexistent in shortgrass prairie (Coffin et al. 1996; Hyder et al. 1971), mixed prairie (Fuhlendorf et al. 2002b), and tallgrass prairie (Collins and Adams 1983). Ecosystem processes, such as nutrient cycling, are irreversibly altered and nutrient status is reduced and cannot be restored even 50 + years after restoration seeding (Burke et al. 1989; Lauenroth et al. 1994; Fuhlendorf et al. 2002b).

Because of the long-term impacts of cultivation, conservation in the Great Plains must consider historical and current patterns of land conversion. In fact, the historical cultivation of native grasslands and shrublands is considered the primary factor in the decline of many sensitive conservation species within the Great Plains during the first century of European settlement. As an example, declines in prairie-chicken populations primarily occurred during this period as cropland exceeded thresholds suitable for maintaining natural cover necessary for nesting and brood-rearing (Crawford and Bolen 1976; Taylor and Guthery 1980; Johnsgard 2002). Establishing perennial grass and forb cover on former croplands has clearly benefited grassland passerines and prairie-chickens (Reynolds et al. 1994; Coppedge et al. 2001a; Matthews et al. 2013), but restoration of cultivated landscapes remains costly and socially constrained, suggesting that focusing on restoration of cropland may be less efficient (i.e., lower benefit-to-cost ratio) than other conservation activities (see Fig. 2) (Fuhlendorf et al. 2002a; Hellerstein and Malcolm 2011; Sohl et al. 2012; Feng et al. 2013). Identifying areas of high biological value that are at risk of conversion

to cropland can help prioritize regional conservation efforts (Stephens et al. 2008).

From Texas to the eastern deciduous forest that borders the Great Plains, woody plants have encroached northward and westward because of changes in climatic conditions and widespread fire suppression (Briggs et al. 2005). This gradual and insidious encroachment has been described as a “green glacier” (Engle et al. 2008) and has converted grasslands and shrublands to woodlands, altering livestock production, ecological processes, and wildlife habitat (Coppedge et al. 2001a; Fuhlendorf et al. 2008). Conversion of grasslands to woodlands began more than 100 years ago and continues today on rangelands throughout North America and beyond (Twidwell et al. 2013). This increase has had profound impacts on grassland birds and prairie grouse in particular (Coppedge et al. 2001a). Specifically, landscapes with declining populations of Lesser Prairie-Chickens experience more large-scale fragmentation from factors like woody plant encroachment than landscapes with sustained populations (Fuhlendorf et al. 2002a). Similarly, Greater and Lesser Prairie-Chickens tend to maximize distance from trees when selecting nesting sites (Hovick et al. 2015a). So, while cultivation may have been the early contributor to fragmentation and may continue in some local areas, from a prairie-chicken perspective in the southern half of the Great Plains, the majority of active fragmentation is due to woody plant encroachment.

Multiple types of fragmentation exist throughout the Great Plains, and many of them are increasing (Engle et al. 2008; Fargoine et al. 2009). Woody encroachment throughout much of the Central and Southern Great Plains is approaching a threshold that will prevent the reintroduction of fire for effective management, thereby reducing the capacity for these areas to function as habitat for grassland obligate species (Fuhlendorf et al. 1996; Coppedge et al. 2001a; Fuhlendorf et al. 2008). Additionally, other sources of fragmentation exist as a result of landowner choice and federal programs where much of the cultivated land has been converted to monocultures of exotic perennial grasses (Laycock 1988; Leathers and Harrington 2010). Moreover, land use such as cultivated crops, biofuels production, energy development, and urban expansion are projected to dominate the Great Plains, which could further reduce native plant cover up to 36% by 2100 (Sohl et al. 2012). Large tracts of prairie will likely be restricted to land parcels where fire is a landscape management practice and where cultivation is not feasible or desirable. These changes have the potential to further reduce populations of obligate grassland fauna of the Great Plains and as a consequence reduce the effectiveness of local

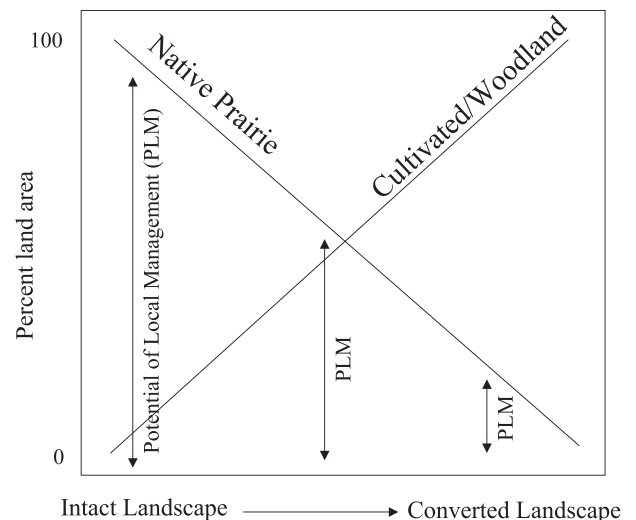


Figure 3. A model illustrating the application of hierarchy theory in which large-scale, regional factors (cultivation of grasslands or tree encroachment into grasslands) constrain the influence of local factors (management practices such as grazing or prescribed burning).

management practices applied for conservation purposes (Fig. 3). The cumulative sum of these changes to rangelands across the Great Plains has led to the endangered status of the Attwater's Prairie-Chicken (*Tympanuchus cupido attwateri*), which is a subspecies of the Greater Prairie-Chicken; formerly threatened status of the Lesser Prairie-Chicken; and reduced distribution and many statewide listings as a species of conservation concern for the Greater Prairie-Chicken (Robel 2004; USFWS, 2014).

An emerging and expanding constraint on prairie grouse inhabiting the Great Plains is the industrialization of rangelands through energy development. High levels of energy development are contributing to additional fragmentation for prairie-chickens, but additional data are needed to determine how and under what circumstances energy development constitutes fragmentation for these species. Existing data have reported mixed impacts of energy development on Greater Prairie-Chickens depending on the sex, life history stage, and other factors (Winder et al., 2013, 2014, 2015a, 2015b), but globally, energy development appears to have consistent, negative influence on grouse survival and behavior (Hovick et al., 2014a, 2014b). Moreover, it is apparent that a large amount of net primary production (i.e., biomass that functions as cover and food for prairie grouse) is lost to oil and gas development specifically, and this undoubtedly has direct effects on native flora and fauna as a result of direct habitat loss (Allred et al. 2015).

Proximal Management

Proximal management is focused on local objectives that could be based on the premise of improving livestock production or other local goals without consideration for effects at broader scales. These practices include most of the local management activities conducted by managers on rangelands, and while they can be locally successful for some objectives such as changing forage yield for livestock production, their success for other objectives is largely dependent on the constraining effect of landscape context. This is particularly true when considering prairie-chicken populations and the immediate effects of local landscape management interacting with short-term weather variables across landscapes with variable capacities to buffer these fine-scale effects (Hovick et al. 2015a; Winder et al., 2015a, 2015b; Hagen & Elmore, 2016).

When considering the potential effects of proximal management and the constraining effect of higher-order landscape features, it is necessary to understand the dominant historic disturbances within the Great Plains, which were fire (anthropogenic and lightning caused), climatic fluctuation, and grazing by mammalian herbivores (Anderson 2006). Additionally, the interaction between grazing animals and fire led to a feedback that resulted in heterogeneous landscapes that included burned and heavily grazed plant communities and ungrazed, unburned plant communities interspersed among many patches in variable successional stages (Fuhlendorf et al. 2009; Fuhlendorf and Engle 2001). This disturbance regime resulted in some level of local heterogeneity in terms of variable vegetation structure and composition, while limiting coarser fragmentation of grasslands by restricting most trees and fire-intolerant plants to drainages and rocky outcrops where fine fuels limited fire frequency. Great Plains landscapes were therefore dominated by grasslands that were a shifting mosaic of patches of various structure and composition following fire and grazing (Fuhlendorf and Engle 2001). For grassland birds, some species were best adapted to particular patches resulting from various time post disturbance while others with broader niche breadth occurred in all or most patch types (Knopf 1996a). The heterogeneity of vegetation types was critical to maintaining floral and faunal diversity across Great Plains landscapes. Some wildlife species such as prairie-chickens (see Fig. 1) and upland sandpipers (Sandercock et al. 2015) require multiple vegetation structure types to complete the annual stages of their life history. This shifting mosaic provided the vegetation structure required for the entire suite of breeding and nonbreeding birds that

occupy grasslands in a particular region (Fuhlendorf et al. 2006; Hovick et al., 2014a, 2014b).

Over the past century, the rangeland profession has encouraged managing these landscapes with uniform grazing, and in some cases fire and herbicides, to promote homogenous plant communities dominated by a few key forage plant species (Fuhlendorf and Engle 2001; Fuhlendorf et al. 2012). On rangelands of the Great Plains, grazing and fire effects are largely reversible unless grazing intensity and duration are sufficient to promote erosion (Milchunas et al. 1988; Milchunas and Lauenroth 1993; Milchunas et al. 1994; Fuhlendorf and Smeins 1997; Fuhlendorf and Engle 2001; Fuhlendorf et al. 2009). On most grasslands, the dominant effect of grazing is altering the structure of vegetation that may be important for some wildlife species (Lauenroth et al. 1994; Knopf 1996b).

Herbicide applications for weed and brush control is another form of proximal disturbance that is widely recommended and frequently adopted to reduce species that are perceived as undesirable for maximizing cattle production (Vallentine 1989; Hanselka et al. 1990; New 1997). Herbicides used on woody plants in the Great Plains are often used to reduce the inherent structural complexity of the vegetation (Vinton and Collins 1997), which in some cases has been altered from historic conditions due to changes in both fire and grazing regimes (Fuhlendorf and Engle 2001). Changes in the woody plant structure and composition can change the availability of food and cover for some wildlife including prairie-chickens (Koerth 1996). As mentioned earlier, limiting woody plants can maintain connectivity of grasslands, and in the case of some species like mesquite (*Prosopis glandulosa* Torr.), herbicides are an important option for management. For other plants, such as juniper species in the Great Plains, herbicides are largely ineffective and fire may be more appropriate. Other species that may be targeted by herbicides include edaphically limited native shrubs such as shinnery oak (*Quercus havardii* Rydb.) and sand sagebrush (*Artemisia filifolia* Torr.), which are critical to conservation of some populations of prairie chickens in the Central and Southern Great Plains (Lauenroth and Milchunas 1991; Boyd and Bidwell 2001; Harrell et al. 2001; Patten et al. 2005; Thacker et al. 2012). Beyond application of herbicides for woody plants, herbicide is often targeted toward herbaceous dicot species (Fuhlendorf et al. 2009). Unfortunately, many of these targeted dicot species provide food both directly and indirectly to prairie-chickens, as well as provide important cover for broods. Herbicide application can produce variable-edge contrasts and have variable resistance to recovery depending on the specific action and the conditions at time of application. Therefore, it may constitute either low or moderate severity of disturbance, but in some cases these vegetation types can cross a recovery threshold that will take decades to change (Thacker et al. 2012).

All of these proximal management practices have variable effects on conservation of landscapes, and some are more useful depending on conservation and other societal objectives. In general, these traditional management actions are usually applied for local management objectives rather than focused on promoting connectivity of the landscape. There are various reasons that local management is often the focus, including parcel size, additional objectives such as livestock grazing, and cost-share programmatic structure. Nevertheless, it is critical to recognize that grazing and vegetation management that is focused on conservation will have limited positive influence when broader-scale patterns have not been considered.

Conservation Priorities and Management Implications

For long-term sustainability of rangeland endemic fauna, conservation strategy must shift from focusing primarily on locally recommended management to a regional focus on preventing high-severity change that contributes to nearly irreversible fragmentation of the Great Plains. Application of hierarchy theory suggests that regional processes will constrain lower-level processes and reduce the success of proximal or local management (see Fig. 3). Because fragmentation is a regional

process, local management focused on prescribed grazing and grassland condition will fail to maintain populations of rangeland endemic wildlife when higher-level processes such as tree encroachment and land conversion are fragmenting large landscapes (Hovick et al. 2015a).

Resources are limited to support conservation and management. Therefore, we propose setting conservation priorities based primarily on a site's capacity to recover from changes that have occurred. Although severity of effects or landscape change is generally a local concern for land management, the overriding issue for regional conservation is the propensity for rangelands to recover from a particular event (see Fig. 2). Landscape change on sites that have the lowest likelihood of recovering should be given the lowest priority because without reversal, the impacts on Great Plains endemic fauna such as prairie-chickens may be nearly irreparable. Change that fragments rangelands such as conversion to cropland, increased dominance of trees, industrialization, some herbicide applications, seeding of invasive herbaceous monocultures, and increased dominance of exotic invaders are all examples of landscape-level change in the top-tier hierarchy that should be the primary conservation focus if prairie-chickens are an objective. Measurements of and management to change metrics such as stubble height, litter depth, bare ground, plant diversity, and percent cover by functional group are of secondary concern for prairie grouse. Conservation discussions, planning, and expenditure of resources should therefore follow in a logical hierarchical approach. Some changes, especially exotic plant invasions and native tree encroachment, contribute to habitat loss and the demise of many bird populations (Coppedge et al. 2001b; Fuhlendorf et al. 2002a), and others (fire and the fire-grazing interaction) contribute to habitat restoration and can increase diversity and stability in native communities (Hovick et al. 2015b; McGranahan et al. 2016). Fire and grazing management may be locally important to conservation, but these disturbances rarely cause irreversible fragmentation of grasslands (see Fig. 2). In fact, periodic fire and the fire-grazing interaction are processes critical to the maintenance of grassland dominance (Vinton and Collins 1997; Fuhlendorf and Engle 2001; Anderson 2006).

The most efficient approach to conserving the endemic biota of the Great Plains is to prevent changes that are long term and challenging to reverse for socioeconomic reasons. Restoring cultivated land and rangelands that have been invaded by exotic species or mature woody plants is expensive and is unlikely to meet the goal of complete restoration within a meaningful management timeframe (i.e., several decades). Cultivation has largely fragmented the Great Plains, yet over the past several decades, cultivated land has decreased in some regions because of government programs and many of the remnant prairies remain uncultivated because of topo-edaphic limitations. In contrast, invasive exotic species and encroaching trees have increased on remnant, native grasslands throughout the Great Plains (Briggs et al. 2002; Briggs et al. 2005; Engle et al. 2008). Thus, a top conservation priority for the long-term persistence of native Great Plains' biota, especially prairie-chickens, should be focused on limiting future cultivation of rangeland and encroachment by woody plants that would increase fragmentation of these landscapes.

A common logical error in reasoning that is relevant to developing conservation priorities is the survivorship bias, which focuses on people or things (i.e., stocks or companies) that have survived and inadvertently ignores those that have not persisted (Gazley and Guo 2015). In wildlife conservation, we often focus on studying species in landscapes where the species has persisted rather than trying to understand where it once existed but is no longer present. For example, the vast majority of the historical distribution of the Lesser Prairie-Chicken has experienced woody plant encroachment from fire suppression, and this encroachment has been a primary cause of decline in the species across its historical range (Fuhlendorf et al. 2002a). Changing grass height or litter depth or increasing the cover of forbs may impact a few remaining prairie-chickens, but it will not create useable space at a scale relevant to the historic conditions that existed before land conversion and fire suppression. Without a retrospective perspective, studies of a species response

to changing landscapes will rarely be able to demonstrate the primary causes of the decline. For prairie-chickens, the factor that has driven landscape changes for the past 50 years (encroachment of woody plants) is also currently the dominant driver of fragmentation of the Southern Great Plains and when combined with historical patterns of cultivation encroachment of woody plants remains the dominant threat to rangelands of the region. In this context, the study of vital rates in response to proximal management that changes herbaceous vegetation structure is trivial when compared with conversion of millions of hectares of rangelands to nonhabitat for grouse. In summary, if prairie-chicken persistence is a conservation goal, a continuing focus on local conditions has a low probability of success but also diverts limited resources from addressing the driving sources of continued decline. While many in the conservation community have acknowledged that landscape factors are critical, it is time to act on these convictions if imperiled prairie grouse are to recover.

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Desert and Prairie Ranching Profitability

Jerry L. Holechek and Jerry Hawkes

During the 1980's and early 1990's the ranching industry in the United States has been in a deflationary mode compared to a highly inflated economy in the 1970's. How are these changing economic conditions affecting ranch values and profitability? Knowledge of the general economic conditions can be useful in decisions regarding implementation of range improvements such as grazing systems or brush control.

To make valid comparisons of ranching profitability under changing economic conditions, information is required from both public and private land ranches. To examine the financial aspects of ranching under the inflationary conditions of the 1970's and the deflationary conditions of the 1980's and 1990's we used the average New Mexico cold desert ranch (250 AU) where the land is primarily publicly owned and the average shortgrass prairie ranch (250 AU) where the land is primarily privately owned. These comparisons are possible because large amounts of both range types occur in the state, with long-term (65 years) detailed financial characterizations of ranches in each range type. The cold desert ranches are in the northwestern corner of New Mexico and shortgrass prairie ranches are in the northeastern corner. The Rocky Mountains in the center of the state separate the two range types. It is important to recognize these comparisons are for the average ranch, and there are individual ranchers who do substantially better or worse.

Methods

Our analysis comes from a series of reports by agricultural economists at New Mexico State University dating back to 1925 plus analyses we've performed using a computer model developed by Allen Torell, agricultural economist, NMSU. The financial structure of the two ranch types, cold desert and shortgrass prairie ranches, for the periods of 1978–1980 and 1990–1992 is based on rancher interviews and range surveys directed by James Gray, John Fowler, Allen Torell, and the authors. Average prices and costs were used for the 1978–1980 and 1990–1992 periods to avoid aberrations associated with particular years not representative of the period.

Production characteristics such as calf crop, calf weights, death loss, etc., at 1990–1992 levels were used for both 1978–1980 and 1990–1992 periods so the influence of cost/price structure changes could be separated from managerial improvements. Generally modest increases were made in production characteristics between the 1978–1980 and 1990–1992 periods (Table 1).

Table 1. Production and efficiency characteristics for average medium sized cold desert and shortgrass prairie ranches in New Mexico in the 1978–1980 (inflationary) and the 1990–1992 (deflationary) periods.

Characteristic	Average Cold Desert Ranch		Average Shortgrass Prairie Ranch	
	1978–1980	1990–1992	1978–1980	1990–1992
Ranch size (acre)	28,614	28,614	7,750	7,750
Number of AU	250	250	250	250
Number of mature cows	186	193	192	187
Replacement rate (%)	12	14	13	15
Bull to cow ratio	1:18	1:15	1:20	1:20
Calf crop %	75	80	77	87
Calf death loss (%)	2.7	2.5	3.5	2.5
Steer calf weight (lb)	410	450	390	460

Ranch Values

Between 1978–1980 and 1990–1992, the average cold desert ranch with cattle excluded lost approximately 38 percent of its value (Table 2). In contrast, shortgrass prairie ranches dropped 9 percent in value in the same period. Generally, values of most types of real estate suffer under deflationary conditions (Batra 1989, Schiller 1991). During the depression of the 1930's, agricultural land and commodity values were much more severely depressed than assets associated with manufacturing and service (USDC 1975, Batra 1989).

The differential reduction in ranch value in the cold



Cold desert zone in northwestern New Mexico.

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Table 2. Financial structure of the average medium sized (250 AU) cow-calf ranch in the cold desert and shortgrass prairie regions of New Mexico in (1978-1980) and (1990-1992).

Item identification	Unit	Quantity	1978-1980	1990-1992	1978-1980	1990-1992
Cold Desert:			\$ value/unit		Total value \$	
Land:						
Owned rangeland	Acres	7,164	54.57	20.00	390,939	143,280
State lease rangeland	Acres	4,070	38.98	4.91	158,648	19,983
Federal lease rangeland	Acres	17,380	—	—	—	—
Federal lease rangeland	AUM's	1,896	60.03	32.74	113,816	62,075
Subtotal	Acres	28,614			663,403	225,338
Dwellings					45,833	55,000
Other buildings					35,752	36,000
Watering facilities:						
Wells	Number	6	8,920	10,000	53,520	60,000
Pipelines	Miles	8	1,697	2,100	13,576	16,800
Tanks & Resources	Number	22	2,362	2,500	51,964	55,000
Subtotal					119,060	131,800
Barbed wire fence	Miles	40	1,712	2,000	68,480	80,000
Machinery					25,500	66,500
Subtotal					958,028	594,638
Cattle:						
Cows	Number	193	438	600	84,534	115,800
Heifers 1-2	Number	27	336	600	9,072	16,200
Heifer calves	Number	50	236	374	11,800	18,700
Bulls	Number	13	844	959	10,972	12,467
Horses	Number	8	670	1,000	5,360	8,000
Subtotal					121,738	171,167
Total Value					1,079,766	765,805
Shortgrass Prairie:			\$ value/unit		Total value \$	
Land:						
Owned rangeland	Acres	6,209	92.00	78.81	571,228	489,352
Private lease rangeland	Acres	540	—	—	—	—
State lease rangeland	Acres	1,001	76.00	19.70	76,076	19,723
Subtotal	Acres	7,750			647,304	509,075
Dwellings					45,833	55,000
Other buildings					35,752	36,000
Watering facilities:						
Wells	Number	5	8,920	10,000	44,600	50,000
Pipelines	Miles	2	1,697	2,100	3,394	4,200
Tanks & Resources	Number	8	2,362	2,500	18,896	20,000
Subtotal					66,890	74,200
Barbed wire fence	Miles	18	1,712	2,000	30,816	36,000
Other range facilities					1,943	4,000
Machinery					26,380	46,500
Subtotal					854,918	760,775
Cattle:						
Cows	Number	188	438	600	82,344	112,800
Heifers 1-2	Number	27	336	600	9,072	16,200
Heifer calves	Number	59	236	374	13,924	22,066
Bulls	Number	11	844	688	9,284	7,568
Horses	Number	5	670	1,000	3,350	5,000
Subtotal					117,974	163,634
Total Value					972,892	924,409

desert compared to the shortgrass prairie is primarily because most of the land is publicly owned. Policy changes by the federal government account for this differential reduction. The uncertainty associated with grazing fees and tenure of grazing privileges and the lower financial returns in the 1980's on public land ranches has caused buyers to reduce prices they are willing to pay per animal unit (AU) compared to that on private land ranches (Torell and Doll 1990).

Land values of the privately owned land portion on the cold desert ranches have also dropped sharply since the 1982 highs. Declining real personal income, saturation of the market with ranchettes, reduced oil revenues, high

real interest rates, lower ranch returns, and a change in the tax code in 1986 caused a collapse in the market for southwestern rangeland in the mid-1980's. Present land prices reflect mainly grazing value rather than future development potential. In the shortgrass prairie, ranches have dropped much less in value because they occur in the area which is not attractive for retirement. Historically, land in the Great Plains has been appraised mainly on the basis of income from livestock and farming, rather than development potential.

Nearly four times the amount of land is required per AU in the cold desert compared to the shortgrass prairie due



Shortgrass prairie range in good condition in northeastern New Mexico.

to lower precipitation and more rugged terrain. In the cold desert ranges, forage production is between 100–400 lbs per acre compared to 600–1,400 lbs per acre in the shortgrass prairie (Holechek et al. 1989). The larger area means that total fencing and watering point values are much higher on the cold desert compared to the shortgrass prairie ranches.

The value of ranch fences and watering points have appreciated at about one percent per year (1978–1992) compared to an average annual inflation rate for the U.S.

economy of 5 percent. Annual maintenance costs range from 5 to 10 dollars for a mile of fence and 200 to 350 dollars for a well. The failure of these assets to keep up with inflation and high annual maintenance costs makes it financially essential to keep fence and water developments at minimum levels necessary to effectively utilize the forage resources of the ranch. This is particularly true in the cold desert where these assets occur primarily on federal lands, and future grazing privileges are uncertain.

Table 3. Budgeted costs for the average medium sized (250 AU) cow-calf ranch in the cold desert and shortgrass prairie in New Mexico in 1978–1980 and 1990–1992.

Cost type	Cold Desert		Shortgrass Prairie	
	1978–1980	1990–1992	1978–1980	1990–1992
	----- \$ -----		----- \$ -----	
A. Variable costs				
1. Grazing fees				
Private lease	367	0	800	1350
State lease	395	2,431	250	777
BLM/Forest Service fees	2,277	2,883	—	—
2. Supplement feed	4,000	10,672	9,000	12,982
3. Livestock expenses				
2 purchased bulls	1,026	2,700	1,296	2,600
Fuel & repairs	5,706	5,410	4,020	4,500
Veterinary & medicine	462	1,546	650	1,425
Property taxes (livestock)	126	1,212	178	1,130
Maintenance	2,156	3,276	1,627	3,000
Other	360	500	540	1,600
4. Hired labor	2,692	5,400	2,500	4,000
Total variable costs	19,567	36,030	20,861	33,364
B. Fixed costs				
Electricity	1,111	1,440	993	1,800
Telephone	142	800	240	840
Butane & heating	60	1,200	280	1,000
Insurance	690	5,200	640	3,600
Depreciation	6,567	14,535	5,570	8,146
Property taxes (land)	1,026	1,182	1,439	1,179
Total fixed costs	9,596	24,357	9,162	16,566
TOTAL COSTS	29,163	60,387	30,023	49,930

Ranching Costs

Between 1978–1980 and 1990–1992, total ranching costs in the cold desert have increased about 100 percent (7 percent per year) (Table 3). In the shortgrass prairie total costs have increased about 60 percent (5%/year). Insurance, electricity, taxes, livestock health care, supplemental feeding costs, and state lease grazing fees all showed major increases on both types of ranches. Supplemental feed costs increased more sharply on the cold desert than on the shortgrass prairie. Research indicates under proper stocking rates supplemental feed costs of \$15–20 per AU will maximize cow-calf performance on most New Mexico ranges (Wallace 1988, Holechek 1992). However, the average rancher is spending \$40–45/AU on supplemental feed (Torell and Word 1991a, 1991b). It has been our experience based on visits to both cold desert and shortgrass prairie ranches that supplemental feed programs are often poorly thought out. Ranchers err in using inappropriate supplements and applying them at the wrong times and to the wrong classes of livestock. We believe supplemental costs could be reduced by 50 percent or more on most ranches with no reduction in cattle productivity.

Grazing fees on federal lands have been a subject of much controversy. However, they represent a small part of total costs (4 to 5%) in the cold desert. It is our impression that many ranchers are disproportionately concerned about increases in grazing fees relative to other production costs. Generally, ranchers believe major reductions in ranch valuations will occur if grazing fees are increased. This concern has validity on the basis of Torell and Doll's (1990) report.

Return on Investment

Both net income and return on investment were substantially higher on the shortgrass prairie compared to cold desert ranches (Table 4). This is due to higher cattle productivity and lower production costs in the shortgrass prairie. Longer periods of green feed, flatter terrain, lower frequency and severity of drought and easier application of intensive herd management practices when livestock are concentrated in smaller areas all explain the superior economic returns from the shortgrass prairie. Based on our analysis, the shortgrass prairie is a more efficient area for beef production than the cold desert.

Nominal cattle prices were at historic highs in the 1990–1992 period. However, when adjustment is made for

Table 4. Returns for average medium (250 AU) cow-calf ranch in the cold desert and shortgrass prairie in New Mexico in 1978–1980 and 1990–1992.

Receipts (Sale of livestock)	1978–80	1990–92	1978–80	1990–92	1978–80	1990–92	1978–80	1990–92
	Number		\$/Cwt		Lbs. Sale wt. (avg)		Total \$	
Cold Desert:								
Yearlings	23	23	67.00	82.00	550	550	8,476	10,373
Calves	121	121	76.00	96.00	425	425	39,083	49,368
Cull bulls	3	3	56.90	60.00	1,475	1,475	2,517	2,655
Cull cows	24	24	44.00	46.00	900	900	9,504	9,936
Total (\$)							59,580	72,332
Expenses								
Variable costs							19,567	36,030
Fixed costs							9,546	24,357
Total costs							29,163	60,387
Returns								
Total net return (\$) ¹							30,417	11,945
Net return AU (\$) ¹							121.67	47.78
Net return acre (\$) ¹							1.06	0.42
Return on investment (%) ¹							2.82	1.56
Total net return adjusted for inflation (1980–1992) (\$) ¹							45,546	11,945
Shortgrass:								
Yearling heifers	2	30	67.00	82.00	685	6.85	918	16,851
Calves	150	122	76.00	96.00	450	4.50	51,300	52,704
Cull bulls	2	2	56.90	60.00	1,500	15.00	1,707	1,800
Cull cows	27	27	44.00	46.00	950	9.50	11,286	11,799
Total (\$)							65,211	83,154
Expenses								
Variable costs							20,861	33,364
Fixed costs							9,162	16,566
Total costs							30,023	49,930
Returns								
Net income ¹							35,188	33,224
Net return AU (\$) ¹							140.75	132.90
Net return acre (\$) ¹							4.54	4.29
% return on investment (%)							3.62	3.59
Total net return adjusted for inflation (1980–1992) (\$) ¹							57,317	33,224

¹No value is subtracted for operator labor and management or opportunity cost.

inflation (5% per year average 1980–1991) real cattle prices since WWII peaked 1951. Real income adjusted for inflation has decreased about 74% on cold desert and 42% on shortgrass prairie ranches between 1978–1980 and 1990–1992 periods.

The problems confronting western range cattle ranchers in recent years are an oversupply of beef due to a low population growth rate, changes in consumer eating habits, expanded world beef supplies, and beef production increases from new technologies. The new beef production technologies involve better cattle health care, embryo transplants, improved breeding programs and intensive nutritional management. Many of these operations are best suited to humid areas where low amounts of land are required per animal unit.

Compared to other investments, western cattle ranching is definitely a high risk-low reward proposition. Presently, yields on 1- to 30-year treasury bonds are around 3.5 to 7.5 percent, respectively. Yields on triple A rated corporate bonds go 1 to 3 percent higher than treasury bonds. Annual returns in the stock market have averaged around 10 percent over the last 40 years. Profits of large corporations in America have averaged about 12% on investment. These returns are all well above the 3.6% and 1.6% that characterized shortgrass prairie and cold desert ranches, respectively.

Historically, ranching returns in New Mexico have ranged between -3 to 5% on investment. Generally, profitability has been higher on large ranches than small ones due to economies of scale. Since World War II profitability of New Mexico ranches has gradually trended downward with the low point occurring in 1986 when return on investment averaged -1 percent.

Sustaining Cattle Ranching in the West

Our analysis indicates the profitability (net real income adjusted for inflation) of cattle ranching on both public and private lands in New Mexico has declined over the last 15 years. This decline has been most drastic on arid public land ranches. Failure of cattle prices to keep up with production cost increases is the reason for the decline. The decline in profitability has been accompanied by falling ranch values.

Under present conditions economic survival appears to depend more on cutting costs than increasing production. Generally, management has been oriented to the approach of grazing systems, brush control and expanding ranch size. All three of these approaches generally involve heavy capital outlays and work best in an inflationary economy.

Many economists project deflationary conditions to last well into the 1990's due to excessively high levels of government and consumer debt. This problem is further exacerbated by a depressed world economy. Present overall economic conditions have many similarities to the late 1920's prior to the 1930's depression (Batra 1989).

The present economic downturn could cause major changes in ranching and range management in the west-

ern USA. If the present downturn continues, many highly leveraged ranchers could be forced out of business by the mid-1990's, unless they are able to sustain the ranch with outside income. There has already been considerable shake-out in the ranching industry in New Mexico (Fowler and Torell 1987, Torell and Doll 1990). Conservative ranchers that avoided capital intensive range management practices such as intensive grazing systems and/or brush control are generally in the best financial condition in terms of debt to equity. As long as deflationary conditions persist, it is our view professional range managers need to shift their emphasis from capital intensive practices that increase production to low input practices that maximize profit with low risk, such as more careful stocking rate selection, better breeding programs, livestock behavioral modifications to improve distribution and reduce poison plant death losses, better placement of watering points, and improved supplemental feeding programs.

Common-use grazing and diversification into recreation are two other approaches that show considerable potential to improve profitability for some ranches. Integrated cattle and sheep ranches in New Mexico have been more profitable than straight cow-calf operations over the last 10 years (Torell and Word 1991a, 1991b). Increasingly New Mexico ranchers are finding fee hunting for both big game animals and gamebirds to be lucrative side endeavors that involve low risk and small capital outlay. Fee hunting works best on ranches that are largely in private ownership and naturally have high game populations. Several ranches in New Mexico now generate \$2,000 to \$30,000 in additional income from fee hunting.

Cowboying as a recreational experience is in its infancy as a western ranch enterprise. Some ranches are now providing a week of cowboying or dude ranching as in the recent movie *"City Slickers"* for around \$2,000–\$3,000 per person. Other aspects of this type of enterprise such as wilderness pack trips and nature tours are also being offered. The fact these enterprises (fee hunting, dude ranching, nature tours) are doing fairly well even under recessionary conditions reflects their potential to boost ranch income in the future.

Western ranches are not as efficient as ranches in the Great Plains and southeastern USA for cattle production but they have tremendous potential to provide high quality recreational experiences for an increasingly crowded, stressed out, urbanized society hungry to experience its colorful past. It is our opinion that cattle ranching will continue to be an important part of western economies but the future will belong to those ranchers who successfully diversify into recreation.

In closing we think the range profession needs to consider these trends and make appropriate adjustments. A strong understanding of the financial consequences of management interventions and knowledge of how to help ranchers develop and manage recreational enterprises will probably be important skills for tomorrow's range managers.

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Succession in Sagebrush

T. Lommasson

Editor's Note:

To truly make progress in research it is necessary to be aware of information found in the past. All too frequently we keep rediscovering the wheel. The following article is a case in point. During the past few years there have been several articles on plant succession published in the *Journal of Range Management*. I selected one article for reprinting. There is much good information in this article on factors which affect plant succession. I wonder what would have been concluded if the study had been for only 5 years at some period during the 31 years that this study represents.

Common sagebrush (*Artemisia tridentata*) on the grasslands of the Beaverhead National Forest in southwestern Montana apparently will maintain itself indefinitely under natural conditions. This conclusion is the result of a 31-year-old study conducted by the Forest Service to determine the possibility of sagebrush giving way to grass under good management of rangeland.

The study area occupies a basin of deep loam soil at the head of Cherry Creek on the east side of the Gravelly Range. Before and during the period of early settlement of this section of the State, this entire range was grazed by herds of buffalo during the summer months. The last buffalo in the adjoining valley was killed in 1882. At this time the heads of the streams and the gently sloping grasslands had been reduced to areas of bare soil pocked with the wallows of the buffalo. On these areas they rolled, pawed, and threw dust for protection against insects. The wallows are still a feature of the landscape.

From 1882 until about 1914, little grazing use was made of the range and the bare soil was allowed to revegetate almost unhindered. During this period sagebrush gained a foothold and became established in favorable locations. Since 1914 the area has been grazed by sheep. In 1926 it was placed under systematic management, following a range survey.

Sagebrush plants in the stand had an average age of 61 years in 1945, by growth ring count. They became established, therefore, in 1885, and in 1915 when the study began, they were 31 years old. At that time they were 24 to 30 inches tall, and were thick and thrifty. A 30-foot square area supported 167 mature plants, having 659 basal branches extending from the plant bases. No other shrubs were present.

In 1932, 18 years after the study started, the plants had decreased in number to 114, with 224 basal branches, a loss of 32% and 66%, respectively. No new plants were present. In 1936 only 93 old plants with 200 basal branches remained. However, the stand was beginning to show openings, and 5 seedlings were present in the open spots. The appearance of seedlings marked the turning point between sustained loss over a long period of years and the beginning of replacement of the stand. At this time the reduction of old plants had reached 44% and the loss of basal branches 70%.

In 1945, 88 old plants with 151 basal branches remained. In addition, the seedlings of 1936 had become well-established plants. The old plant loss since 1915 amounted to 47%, and the basal branch loss 77%.

Total vegetation density and percentages composition of sagebrush, grasses and grasslike plants, and weeds present on the plots for each of the periods were as follows:

	1915	1932	1936	1945
Total vegetation density	.8	.7	.65	.5
Sagebrush (% composition)	40	57	44	27
Grasses and grasslike plants (% composition)	40	32	40	58
Weeds (% composition)	20	11	12	15

Studies were made also of sagebrush invasion on a companion plot. In 1932 all the sagebrush on this plot was

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Organisms as Ecosystem Engineers

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Organisms as ecosystem engineers

Clive G. Jones, John H. Lawton and Moshe Shachak

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Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and create habitats. Autogenic engineers (e.g. corals, or trees) change the environment via their own physical structures (i.e. their living and dead tissues). Allogenic engineers (e.g. woodpeckers, beavers) change the environment by transforming living or non-living materials from one physical state to another, via mechanical or other means. The direct provision of resources to other species, in the form of living or dead tissues is not engineering. Organisms act as engineers when they modulate the supply of a resource or resources other than themselves. We recognise and define five types of engineering and provide examples. Humans are allogenic engineers par excellence, and also mimic the behaviour of autogenic engineers, for example by constructing glasshouses. We explore related concepts including the notions of extended phenotypes and keystone species. Some (but not all) products of ecosystem engineering are extended phenotypes. Many (perhaps most) impacts of keystone species include not only trophic effects, but also engineers and engineering. Engineers differ in their impacts. The biggest effects are attributable to species with large per capita impacts, living at high densities, over large areas for a long time, giving rise to structures that persist for millennia and that modulate many resource flows (e.g. mima mounds created by fossorial rodents). The ephemeral nests constructed by small, passerine birds lie at the opposite end of this continuum. We provide a tentative research agenda for an exploration of the phenomenon of organisms as ecosystem engineers, and suggest that all habitats on earth support, and are influenced by, ecosystem engineers.

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Interactions between organisms are a major determinant of the distribution and abundance of species. Ecology textbooks (e.g. Ricklefs 1984, Krebs 1985, Begon et al. 1990) summarise these important interactions as intra- and inter-specific competition for abiotic and biotic resources, predation, parasitism and mutualism. Conspicuously lacking from the list of key processes in most text books is the role that many organisms play in the creation, modification and maintenance of habitats. These activities do not involve direct trophic interactions between species, but they are nevertheless important and

common. The ecological literature is rich in examples of habitat modification by organisms, some of which have been extensively studied (e.g. Thayer 1979, Naiman et al. 1988). However, in general, population and community ecology have neither defined nor systematically identified and studied the role of organisms in the creation and maintenance of habitats. There is not even a word, or words, in common use to describe the process. We will call the process *Ecosystem Engineering* and the organisms responsible *Ecosystem Engineers*.

Beaver (*Castor canadensis*) are familiar examples of

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organisms acting as ecosystem engineers. By cutting trees and using them to construct dams they alter hydrology, creating wetlands that may persist for centuries. "These activities retain sediments and organic matter in the channel, ... modify nutrient cycling and decomposition dynamics, modify the structure and dynamics of the riparian zone, influence the character of water and materials transported downstream, and ultimately influence plant and animal community composition and diversity" (Naiman et al. 1988).

However, beaver are by no means the only ecosystem engineers. As we will show, a vast array of species have effects that are fundamentally similar, albeit often on more modest spatial and temporal scales. Yet there is no common language to describe what ecosystem engineers do, no formal structure to model their effects, and no general theory round which to organise understanding of the process. Examples, which are developed more formally below (for others, see Table 1), include not only beaver and their dams but also gophers, ants and termites that move soil, woodpeckers that drill holes, alligators that make wallows, rock-eating snails, trees, corals, sea-grass beds and *Sphagnum* blanket bogs.

The purposes of this article are fourfold: (i) to define and to give examples of ecosystem engineering by organisms; (ii) to develop a conceptual framework that explains and classifies its effects; (iii) to show how organismal engineering differs from related concepts (e.g. 'keystone species' Paine 1969, Krebs 1985); (iv) and to identify questions for further work on organisms as ecosystem engineers. First we define what we mean by an ecosystem engineer, before providing examples and a conceptual framework for what is, and is not, ecosystem engineering.

Definitions

Ecosystem engineers are organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species, by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and/or create habitats.

The direct provision of resources by an organism to other species, in the form of living or dead tissues is not engineering. Rather, it is the stuff of most contemporary ecological research, for example plant-herbivore or predator-prey interactions, food web studies and decomposition processes.

Autogenic engineers change the environment via their own physical structures, i.e. their living and dead tissues. *Allogenic engineers* change the environment by transforming living or non-living materials from one physical state to another, via mechanical or other means.

Armed with these definitions we can now proceed to consider some detailed examples. We are not, at this juncture, concerned with the magnitude or scale of the

impacts of engineers on communities and ecosystems. We are interested solely in discovering properties that all engineers have in common. We address the scale and magnitude of their effects later.

Classification of organisms as engineers

Table 1 summarises examples of organisms as ecosystem engineers. The table is illustrative, not exhaustive. Additional examples are discussed at greater length in the text.

All the examples of which we are aware can be assigned to one of five possible cases (Fig. 1), or to a combination of two or more of these cases. As in many other areas of ecology, the diversity of biological processes means that precise pigeon-holing is sometimes difficult. The boundaries between types of engineering are occasionally fuzzy and, in the real world, separating engineering from other ecological processes may also be difficult, simply because these non-trophic interactions always co-occur with trophic interactions. We discuss some difficult cases as we proceed. The majority of examples are, however, easy to classify. The legend to Fig. 1 explains the conventional notation used to describe them. For clarity, it is easiest to introduce the arguments using beaver and their dams.

Beaver conform to case 4 in Fig. 1. That is they are allogenic engineers, taking materials in the environment (in this case trees, but in the more general case it can be any living or non-living material), and turning them (engineering them) from physical state 1 (living trees) into physical state 2 (dead trees in a beaver dam). This act of engineering then creates a pond, and it is the pond which has profound effects on a whole series of resource-flows used by other organisms. The critical step in this process is the transformation of trees from state 1 (living) to state 2 (a dam). This transformation modulates the supply of other resources, particularly water, but also sediments, nutrients etc. A critical characteristic of ecosystem engineering is that it must change the availability (quality, quantity, distribution) of resources utilised by other taxa, excluding the biomass provided directly by the population of allogenic engineers. Engineering is not the direct provision of resources in the form of meat, fruits, leaves, or corpses. Beaver are not the direct providers of water, in the way that prey are a direct resource for predators, or leaves are food for caterpillars.

Now consider the autogenic equivalents of beaver (Fig. 1, case 3). Simple examples are the growth of a forest or a coral reef. Trees and corals are direct sources of food and living space for numerous organisms, but the production of branches, leaves or living coral tissue does not constitute engineering. Rather, it conforms to case 1 in Fig. 1 (the direct provision of resources). However, the development of the forest or the reef results in physical structures which do change the environment and modulate the distribution and abundance of other resources.

Table 1. Examples of organisms acting as ecosystem engineers. Classification according to Fig. 1. Additional examples are discussed in the text.

Organism	Habitat	Activity	Impact	Refs.
Case 2 (allogenic)				
American alligators, <i>Alligator mississippiensis</i>	Everglades National Park	create wallows	retain water in droughts; provide refuges for fish, fish-eating birds, etc.	Finlayson & Moser (1991)
Rabbits, <i>Oryctolagus cuniculus</i> , badgers, <i>Meles meles</i>	Europe	dig extensive burrows (rabbit warrens, badger setts)	burrows occupied by other species, e.g. fox, <i>Vulpes vulpes</i> , and by many invertebrates	Southern (1964); Neal & Roper (1991)
Case 3 (autogenic)				
Marine phytoplankton	Gulf of Maine	blooms of phytoplankton particles scatter and absorb light in upper layers of water column	enhance warming of surface waters that may initiate development of thermocline	Townsend et al. (1992)
Microalgae in sea ice	Antarctica	scatter and absorb light within ice and underlying seawater; reduce strength of ice	enhance melting and break up of ice	Buynitskiy (1986); Arrigo et al. (1991)
Freshwater phytoplankton	Lake St. George, Ontario	intercept light in upper water column; small algal spp. more effective than large spp.	light interception leads to shallower mixing depth, lower metalimnetic temperatures and lower heat content of water column	Mazumder et al. (1990)
Cyanobacteria and other nonvascular plants	desert and semi-desert soils	exude mucilaginous organic compounds	glue the organisms, organic matter and soil particles together to form a microphytic crust; change infiltration, percolation, retention and evaporation of water; reduce soil erosion; affect seedling emergence	West (1990)
Bog moss, <i>Sphagnum</i> spp.	Northern and western Britain	build 'blanket' and 'raised' bogs via accumulated peat	major changes in hydrology, pH, and topography	Tansley (1949)
Submerged macrophytes	freshwater lakes, ponds and rivers	grow to create weed beds	attenuate light; steepen vertical temperature gradient; retard flow; enhance sedimentation; oxygenate rhizosphere	Carpenter & Lodge (1986)
Forest trees (broad-leaved and coniferous)	Hubbard Brook Experimental Forest, New Hampshire	shed branches and trunks into streams	create debris dams; alter morphology and stability of stream channels, storage and transport of dissolved organic matter and sediments; different tree species may create dams which differ in persistence	Likens & Bilby (1982); Hedin et al. (1988)
Higher plants	ubiquitous	dead leaves etc. accumulate as litter	alter microenvironment of soil; change surface structure, affecting drainage, and transfer of heat and gasses; act as physical barrier for seeds and seedlings; numerous impacts on structure and composition of plant communities	Facelli & Pickett (1991)
Terrestrial plants in 29 families, with >1,500 species	ubiquitous	grow structures (modified leaves, leaf axils etc.) that impound water	create small aquatic habitats, supporting a highly specialised insect fauna	Fish (1983)
Case 4 (allogenic)				
Marine meiofauna (protozoa and representatives of many invertebrate phyla)	ubiquitous	biodeposition, bioturbation, porewater circulation, and faecal pellet production	change physical, chemical and biological properties of sediments; change direction and magnitude of nutrient fluxes; increase oxygenation of sediments	Reichelt (1991)
Marine burrowing macrofauna	ubiquitous	burrow into and redistribute sediments; bioturbation; burrow ventilation	create dynamic sediment mosaics; actively transport solutes into burrows; increase oxygenation of sediments; stimulate microflora; increase decomposition rates	Anderson & Kristensen (1991); de Wilde (1991); Meadows & Meadows (1991b)

(cont.)

Tab. 1. (cont.)

Organism	Habitat	Activity	Impact	Refs.
Marine zooplankton	ubiquitous	filter living, dead organic and inorganic (e.g. clay) particles, and concentrate into faecal pellets	sinking faecal pellets important in vertical transport and exchange of elements and organic compounds in oceans	Dunbar & Berger (1981); Wallace et al. (1981); Fowler & Knauer (1986)
Fiddler crab, <i>Uca pugnax</i>	New England salt marsh	dig burrows	increase soil drainage and oxidation-reduction potential; increase decomposition rates; increase primary production at intermediate tidal heights	Bertness (1985)
European periwinkle, <i>Littorina littorea</i>	New England rocky beach	bulldoze sediments from hard substrates	prevent sediment accumulation and hence growth and establishment of algal canopy; algae are case 3 engineers and further increase sedimentation rates; faunal composition markedly different with and without snails	Bertness (1984a)
Snails, <i>Euchondrus</i> spp.	Negev desert	eat endolithic lichens and the rock they grow in	increase rate of nitrogen cycling, soil formation and rock erosion	Shachak et al. (1987); Jones & Shachak (1990)
Bagworm caterpillars, <i>?Penestoglossa</i> sp.	Golden Gate Highlands, South Africa	eat endolithic lichens and construct larval shelters ('bags') from quartz crystals	small increase in erosion rate, nutrient cycling and soil formation	Wessels & Wessels (1991)
Mound-building termites, Isoptera	widespread in tropics and subtropics	mound and subterranean gallery construction; redistribution of soil particles	change mineral and organic composition of soils; alter hydrology and drainage	Wood & Sands (1978); Lal (1991)
Ants, Formicidae	ubiquitous	nest and subterranean gallery construction; redistribution of soil particles	change local structure and composition of soils; alter 'above nest' vegetation; produce microsite enrichment	Elmes (1991)
Earthworms, Lumbricidae, Megascolecidae	ubiquitous	burrowing, mixing and casting	change mineral and organic composition of soils; affect nutrient cycling; alter hydrology and drainage; affect plant population dynamics and community composition	Lal (1991); Thompson et al. (1993)
Blind mole rats, <i>Spalax ehrenbergi</i>	Israel	digging and tunnelling	move large quantities of soil; increase aeration; create distinctive ecosystem	Heth (1991)
Mole rats, Bathyergidae (several genera)	South African lowland fynbos	digging and tunnelling	create impressive, cratered landscapes, with effects on soil formation, plant productivity and species composition	Richardson et al. (in press)
Prairie dogs, <i>Cynomys</i> spp.	North American short and mixed grass prairie	continual intense disruption by burrowing, creating soil mounds	change physical and chemical properties of soil persisting for 100–1000s of years	Whicker & Detling (1988)
Pocket gophers, <i>Geomys bursarius</i>	North American grasslands and arid shrublands	construct tunnels and move soil to surface mounds	alter patterns and rates of soil development, nutrient availability and microtopography; change plant demography, diversity and primary productivity; affect behaviour and abundance of other herbivores	Huntly & Inouye (1988); Moloney et al. (1992)
Indian crested porcupine, <i>Hystrix indica</i>	Negev desert	digging for food	dig up to 2–3 holes m ⁻² ; diggings accumulate organic matter, runoff water; create favourable sites for seed germination	Yair & Rutin (1981); Gutterman (1982)
Elephants, <i>Loxodonta africana</i>	East African woodland and savannah	physical disturbance and destruction of trees and shrubs	widespread vegetation changes; alteration of fire regime; effects on food supply and population dynamics of other animals; ultimately changes in soil formation, riparian zones, and biogeochemical cycling	Naiman (1988)

(cont.)

Tab. 1. (cont.)

Organism	Habitat	Activity	Impact	Refs.
Case 5 (autogenic) and case 6 (allogenic) (examples combining elements of both)				
Crustose coralline algae, <i>Porolithon</i> , <i>Lithophyllum</i>	coral reefs	overgrow and cement together detritus on outer algal ridge of barrier reef	break force of water and protect corals against major wave action; effect via own bodies (case 5) and secretion of 'cement' (case 6)	Anderson (1992)
Ribbed mussels, <i>Geukensia demissa</i>	Rhode Island <i>Spartina</i> salt marsh	secrete byssal threads, and form dense mussel beds	on marsh edge, dense beds of mussels (case 5) and byssal threads (case 6) bind and protect sediments and prevent physical erosion and disturbance, e.g. by storms	Bertness (1984b)

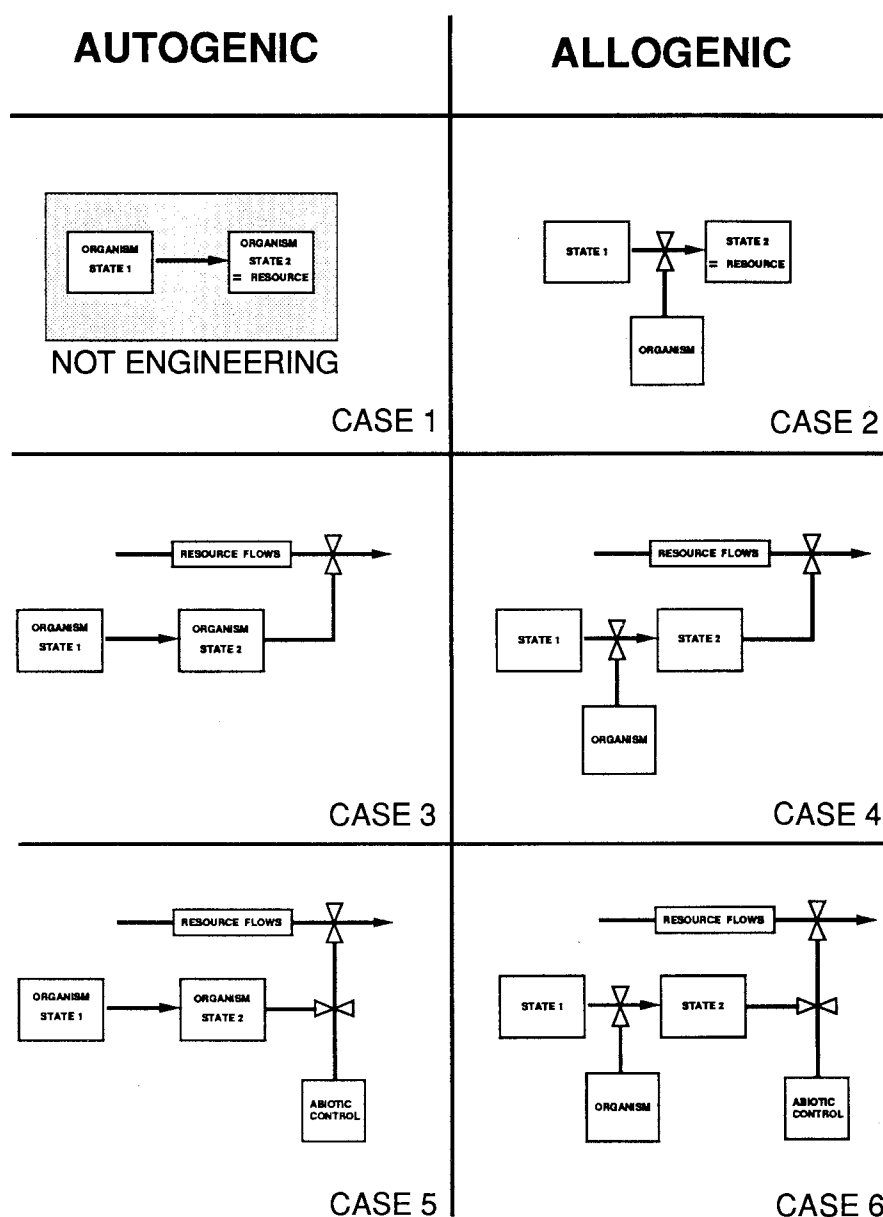


Fig. 1. Conceptual models of autogenic and allogenic engineering by organisms. For definitions and examples see text and Table 1. The symbol $\times$ defines points of modulation. For example, allogenic engineers transform living or non-living materials from state 1 (raw materials) to state 2 (engineered objects and materials), via mechanical or other means. The equivalent (state 2) products of autogenic engineering are the living and dead tissues of the engineer. These products of both autogenic and allogenic engineering then modulate the flow of one or more resources to other species (cases 2–4) or modulate a major abiotic controller (e.g. fire), which in turn modulates resource flows (cases 5–6). Case 1, the direct provision of resources by one species to another is not engineering, and involves no modulation of resource flows.

This modulation constitutes autogenic engineering. Trees alter hydrology, nutrient cycles and soil stability, as well as humidity, temperature, windspeed and light levels (see Holling 1992); corals modulate current speeds, siltation rates and so on. It is obvious, but surprisingly rarely explicitly stated, that numerous inhabitants of the habitats so created are dependent upon the physical conditions modulated by the autogenic engineers, and upon resource flows which they influence but do not directly provide; without the engineers, most of these other organisms would disappear.

One further example may help to clarify the distinction between case 1 and case 3. The growth of seagrass beds modulates ocean currents, which in turn may alter sedimentation rates and hence food supplies for other organisms with substantial effects upon their performance (e.g. growth and survival in the clam *Mercenaria mercenaria* (Irlandi and Peterson 1991)). The direct provision of food or living space by seagrasses (case 1) is not critical for *Mercenaria* but the clam's survival is nonetheless dependent upon these plants.

It could be argued that the growth of tree-trunks, branches, reefs or similar substantial biological structures (case 1, Fig. 1) itself constitutes ecosystem engineering. Inclusion or exclusion is a matter of choice. We have chosen to exclude it (whether it is the provision of food or of 'architecture' (Southwood et al. 1979 and Lawton 1983)) when the structures are considered solely and directly as resources, because this differs in kind from the remaining cases in Fig. 1. To qualify for our definition of an ecosystem engineer, an organism must modulate the supply of other resources for other species, rather than be the direct provider of resources. The growth of biological structures is thus a necessary but not a sufficient requirement for autogenic engineering.

We can illustrate our arguments further by considering the simplest kind of allogenic engineering (case 2, Fig. 1). Various organisms make holes in tree trunks and branches, some quickly (woodpeckers), others more slowly (rot fungi). They transform wood without holes into wood with holes, and indirectly provide resources for other creatures, nesting and roosting cavities for birds and bats for instance. The holes are the resource, not the organisms that make them. Notice that if some of the holes fill up with water (Kitching 1983), the little ponds so created are examples of case 4, and are conceptually identical to beaver dams.

Inevitably there are some grey areas in this classification and at the risk of being pedantic it is worthwhile considering just one. The natural hollows and cavities formed at branch junctions and root bases as the tree grows, and which may subsequently fill up with water ('pans' sensu Kitching (1983)) are not the same as rot- or woodpecker-holes and they do not belong in case 4; rather they conform to case 3 (trees are now autogenic engineers because their biomass gives rise to water-filled hollows). Numerous examples of these 'phytotelmata' are summarised by Fish (1983) (Table 1).

It is not universally the case that plants are allogenic and animals are autogenic engineers. Enhanced rates of physical and chemical weathering of rocks into soil by algae or higher plants (Bloom 1978) constitute allogenic engineering (case 4). Plants may act either as autogenic or as allogenic engineers, and provide some of the most complex cases of ecosystem engineering, to which we now turn.

Autogenic (case 5) and allogenic (case 6) engineering are at the extremes of continua that merge with cases 3 and 4 respectively. Cases 5 and 6 have the common property that autogenic or allogenic engineers interact with, and modulate powerful abiotic forces, for instance fires or hurricanes. Examples in cases 5 and 6 are distinguished from cases 3 and 4 by the extreme magnitude of the processes modulated by the engineers, and by the fact that these major abiotic forces are themselves fundamental modulators of the distribution and abundance of resources.

Fire provides a particularly interesting case. It is logical, albeit unconventional, to regard the production of combustible living and dead biomass as autogenic engineering (case 5). Different species of plants produce different qualities and quantities of living and dead fuel, modulating the magnitude, intensity and duration of fire and, in turn, profoundly altering the supply of resources for many other species (Christensen 1985). High grassland productivity in Serengeti-Mara in the 1960s markedly increased the incidence of fire, resulting in conversion of savannah woodland to an alternative state – grassland – which is now maintained by elephants (Dublin et al. 1990). The effects of elephants as allogenic engineers are summarised in Table 1.

Plants also act as allogenic engineers (case 6). In Puerto Rico *Dacryodes excelsa* trees are able to withstand hurricanes because their extensive roots and root grafts bind and stabilise bedrock and superficial rocks; this species therefore dominates tropical mountain forests where hurricanes are common (Basnet et al. 1992).

Difficult cases: Pollinators, gall formers and cows

The richness of biological processes means that a completely satisfactory, comprehensive yet exclusive definition of ecosystem engineering may be impossible to achieve, although numerous examples are easy to classify (Table 1). Given the diversity of species interactions in nature, efforts to classify many other ecological phenomena suffer similar problems 'at the margin'.

Pollinators and gall-formers present an interesting challenge for our definition of engineering. Both have profound effects on the growth of plant tissue; in so doing, pollinators modulate the supply of resources for seed predators, and gall-formers create structures that are used not only by themselves for shelter and food, but also by inquilines (e.g. Askew 1975). Both types of interaction conform broadly to case 2 (Fig. 1). However, we do not find it helpful to regard pollinators as engineers, not least since self-pollination is case 1 and not engineering.

But it is possible to regard gall-formers as engineers for inquilines; they physically modify plant-tissues, and create new habitats and resources for other organisms. The distinction between pollinators and gall-formers is, however, a fine one.

Our definition of engineering also embraces other, unexpected ecological phenomena, for example dung masses produced by large herbivores. Cows turn grass into cow pats, which are then colonised by a rich community of invertebrates, dependent upon the pats for food and shelter (Mohr 1943). The physical structure and environment provided by the droppings is at least as important to its inhabitants as the concentration of food resources (Elton 1966). It does not stretch the definition of engineering too far to regard cows as allogenic engineers, turning grass into cow pats (case 2). We would be the first to admit, however, that it is an unconventional perspective. Similar remarks apply to faecal pellet production by oceanic zooplankton (Table 1). For these and other borderline cases, the common sense way to view the issue is to ask whether understanding the ecological interactions is enhanced by recognising the engineering dimension.

Human analogues

The parallels between ecological and human engineers are, not surprisingly, very close. Humans are tool-using organisms that specialise in engineering. While human engineering often has intent or purpose, it is probably true to say that the major reason why humans have such adverse effects on the environment is because of the unintended consequences of our activities as engineers. Indeed people are now the primary agents of environmental change in most areas of the world (Naiman 1988, Likens 1992). Many human activities, from dam-building and skyscraper construction to forest clearance and the dredging and canalization of water courses, conform exactly to cases in Fig. 1, in which humans are allogenic engineers, altering the physical environment and modulating the flow of resources to other species.

Construction of nesting boxes for birds and hives for bees are examples of case 2. Ploughing by farmers and the construction of dams and reservoirs by water engineers provide examples of case 4. Building harbours and sea walls to reduce storm damage from waves are examples of case 6. Humans mimic autogenic effects, using tools to construct glasshouses and build air conditioning plants (mimicking case 3), and by bulldozing fire breaks to counteract fire (mimicking case 5). We classify human engineering activities as heavy or light, construction, civil, heating, plumbing, and air-conditioning to name but a few. Organisms do all these jobs, and from a functional perspective we see no fundamental difference between human and non-human engineering.

Related concepts

The idea that some organisms alter the physical structure of their environment, with impacts on their own and other populations is not new. But earlier work either focuses on particular species and habitats and lacks generality, or takes a more general view but fails clearly to define ecological engineering, or to distinguish it from other processes. For example, in an important set of reviews dealing with animal influences on ecosystem dynamics, co-ordinated by Naiman (1988), engineering and direct trophic effects are interwoven. Within this series of papers, Huntly and Inouye (1988) explicitly describe pocket gophers *Geomys bursarius* as “soil engineers” because of their role as earth-movers. Gophers are, indeed, excellent examples of allogenic (case 4) engineers (Table 1).

Ecologists in general have paid surprisingly little attention to how environments are created and maintained; most appear content to follow Andrewartha and Birch (1954) in recognising “a place to live” and “weather” as two of the four essential features of species’ environments, without formally considering the role of engineering in habitat modification, creation and maintenance.

Bioturbators

In marine benthic environments the activities of large burrowing animals are known to play a dominant role in determining the physical structure of sediments, altering habitat suitability for other species (Rhoads and Young 1970, Thayer 1979, Lopez and Levinton 1987, Meadows and Meadows 1991a, see also Table 1). Rhoads and Young (1970) called the process ‘trophic amensalism’ when large deposit feeders create unstable sediments, restricting the presence of suspension feeders and attachment by sessile epifauna. The term amensalism is reasonable, because the effect is asymmetrical and is a form of competitive exclusion (Lawton and Hassell 1981), but the mechanism is not trophic and clearly differs from normal exploitation competition for food. ‘Trophic amensalism’ is actually another good example of case 4 allogenic engineering brought about by bioturbation of sediments.

Patch dynamics

Numerous studies recognise the importance of patches of bare or different substrates in otherwise closed communities (e.g. Dayton 1971, Wiens 1976, Paine 1979, Pickett and White 1985). Patches may be created by physical disturbance (waves, fire, landslips) or by the activities of organisms (grazing, predation or engineering), or by interactions between engineering, trophic and physical processes. For some applications of patch dynamic theory the way in which patches are created may be less important than their existence. In general, however, we believe that it is desirable to recognise engineering as one of several distinct ways in which patches are created and maintained, particularly since the factors that control patch formation by engineers are often different from those controlling patch formation by abiotic forces.

Animal and plant artifacts

In their *Theory of Environment* Andrewartha and Birch (1984) define a framework for examining all the processes that impinge upon a single species population. This target species occupies the centrum of a web of directly and indirectly acting components, and Andrewartha and Birch point out that a link in the web may be another living organism or its artifact or residue. The Theory of Environment therefore clearly allows for engineering, without explicitly identifying it as a defined modifier in the web, or as a process worthy of study in its own right.

Meadows and Meadows (1991a) and Meadows (1991) review the environmental impacts of animal burrows and burrowing animals, and Hansell (1993) the ecological consequences of animal burrows and nests. Many of these artifacts (e.g. meiofaunal burrows, megapode nests, termite mounds and mole rat colonies) have landscape level effects, and serve to concentrate and redistribute resources for other species – that is they are classic examples of ecological engineering (Table 1).

Meadows (1991) points out that there are “underlying similarities between the impact of [burrowing] animals from different terrestrial and aquatic habitats on environmental change and modification.” He provides a formal system to quantify the impacts of burrowing, distinguishing between animals with large per capita but geographically restricted effects (e.g. badgers) and those species with small per capita effects that nevertheless, because of their abundance and distribution, have impacts on entire landscapes (e.g. earthworms). Hansell (1993) recognises that the “services and substances of the builders create a new range of habitat niches which can be exploited by a wide variety of specialists” and suggests that “the presence of nest builders and burrowers can ... significantly contribute to species diversity in habitats.” The examples provided by both authors all conform to either case 2 (other species use the nests and burrows) or case 4 (species respond to changes in distribution and abundance of resources). Their work therefore differs from ours only in its more restricted focus.

Extended phenotypes

The importance of animal artifacts is also recognised by Dawkins (1982), as an example of species' extended phenotypes. Dawkins writes (p.200): “A beaver dam is built close to the lodge, but the effect of the dam may be to flood an area thousands of square meters in extent. As to the advantage of the pond from the beaver's point of view, the best guess seems to be that it increases the distance the beaver can travel by water, which is safer than travelling by land, and easier for transporting wood. ... If this interpretation is right the lake may be regarded as a huge extended phenotype.” Dawkins recognises other products of animal engineering as extensions of species' phenotypes and hence subject to natural selection, including caddis-fly cases, termite mounds and birds' nests.

He also points out that not every example of what we are now calling allogenic engineering can be regarded as an extended phenotype, because impacts on the environment are of no consequence to the engineer's fitness and hence are not subject to natural selection. A good example would be water-filled footprints made by an ungulate. The distinction between engineering that is subject to natural selection (because it is an extended phenotype) and engineering that is not ('accidental' engineering) appears to be unimportant in terms of its shorter-term ecological consequences; all types of engineering modify and modulate resource flows for other organisms. But there may be interesting longer-term differences, particularly in the nature of the feed-back loops that operate on 'extended phenotype' versus 'accidental' forms of engineered artifacts. We return to this point later.

Keystone species

Keystone species (Paine 1969, Krebs 1985, Daily et al. 1993) play a critical role in determining community structure. By definition, removal of keystone species causes massive changes in species composition and other ecosystem attributes. The critical links are usually regarded as trophic and therefore within the realm of traditional ecological thinking. For example, removing top predators has a cascading effect throughout the foodweb, altering species composition and hence physical structure and nutrient cycling at lower levels (Estes and Palmisano 1974, Carpenter et al. 1987).

But critical effects frequently involve engineering, for example via disturbance (e.g. bioturbators (Thayer (1979), above; case 4). In the frequently cited example of sea-otters *Enhydra lutris*, removal of otters leads to an increase in sea urchins (*Strongylocentrotus* sp.) and hence to the disappearance of kelp beds, which in turn changes wave action and siltation rates, with profound consequences for other inshore flora and fauna (Estes and Palmisano 1974). Kelp are autogenic engineers (case 3); removal of kelp by urchins is, amongst other things, allogenic engineering (case 4). In other words, in this familiar example, the species traditionally regarded as the keystone (sea otter) has major effects because it changes the impact of one engineer (urchin) on another (kelp), with knock-on effects on other species in the web of interactions. The equally well known impact of kangaroo rats (*Dipodomys* spp.) on desert vegetation occurs because the rodents not only eat seeds but also cause considerable physical disturbance. By burrowing and moving large quantities of soil they create many shallow pits and little mounds, which facilitate decomposition and the establishment of annual plants (case 4 engineering) (Brown and Heske 1990).

Direct effects of keystone species via their role as engineers have recently been reported by Daily et al. (1993). Red-naped sapsuckers *Sphyrapicus nuchalis* (a type of woodpecker) act as keystone species in two ways in Colorado subalpine meadows. Their nesting holes

drilled in aspens, *Populus tremuloides*, are essential nesting sites for two species of swallows (case 2); the swallows are missing from the community in the absence of sapsuckers. Feeding holes drilled by the sapsuckers in willows, *Salix* spp., also make sap flows available to several birds, mammals and insects (directly changing the distribution and abundance of this resource for other species – and therefore again conforming to case 2).

It is theoretically possible (though we think it will be uncommon in practice) for a keystone species to exert its effects entirely trophically, without also acting as an engineer, or without changing the engineering role of other species in the web. On the other hand, many engineers are keystone species even though they play relatively minor roles in community food webs.

Krebs concludes his textbook review of keystone species as follows: “Keystone species may be relatively rare in natural communities, *or they may be common but not recognised* (our emphasis). At present, few terrestrial communities are believed to be organised by keystone species, but in aquatic communities keystone species may be common”. We believe that such views probably reflect a consensus among ecologists. They persist because we have failed to recognize the role of ecosystem engineers as keystone species. It is trite, but true, that a forest is a forest because it has trees, which not only provide food and living space but which also autogenically engineer the forest climate, and modulate the flows of many other resources to forest inhabitants, both above- and below-ground. Many single species of trees in temperate or boreal forests (with low tree-species richness) are both keystone species and significant ecosystem engineers.

Our views are very close to Holling’s (1992) *Extended Keystone Hypothesis*, in which he argues that “all terrestrial ecosystems are controlled and organised by a small set of key plant, animal, and abiotic processes that structure the landscape at different scales.” We would add two points. First a critical, but not exclusive controlling mechanism is some form of engineering; and second, we believe that keystone engineers occur in virtually all habitats on earth, not just terrestrial ones.

‘Top down’ vs ‘bottom up’, asymmetrical and indirect effects

Traditional population models focus on reciprocally coupled pairs of interactions, interspecific competition (-/-), enemy-victim (-/+) and so on (Williamson 1972). Highly asymmetrical competitive interactions (amensalism; 0/-) are common, possibly the norm, in some situations (Lawton and Hassell 1981). Enemy-victim interactions may also be asymmetrical (donor-controlled; 0/+), that is prey abundance controls predator abundance, but not vice versa (Lawton 1989, Hawkins 1992), with a growing debate in ecology about the relative importance of such ‘bottom up’ vs ‘top down’ effects (Hunter and Price

1992). Ecological engineering adds enormously to the catalogue of important, highly asymmetrical species interactions, because engineers impact upon many taxa (positively or negatively), but there may often be no direct, reciprocal effects of the impacted species upon the population of engineers.

One example will suffice. Beaver beneficially influence the abundances of aquatic biota, but not vice versa; that is they have massive ‘bottom up’ effects (0/+) that benefit numerous other aquatic organisms. Their activities are also detrimental to terrestrial species living upstream (and perhaps downstream) from the dam (0/-) just as bioturbators exclude sessile epifauna requiring stable substrates (see above). Generally we expect both the positive and negative effects of engineers to be highly asymmetrical.

This is not to say that there cannot be any feedbacks from organisms in the engineered habitat, back to the engineer. Undoubtedly there are, although feedback pathways are probably often rather long, indirect, and frequently slow. They remain virtually unstudied. For some engineers, it is difficult to imagine any reciprocal effects. For instance, the insect inhabitants of abandoned birds’ nests (e.g. some tineid moths in the genus *Monopis* and staphylinid beetles in the genus *Microglotta* (Walsh and Dobb 1954, Emmet 1979)) probably never encounter the builder. Gophers, in contrast, engineer soil and change vegetation composition, biomass and productivity (Table 1); in turn, grasshopper populations become more abundant in the vicinity of gopher mounds (Huntly and Inouye 1988). Two feedbacks may operate on gophers. The first is reasonably well documented, positive and relatively direct, via plants that are food for gophers; soil disturbance favours the plant species that gophers prefer to eat. Second, it is at least conceivable, but untested, (D. Tilman, pers. comm.) that grasshoppers compete with gophers for food, providing a longer, negative feed-back loop on gopher numbers.

We predict that if feed-backs exist at all between engineers and the organisms they affect, they will characteristically be indirect, involving several intermediate processes and species.

Spatial and temporal scales

The impact of an ecological engineer depends upon the spatial and temporal scale of its actions. Water filled woodpecker holes and beaver dams may both be examples of case 4 engineering, but there is not much doubt about which is the more significant ecological phenomenon. Six factors scale the impact of engineers. They are:

- (i) Life time per capita activity of individual organisms.
- (ii) Population density.
- (iii) The spatial distribution, both locally and regionally, of the population.

- (iv) The length of time the population has been present at a site.
- (v) The durability of constructs, artifacts and impacts in the absence of the original engineer.
- (vi) The number and types of resource flows that are modulated by the constructs and artifacts, and the number of other species dependent upon these flows.

Thus, the most obvious ecological engineering is attributable to species with large per capita effects, living at high densities, over large areas for a long time, giving rise to structures that persist for millennia and which affect many resource flows – for instance mima mounds created by fossorial rodents, including gophers (Cox and Gakahu 1985, 1986, Cox et al. 1987, Naiman 1988). Autogenic engineers may also have massive effects; as Holling (1992) succinctly states: “To a degree, ... the boreal forest ‘makes its own weather’ and the animals living therein are exposed to more moderate and slower variation in temperature and moisture than they would otherwise be.” Boreal forest trees have large per capita effects on hydrology and climatic regimes, occur at high densities over large areas, and live for decades. But their impacts as autogenic engineers may have a relatively short memory if the forest is logged.

Organisms with small individual impacts can also have huge ecological effects, providing that they occur at sufficiently high densities over large areas, for sufficient periods of time. Burrowing meiofauna and bogforming *Sphagnum* mosses (Table 1) are good examples. Accumulated *Sphagnum* peat may persist for hundreds to thousands of years after the death of the living moss.

Ecological engineers may also enhance and speed up large scale physical processes, including geological erosion and weathering (Yair and Rutin 1981, Krumbein and Dyer 1985, Hoskin et al. 1986). Examples of rock-eating snails and caterpillars are listed in Table 1. Worldwide, but especially in the tropics, heavily undercut coastal cliffs of sedimentary rock are apparently being eroded by tides and storms. In fact the process is greatly accelerated by two groups of engineers, both with low per capita effects, but very abundant. Cyanobacteria (*Hyella* spp.) bore the rock and are food for chitons which rasp away the rock to reach them, apparently speeding up coastal erosion by an order of magnitude or more (Krumbein and Dyer 1985). Similarly, organisms whose shells, body parts and dead tissues help form sedimentary rocks, coal and soil (e.g. molluscs, diatoms and many higher plants) create structures whose effects on ecosystems persist for eons.

Engineering impacts are often greatest when the resource flows that are modulated are utilised by many other species, or when the engineer modulates abiotic forces that affect many other species. Not surprisingly, engineering that affects soils, sediments, rocks, hydrology, fire and hurricanes provides some of the most striking examples.

We know of very few field manipulation experiments

designed to quantify the impact of ecosystem engineers by removing or adding species. Studies by Bertness (1984a,b, 1985) are excellent examples of manipulative experiments on both allogenic (cases 4 and 6) and autogenic (case 5) engineers (Table 1). A recent study by Hall et al. (1993) shows the potential power of field manipulations for disentangling per capita impacts from population impacts (although in the present context it is not ideal because predation and disturbance [case 4 engineering] effects are confounded). Edible crabs (*Cancer pagurus*) hunting for prey dig pits in shallow subtidal areas of the west coast of Scotland. The pits are conspicuous features of the seabed topography, yet exclusion of crabs from areas of the sea bed for twelve months failed to reveal any landscape-level effects of crab pits, either on substrate structure and composition (particle sizes, organic carbon etc.) or faunal diversity, composition and abundance. Crabs appear not to be abundant enough to significantly alter community structure, either by predation or by engineering, despite large and visually conspicuous individual impacts. This example contrasts markedly with the substantial effects of fiddler crabs (*Uca pugnax*) on productivity, decomposition, oxygenation and drainage in a New England salt marsh, revealed by experimental removal of crabs (Bertness 1985) (Table 1).

Another extremely poorly researched problem is the way in which the persistence of the products or effects of engineering influence population, community and ecosystem processes. If engineers make long-lived artifacts, then their effects will usually, also, be long lived. But ephemeral products can also have long-term impacts. For example, faecal pellets produced by marine zooplankton (Table 1) decompose relatively quickly, but not before they have sunk into the deep ocean, removing nutrients from surface waters for millennia.

A useful thought experiment is to consider taking the engineers away and imagining the consequences. In many cases their impacts are ephemeral, operating on timescales shorter than, or similar to, the lifetime of the organism itself (e.g. the nests of small passerine birds). But in other cases, the engineers leave monuments with impacts that extend many lifetimes beyond their own – mima mounds, termite nests, buffalo wallows, beaver dams, peat, sedimentary rocks and so on. These persistent effects must greatly slow down rates of ecological change, and impose considerable buffering and inertia on many ecological systems and processes. Rates of decay, the ‘half-lives’ of the products of ecological engineers, and their contributions to population, community and ecosystem stability, resistance and resilience (Pimm 1984) deserve much more attention from theoretical and experimental ecologists.

Evolutionary effects

Earlier, we distinguished between engineered artifacts subject to natural selection as extended phenotypes, and 'the rest' – by-products of some other activity that are not themselves directly subject to selection; water-filled ungulate hoof prints were given as an example. Extended phenotype engineering, by definition, creates structures or effects that directly influence individual fitness (or colony fitness in social insects), for instance a beaver dam, woodpecker hole or termite mound. But the evolutionary effects of extended phenotype engineering, other 'accidental' engineering, and of organisms in the engineered habitat upon the engineer are far from straightforward, and generally unstudied. For example, the extended phenotype may be subject to selection from the physical environment, implying no biotic feedbacks. Or it may be subject to selection from polyphagous predators (e.g. nest-robbing snakes) that are in no way dependent upon the engineered habitat for their existence. On the other hand, engineering might generate habitats with species populations that, ultimately, feed back positively or negatively upon the engineers, via predation, disease, competition, or the invasion of additional species of engineers.

Some engineering undoubtedly has had evolutionary effects on other organisms. One of the best documented examples in the fossil record is a decline, from the Devonian onwards, in the diversity of immobile suspension feeders living on soft marine substrata, as mobile taxa diversified (Thayer 1979). Thayer attributes these major changes in the structure of marine benthic communities to the evolution of 'biological bulldozers' – bioturbators or engineers – that disturb sediments (see above), fouling, overturning and burying immobile suspension feeders, which are now largely confined to hard substrates. Thayer also speculates that by increasing the turnover rate of nutrients in sediments of continental shelves, bulldozers may have contributed to the Mesozoic diversification of phytoplankton (coccoliths, diatoms and dinoflagellates) and, via trophic linkage, to diversification of zooplankton (radiolaria and foraminifera).

An intriguing, but rarely considered problem is the degree to which engineering by other taxa might similarly have changed major patterns in the radiation and extinction of earth's biota. To the extent that engineers shape and modify most, possibly all, habitats on earth (see below), and given the trite but true observation that all organisms are adapted to their environment, engineering in some form or other must have driven, or contributed to, the evolution of myriads of species. But the extent to which major patterns of evolution might have been different if some types of ecological engineering had not evolved, or had taken a different form, is almost entirely unknown.

Questions

We finish with a haphazard list of open questions.

Are there any ecosystems on earth that have not been physically engineered by one or more organisms to a significant degree? A cautious, preliminary answer is no, there are not. We initially thought that it would be difficult to identify evidence of ecosystem engineering by biota in the open waters of oceans or large lakes, or in snow fields and ice packs, for instance. But the examples in Table 1 show that this prediction was wrong. We currently cannot identify any habitat on earth that is not engineered in some way by one or more species.

How many species (or what proportion of species) in various communities have a clearly defined and measurable impact as engineers? Is it 10%, 1% or 0.1%? What are the relative frequencies of the five classes of engineering identified in Fig. 1, say in terms of the numbers of species acting as engineers? Cases 5 and 6 are presumably rather rare; but how much rarer are they than the others types of engineering? Is the predominance of examples involving burrowing animals in case 4 real (we could easily have included still more examples) or is it because this form of engineering is particularly easy to see?

Are the most physically structured ecosystems (or subsystems, e.g. soil or sediments) the ones in which engineers are most important? How much of the structure have they created and modified?

How many other species are impacted by engineers in any ecosystem? What happens to species richness if we remove or add engineers? How much of the effects of keystone species are due to engineering versus trophic effects? Earlier, we speculated that few keystone effects are purely trophic; is this hypothesis correct? How do engineering and trophic relations interact?

Should conservationists and nature reserve managers pay more attention to the role of ecological engineers in maintaining ecosystem integrity, or do managers largely know which the important species are, without having put a name to the idea, or without having recognising the common themes identified in this paper?

How should we model engineering? The biological details in each case will be complicated, and there are at least five kinds of engineering; but there are also several sorts of interspecific competition, various ways of being a herbivore and a rich catalogue of enemy-victim interactions, none of which has stopped theoreticians from developing appropriate families of relatively simple models to understand and to predict the dynamics of such interactions. There is, in principle, no reason why we cannot write down the equation:

$$d\text{mayfly}/d\text{beaver} = F(x, y, z),$$

where mayfly populations respond to changes in beaver numbers on long time-scales, and where the response is influenced by various key variables, including feedbacks

to beaver from other components in the engineered habitat. Interesting theoretical questions centre on the generation time of the engineer, the half-life of whatever it is that is engineered, the rate of restoration of non-engineered habitat, the generation times of impacted species, and their various interactions. There are intriguing problems of nested time-scales, delayed responses, donor-control, long chains of indirect interactions and so on, that might usefully be explored using relatively simple models.

Extending these arguments, there is no reason in principle why processes driven by engineering should not be coupled to the rich diversity of trophic linkages to create not simply descriptions and models of foodwebs (e.g. Pimm et al. 1991), but of *interaction webs*, that more accurately reflect interactions in communities and ecosystems. The conceptual framework brought together by Carpenter (1988) under the title of 'complex interactions' should clearly embrace engineering as one component.

Intriguingly, once the need to define and study interaction webs is recognised, it also becomes apparent that ecological engineering as we have defined it is only part of the picture. We have focused on physical state changes wrought on biotic and abiotic materials by organisms. But physical engineering is not the only form of ecosystem engineering that organisms carry out. Chemical and transport engineering are two obvious other forms that we consider will conceptually fit into the same general classification scheme. For brevity, we have not examined them here.

Last, but by no means least, what new insights will the concept of engineering bring to ecology? This review attempts to define and classify the phenomenon. But definition and classification are merely a small beginning, not an end. Are there major patterns in the distribution and abundance of organisms that might be explained, at least in part, by ecosystem engineering? What are they? What predictions might we make that would not have been made without the conceptual framework provided here, or something akin to it? We do not, currently, know the answers to these questions. But if the notion of organisms as ecosystem engineers results simply in an accumulation of 'just-so' stories, it will not have been particularly useful.

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The Keystone Role of Bison in North American Tallgrass Prairie

Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes

Alan K. Knapp, John M. Blair, John M. Briggs, Scott L. Collins, David C. Hartnett, Loretta C. Johnson, and E. Gene Towne

Throughout the history of Great Plains grasslands, North American bison (*Bos bison*, also known as *Bison bison*; Jones et al. 1992) and other large herbivores were abundant and conspicuous components of the biota (Wedel 1961, Stebbins 1981). Many of the earliest herbivores, particularly those that were primarily browsers, are now extinct, but their consumption of woody vegetation is thought to have played a critical role in the post-Pleistocene rise of the grassland biome and the subsequent increase in bison populations (Axelrod 1985, Hartnett et al. 1997). Indeed, the large herds of bison encountered by early Europeans on the Great Plains were likely the result of the rapid early-Holocene proliferation of this ungulate into a relatively young and expanding "treeless" grassland biome (Stebbins 1981, Axelrod 1985). In the most productive regions of the Great Plains, the eastern tallgrass prairies, abundant bison herds were noted by early explorers (Shaw and Lee 1997). Although herds were larger in the western shortgrass

Ungulate grazing activities and fire are key to conserving and restoring the biotic integrity of the remaining tracts of tallgrass prairie

steppe, some have speculated that a greater density of bison could be supported in eastern tallgrass prairies than elsewhere in the plains (McHugh 1972). It is unfortunate, then, that despite the historic abundance of bison in tallgrass prairies, their ecological effects in these mesic grasslands are poorly understood.

Knowledge of the bison's role in tallgrass prairies is lacking because the extent of this grassland and the abundance of its dominant ungulate have declined dramatically and in tandem over the last 150 years. Although there is debate over the numbers of bison inhabiting the Great Plains before the 1800s (estimates range from 30 million to 60 million; McHugh 1972, Flores 1991), it is well documented that from 1830 to 1880 the slaughter of bison in the Great Plains reduced their numbers to an estimated low of a few thousand individuals. Widespread cultivation of the plains, which accompanied the near extirpation of the bison, reduced the once-vast tallgrass prairie (approximately 68 million hectares) to less than 5% of its presettlement

range (Samson and Knopf 1994). The near-simultaneous reduction in herbivore abundance and grassland extent left little opportunity to assess bison-tallgrass prairie interactions.

Today, thanks to conservation efforts (Berger and Cunningham 1994), bison numbers in the Great Plains have rebounded (to approximately 150,000), and significant public and private herds are maintained in several mixed- and short-grass prairie preserves and ranches. It is from these semi-arid grasslands, many of which escaped cultivation, that the most extensive knowledge of bison-grassland interactions has been generated (Peden et al. 1974, Coppock et al. 1983). By contrast, the current understanding of tallgrass prairie structure and function has been developed almost exclusively from studies of ungrazed tracts or from sites grazed by domestic cattle (Risser et al. 1981, Collins 1987, Howe 1994, Leach and Givnish 1996). Only recently have bison been reintroduced to tallgrass prairie sites that are large enough to assess both their influence on other biota and ecosystem processes, as well as their interactions with other important features of these grasslands, particularly fire (Collins et al. 1998, Coppedge and Shaw 1998, Knapp et al. 1998b).

The Konza Prairie Research Natural Area in the Flint Hills of northeastern Kansas is the largest tract of unplowed tallgrass prairie (3500 ha) in North America dedicated to research (Knapp et al. 1998b). Konza Prairie was one of the original sites selected in 1981 for inclusion in the

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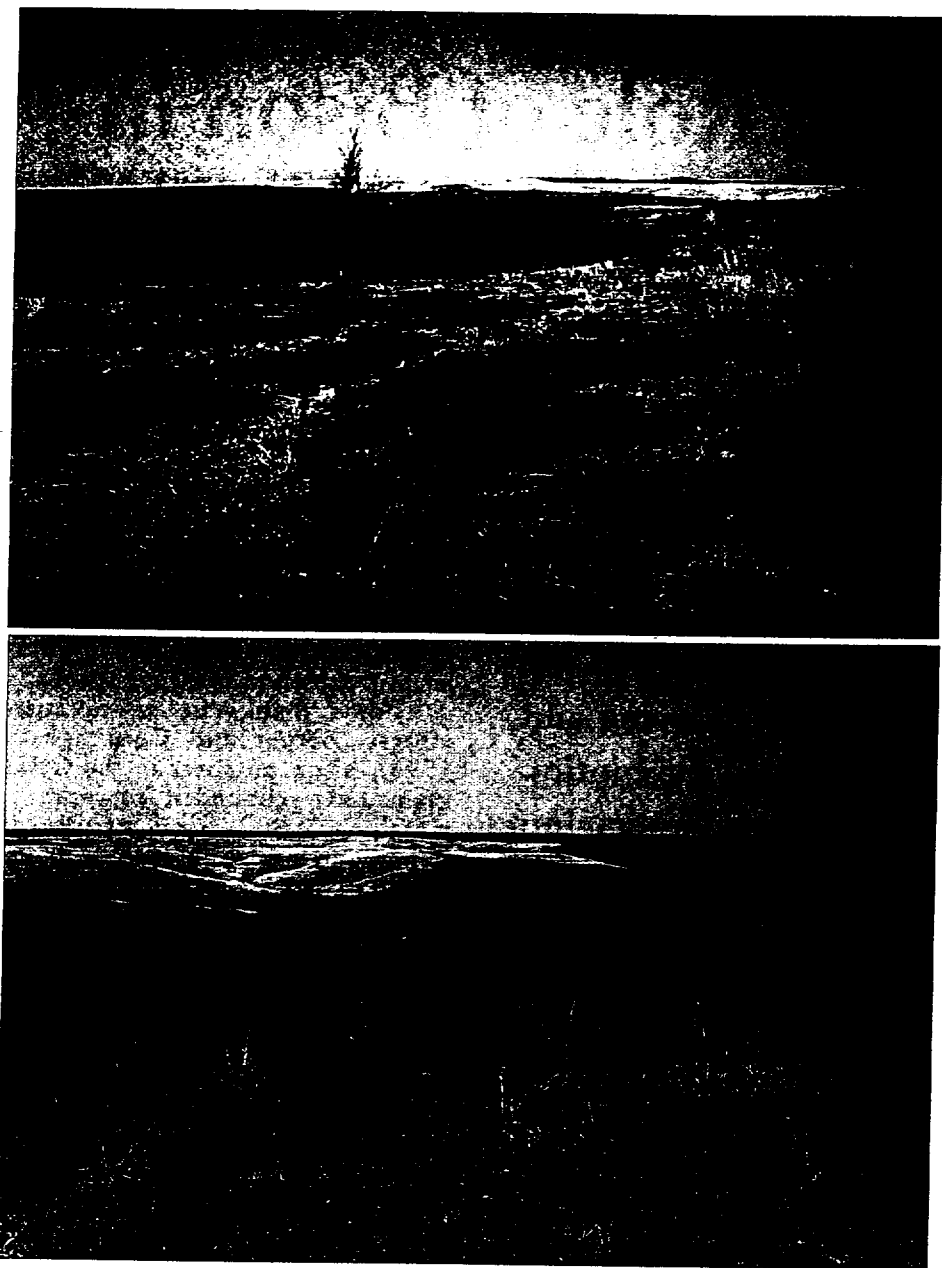


Figure 1. Grazing by bison increases spatial variability in tallgrass prairie. Immediately after fire (April) in grazed watersheds on the Konza Prairie, a native tallgrass prairie in northeastern Kansas, the uneven consumption of fuel by fire in grazed areas (upper photo) is caused by the patchiness of bison grazing the previous year. Dark areas indicate sites where bison did not graze or where grazing was light, and fuel loads were therefore sufficient to carry a fire through the patch. Lighter areas are patches that were grazed repeatedly by bison, such that fuel loads were reduced and the impact of fire was minimal. Later in the season, bison graze preferentially in recently burned watersheds (lower photo). In this late spring (May) view of a burned watershed, unburned watersheds can be seen in the background. Bison at Konza Prairie have access to 10 watersheds that differ in fire regime.

National Science Foundation's Long Term Ecological Research (LTER) program, and ongoing experimental treatments on some parts of the site date to 1972. Past syntheses of research at Konza Prairie have focused on the effects of fire and climatic

variability (Knapp and Seastedt 1986, Knapp et al. 1998b), but a majority of these data were collected in the absence of bison grazing.

In 1987, 30 bison were reintroduced to Konza Prairie, and the herd was allowed to increase until 1992.

Since that time, the herd has been maintained at approximately 200 individuals, who have had unrestricted access to a 1012 ha portion of the landscape. Within this area are 10 watersheds that are subjected to different frequencies of late-spring prescribed fire. The target animal density of 200 animals was selected so that approximately 25% of aboveground primary production is consumed annually. This consumption rate is approximately half that of tallgrass prairie managed for domestic cattle. The bison herd at Konza Prairie is not provided supplemental feed in winter, nor is it actively managed. Thus, this herd provides an opportunity to document the impact of bison on a native tallgrass prairie ecosystem.

Although research on bison-tallgrass prairie interactions began soon after bison were reintroduced to Konza Prairie, comprehensive studies spanning scales from the leaf to the landscape level began in the early 1990s. In this article, we provide the first synthesis of these research efforts, with the goal of highlighting the keystone role (sensu Power et al. 1996) that bison played in the tallgrass prairies of the past. Within this overview, we address two general questions: What are the direct and indirect effects of bison on patterns and processes in tallgrass prairie? What factors influence the spatial and temporal patterns of grazing activities by bison? Perhaps as important as addressing these questions, the data that we present indicate that large-ungulate herbivory can, and should, play a key role in the management and conservation of the remaining tracts of this once-widespread grassland.

Bison grazing activities and plant responses

Like all large herbivores, bison do not graze indiscriminately across the landscape or even within a local area (Senft et al. 1987, Wallace et al. 1995). Rather, they graze in two patterns in tallgrass prairie, creating both distinct grazing patches (typically 20–50 m² in Flint Hills tallgrass prairie; Catchpole 1996) and more extensive grazing lawns (larger than 400 m²; McNaughton 1984). In both

cases, bison revisit grazed sites throughout the season, such that repeated defoliation of grazed plants is the norm and relatively sharp boundaries between grazed and ungrazed vegetation become evident (Figure 1). Bison are primarily graminoid feeders and consume higher proportions of the dominant grasses than would be predicted based on grass availability in the landscape (Peden et al. 1974, Van Vuren and Bray 1983, Steuter et al. 1995). Bison tend to avoid forbs and woody species, which usually constitute less than 10% of their diet. Thus, within a bison grazing area, forbs are often conspicuously left ungrazed and are surrounded by grazed grasses (Fahnestock and Knapp 1993, Damhoureyeh and Hartnett 1997).

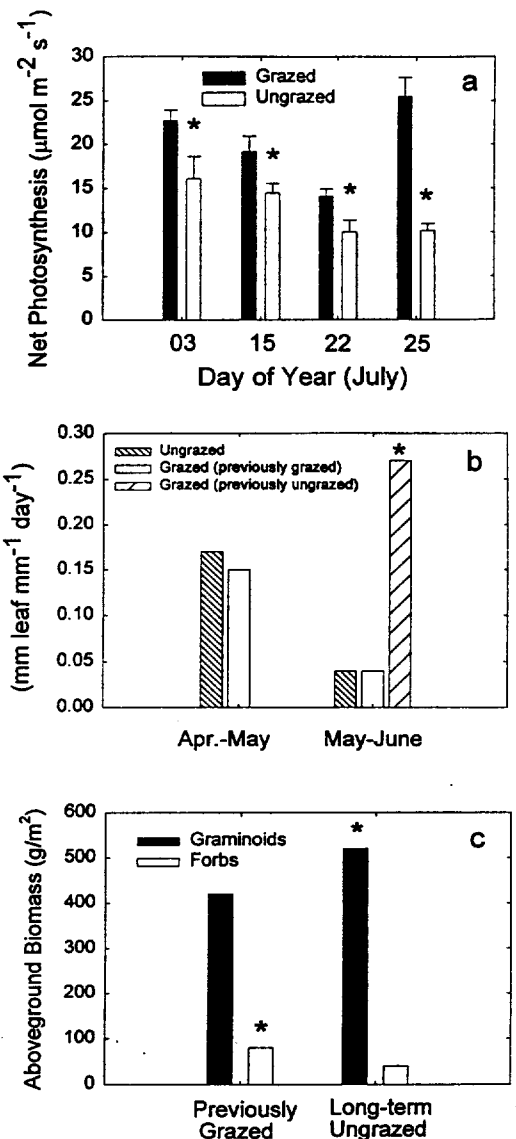
Preferential grazing of the dominant grasses by bison sets the stage for significant alterations in competitive interactions among the C_4 grasses and the C_3 forbs. Such shifts are important for plant community structure because in ungrazed and frequently burned prairie, a small group of grass species (*Andropogon gerardii*, big bluestem; *Sorghastrum nutans*, Indian grass; *Panicum virgatum*, switchgrass; and *Andropogon scoparium*, little bluestem) account for most biomass, density, leaf area, and resource consumption (Knapp 1985, Briggs and Knapp 1995). However, it is the species-rich forb component (more than 350 species are recorded on Konza Prairie; Freeman 1998) that is critical for the maintenance of high levels of biotic diversity in tallgrass prairie (Gibson and Hulbert 1987, Glenn and Collins 1990, Turner et al. 1995). Thus, by grazing on grasses and allowing forbs to flourish, bison have the potential to significantly influence biodiversity in these grasslands (Collins et al. 1998).

The short-term effects of bison herbivory on the most abundant prairie grass, *A. gerardii*, are different from the long-term effects. At the leaf level, short-term responses to leaf removal are typical of many graminoids in grazing systems (McNaughton 1983). Wallace (1990) reported a postgrazing enhancement of photosynthesis in *A. gerardii* in Oklahoma. Similarly, on Konza Prairie, midseason photosynthetic rates

Figure 2. Response of tallgrass prairie vegetation to bison herbivory at three temporal scales. (a) Instantaneous leaf-level photosynthetic responses of *Andropogon gerardii* to grazing (Erin Questad and Alan K. Knapp, unpublished data). (b) Relative growth rates of tillers of *A. gerardii* in sites that differ in grazing history (data from Vinton and Hartnett 1992). Both ungrazed tillers and grazed tillers with a history of grazing had similar growth rates, whereas grazed tillers without a history of grazing had significantly greater growth rates. (c) End-of-season aboveground biomass in ungrazed sites that differ in grazing history (data from Knapp et al. 1998a). Asterisks in panels (a) and (b) indicate significantly different values ($P < 0.05$) for comparisons at specific dates; in panel (c) they indicate comparisons within growth forms.

averaged 53% higher in grazed tillers (individual grass stems) than in ungrazed plants, with a maximum stimulation of 150% (Figure 2a). Mechanisms for this enhancement of photosynthesis include increased light availability and reduced water stress for all species in grazed patches (Fahnestock and Knapp 1993) and greater tissue nitrogen concentration in *A. gerardii* leaves as nitrogen is reallocated from roots.

These potential compensatory increases in photosynthesis after grazing may be augmented by the translocation of carbon reserves from belowground to aboveground tissues. Vinton and Hartnett (1992) found that in the first year of grazing, growth and biomass of grazed *A. gerardii* tillers had completely compensated for the loss to grazing by season's end. But after several years of grazing, the ability of tillers to compensate for lost tissue was reduced (Figure 2b). Vinton and Hartnett (1992) attributed these differences in short- and long-term responses to reductions in belowground carbon allocation and stored carbohydrate reserves after several years of grazing. Turner et al. (1993) also demonstrated the importance of



grazing history on productivity in tallgrass prairie by measuring aboveground primary production in a number of sites with different grazing histories. They found that compensatory regrowth of biomass occurred in sites with little history of grazing but not in sites that had been grazed heavily in previous years.

Some researchers have argued that the inability of tallgrass prairie grasses to compensate for the biomass lost in frequently grazed areas is evidence that prolonged, intensive bison grazing did not occur in these grasslands (Shaw and Lee 1997). If this hypothesis were true, then grass abundance would decline continually following repeated grazing. However, the tallgrass prairie's loss of production potential due to grazing is short lived. At Konza Prairie,

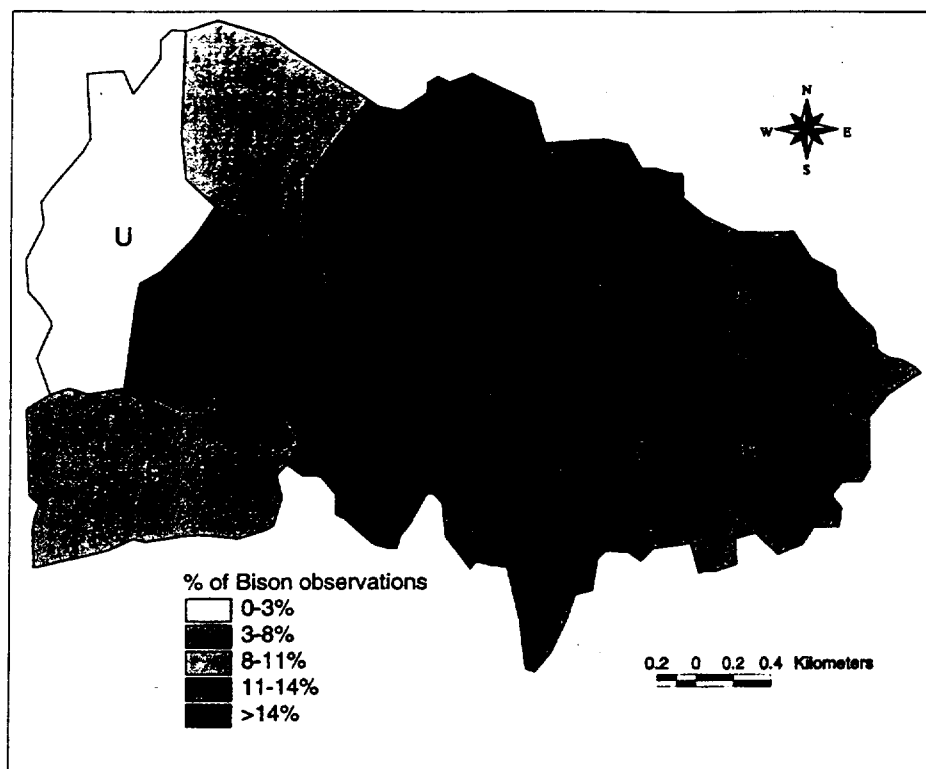


Figure 3. Spatial distribution of bison in 10 watersheds in the central portion of Konza Prairie after the completion of spring burning. During the months of April, May, and June 1992, bison locations were determined twice per week and recorded on large-scale, spatially rectified aerial photographs overlaid with a 30-meter grid. Bison were observed most frequently in the recently burned watersheds. B, burned watersheds; U, unburned watersheds.

permanent fenced exclosures have excluded bison from experimental plots within grazed watersheds for several years. When adjacent grazed sites were also protected from grazing with temporary exclosures, aboveground production in the first year in these newly protected sites was reduced relative to that in the adjoining long-term ungrazed areas (Figure 2c); however, these sites recovered their production potential by the second year. Thus, production potential can recover if bison grazing is sufficiently dynamic, either spatially or temporally, such that sites are grazed intermittently.

Removal of grass leaf area by bison, and reductions in the capability of the dominant grasses to compensate for tissue lost after multiple years of grazing, suggest that the co-occurring subdominant forbs may benefit from bison grazing. Indeed, comparisons of forbs inside grazing patches with those in adjacent ungrazed prairie have shown that gas exchange and aboveground biomass production, density, and cover

can be enhanced by the selective consumption of grasses by bison (Fahnestock and Knapp 1993, Hartnett et al. 1996, Damhoureyeh and Hartnett 1997). Given the importance of past grazing pressures to the direct responses of grasses to herbivory and the indirect responses of forbs, identifying those factors that influence the selection and reselection of grazing patches by bison in tallgrass prairie is critical for understanding the long-term consequences of bison grazing patterns.

Factors influencing bison selection of grazing sites

Historical information regarding bison grazing patterns in the Great Plains is replete with anecdotal accounts of herds attracted to recently burned grasslands (Figure 1; McHugh 1972, Pyne 1982), but quantitative evidence of this preference in tallgrass prairie has been lacking until recently (Coppedge and Shaw 1998). As noted earlier, bison at Konza Prairie have free access to

10 watersheds that are subject to different fire frequencies. Since 1991, twice-weekly observations of the distribution of bison within this area have been made to assess patterns of bison grazing (Nellis et al. 1992). The results confirm that bison do graze preferentially within burned watersheds from April (burning takes place in late March–early April) through June and July, and, in some years, through August (Figure 3; Vinton et al. 1993, Nellis and Briggs 1997). In addition to grazing preferentially in burned sites, bison increase their selective consumption of some grass species in burned sites relative to unburned sites (Pfeiffer and Hartnett 1995). Late in the summer, lowland topographic positions with deeper soils (and therefore greater soil moisture and plant productivity; Knapp et al. 1993) in burned watersheds become preferred grazing locations as the uplands dry. This preference for burned areas in tallgrass prairie is consistent with postfire responses in mixed grass prairie (Coppock and Detling 1986), as well as with large ungulates' winter preference for burned sites in the northern mixed grasslands of Yellowstone National Park (Pearson et al. 1995).

Within a watershed or at a specific topographic position in tallgrass prairie, several factors may influence initial patch selection and reselection (see also Wallace et al. 1995). In addition, patch selection has several long-term consequences. When bison were first reintroduced to Konza Prairie, they encountered a mosaic of burned and unburned watersheds, with significant differences among watersheds in the spatial heterogeneity of plant community composition. For example, frequently burned but ungrazed watersheds are dominated by C_4 grasses and have low species richness and diversity, whereas less frequently burned sites have higher species richness and forb cover (Gibson and Hulbert 1987, Collins 1992). Initial studies on Konza Prairie indicated clearly that bison established grazing patches in areas strongly dominated by C_4 grasses and that these patches were reselected at a high rate (Vinton et al. 1993). Six years later, a survey of floristic composition indicated that established bison grazing patches had

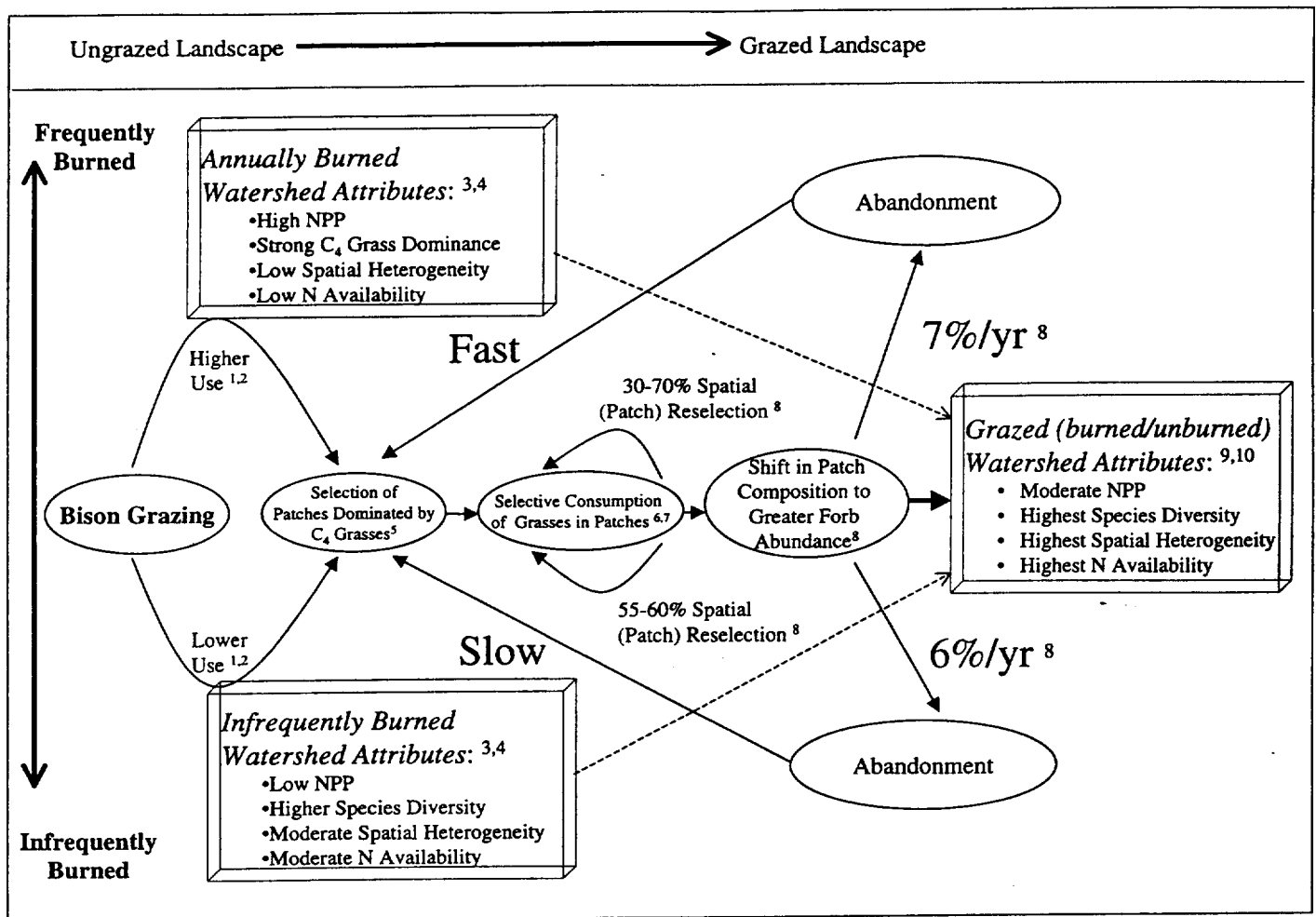


Figure 4. Conceptual model of the spatial and temporal dynamics of bison grazing activities and the responses of tallgrass prairie to the reintroduction of bison. Before the reintroduction of bison, watershed attributes at Konza Prairie differed strongly depending on the fire regime imposed, with frequently burned sites notable for their high productivity but low plant species diversity. Selective bison grazing at the watershed level (preference for burned sites, particularly in the spring) and the patch level (selection of patches dominated by C₄ grasses) has led to increased similarity in watershed attributes despite differences in fire history. Moreover, significant increases in plant species diversity and spatial heterogeneity have been noted in all watersheds. Superscripts denote studies on which this synthesis is based: 1, Nellis and Briggs (1997); 2, Vinton et al. (1993); 3, Briggs and Knapp (1995); 4, Collins (1992), Collins et al. (1995); 5, Vinton and Hartnett (1992), Vinton et al. (1993); 6, Hartnett et al. (1997); 7, Fahnestock and Knapp (1993, 1994); 8, Catchpole (1996); 9, Collins and Steinauer (1998); 10, Hartnett et al. (1996).

a higher abundance of forbs and a lower cover of grasses than adjacent ungrazed patches (Catchpole 1996). Similar small-scale patterns of forb and grass abundance were observed by comparing the floristic composition inside and outside grazing exclosures in grazed watersheds at Konza Prairie (Hartnett et al. 1996). These observations suggest that bison alter plant community composition at the patch scale by selecting species-poor, grass-dominated sites and converting them to sites of locally higher diversity (Figure 4).

A second factor that may influence patch selection and reselection by bison is plant quality. The foliar

nitrogen content of plants is highly variable, both spatially and temporally. Bison contribute to this patchiness through deposition of nitrogen-rich urine. Steinauer (1994) applied synthetic bovine urine at randomly selected locations along eight transects at Konza Prairie (four each in grazed and ungrazed areas). In ungrazed areas, grass cover was significantly higher in plots that were fertilized with urine than in plots without urine. But in the grazed area, by contrast, grass cover was significantly lower on the urine-treated plots than in plots without urine because bison preferentially grazed the grasses on the urine-treated plots.

Day and Detling (1990) have shown that grasses growing on urine patches in mixed-grass prairie have higher leaf nitrogen content, and are therefore more nutritious per bite, than grasses growing on patches without urine. Not only was grass cover lower on urine patches at Konza Prairie, but the total area of grazed patches on the urine-treated transects was significantly larger than the area of grazed patches on transects that were not treated with urine (Steinauer 1994). Thus, the enhanced productivity of grasses growing on urine patches represents a potential stimulus for the initiation and reselection of grazing patches by bison.

Given that bison prefer grazing patches that are initially dominated by C_4 grasses, but that their selective foraging and reselection habits convert these patches to sites with a greater abundance of nonforage species, it is likely that patch locations are spatially dynamic across the landscape. Patches can "move" by two mechanisms: patch abandonment, followed by selection of a new patch; or patch migration, wherein portions of a patch are abandoned and the patch expands into adjacent areas. Over a 3-year period, Catchpole (1996) found the rate of patch abandonment to be approximately 6–7% per year in both burned and unburned watersheds; thus, at least portions of previously established grazing patches were reselected at a high rate (Figure 4). However, when grazing patches were mapped and compared across years, the extent of spatial reselection—although highly variable due to differences in total burned area available to bison in any one year—averaged approximately 50% per year. Thus, grazing patches in both burned and unburned watersheds appear to migrate significantly from year to year. This local migration permits periodic release of portions of the grassland from grazing pressures (Figure 4) and provides a mechanism for recovery of below-ground carbohydrate storage reserves and production potential.

At the watershed and landscape scales, the long-term consequences of bison activities include a reduction in cover, dominance, and productivity of grasses; the competitive release of many subdominant species, resulting in an increase in the abundance of forbs; an overall increase in plant species richness and diversity; and increased spatial heterogeneity (Figure 5; Hartnett et al. 1996). Although alterations in plant community composition can be attributed, in large part, to the direct effects of grazing by bison, increased plant species richness is also likely to be a product of increased microsite diversity generated by nongrazing activities, such as dung and urine deposition, trampling, and wallowing. These and other bison activities contribute significantly to the increase in spatial heterogeneity that is characteristic of grazed tallgrass prairie (Figure 5).

Other impacts of bison in tallgrass prairie

Effects of ungulates, especially grazing, on plant community composition and structure have been studied in many grasslands worldwide (McNaughton 1984, Milchunas et al. 1988, Frank and McNaughton 1992, Milchunas and Lauenroth 1993). Ungulate activities, however, affect many other aspects of grassland structure and function, including the physical structure of the environment and the rates of a number of ecosystem-level processes (McNaughton 1993, Frank and Evans 1997, McNaughton et al. 1997). There are several other important mechanisms by which bison alter ecosystem-level processes and physical habitat structure in tallgrass prairie.

Nutrient redistribution and cycling. Bison can substantially alter nutrient cycling processes and patterns of nutrient availability in tallgrass prairie. Their effects on nitrogen cycling are critical because nitrogen availability often limits plant productivity in these grasslands (Seastedt et al. 1991, Blair 1997, Turner et al. 1997) and influences plant species composition (Gibson et al. 1993, Wedin and Tilman 1993). Simulation models of tallgrass prairie responses to grazing (Risser and Parton 1982) and studies of grazers in other grasslands (Frank and Evans 1997, McNaughton et al. 1997) have demonstrated a disproportionate influence of ungulates, including bison, on the regulation of nitrogen cycling processes. Preliminary data from Konza Prairie suggest that bison are similarly important in controlling nitrogen cycling in tallgrass prairie.

Bison influence nitrogen cycling, conservation, and availability in tallgrass prairie ecosystems by altering several soil and plant processes. Ungulates in grasslands consume relatively recalcitrant plant biomass and return labile forms of nitrogen (i.e., urine) to soils (Ruess and McNaughton 1988), thus bypassing the otherwise slow mineralization of nitrogen in plant litter. Nitrogen in bison urine is largely urea, which can be hydrolyzed to ammonium in a matter of days (Ruess and McNaughton 1988). Indeed, application of

synthetic bison urine increased concentrations of ammonium and nitrate in Konza Prairie soils over 130-fold and 30-fold, respectively, 8 days after application (J. R. Matchett and Loretta C. Johnson, unpublished data).

Bison grazing can decrease the export of nitrogen from tallgrass prairie by altering the magnitudes of two major pathways of nitrogen loss—combustion and ammonia volatilization. Fire is the major pathway of nitrogen loss from ungrazed tallgrass prairie (Dodds et al. 1996, Blair 1997); nitrogen loss from burning averages $1\text{--}4\text{ g}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Blair et al. 1998). Grazing lowers combustion losses of nitrogen in tallgrass prairie by reducing the aboveground plant detritus and increasing the patchiness of a prairie fire (Figure 2; Hobbs et al. 1991). Although volatilization of ammonia can be increased by grazing in other types of grassland (Detling 1988), Hobbs et al. (1991) suggested that any increase in ammonia volatilization in tallgrass prairie will be more than compensated for by a reduction in combustion losses of nitrogen.

Finally, bison grazing affects the amount and quality of plant litter returned to soils. Grazing increases plant uptake of nutrients (Ruess 1984) and shoot nitrogen content in many grasslands (Holland and Detling 1990, Milchunas et al. 1995), including tallgrass prairie (Turner et al. 1993). However, the effects of grazers on root growth and chemistry vary among grasslands (Milchunas and Lauenroth 1993). On Konza Prairie, root productivity and root biomass were 30% and 20% lower, respectively, in bison grazing lawns than in ungrazed exclosures. In addition, the nitrogen concentration of new root growth in bison grazing lawns at Konza Prairie increased significantly, from 0.6% to 0.9%, and the C:N ratio of roots decreased. A lower C:N ratio reduces microbial immobilization and enhances nitrogen availability within grazed areas. Indeed, recent studies on Konza Prairie indicated that net nitrogen mineralization in bison grazing lawns was 153% greater, and net nitrification 126% greater, than in ungrazed prairie (Figure 6). Furthermore, net nitrogen mineralization rates were proportional to the intensity of bison use of a given area. Thus, the

net effect of bison grazing appears to be increased rates of nitrogen cycling, coupled with a significant increase in spatial heterogeneity in nitrogen availability; together, these effects can alter patterns of plant productivity and species composition in tallgrass prairie (Figure 5; Steinauer and Collins 1995).

Wallowing. One aspect of bison behavior that differs from that of cattle, and is primarily a physical activity, is wallowing. Wallows in Flint Hills tallgrass prairie, which are established primarily in level upland or lowland sites, dramatically alter the patch structure of this prairie. Bison wallows develop as the animals paw the ground and roll in the exposed soil. Continued use of wallows by bulls, cows, and calves creates a soil depression of 3–5 m in diameter (and 10–30 cm in depth) that is devoid of vegetation. These denuded patches either gradually revegetate or remain as bare soil, depending on the frequency of revisitation by bison. With the vast numbers of bison that once occupied the Great Plains, these soil depressions were probably abundant and widespread features of the landscape (England and DeVos 1969). For example, a number of relic wallows had to be filled to level the playing field for the first University of Oklahoma home football game in 1895 (University of Oklahoma Athletic Department 1986). Relic wallows still exist in many areas where bison have not occurred in the past 125 years.

Environmental conditions in relic and newly established wallows strongly influence prairie patch dynamics (Polley and Collins 1984, Polley and Wallace 1986). Because of soil compaction, wallows often retain rainwater in the spring, creating localized habitats that are suitable for ephemeral wetland species, similar to vernal pools in California (Holland and Jain 1981, Uno 1989). In the summer, however, the same wallows support only plants that can tolerate severe drought. Vegetation composition and structure in wallows is different from that in the surrounding prairie (Polley and Collins 1984), and these differences are enhanced by fire (Collins and Uno 1983), which may not spread through wallows because of low fuel loads. Consequently, at larger spa-

tial scales, grazed prairie that contains bison wallows has higher plant species diversity than grazed prairie without wallows (Collins and Barber 1985). Thus, bison can physically alter grasslands in ways that increase environmental heterogeneity and enhance both local and regional biodiversity (Hartnett et al. 1997).

Bison carcasses. Bison not only affect vegetation patterns and soil processes through their grazing activities but also have profound and lasting localized effects after they die. Although legal requirements and management practices dictate the removal of carcasses of domestic herbivores from public and private grasslands, native herbivores routinely die of natural causes and their bodies remain in situ. As part of the minimal management strategy at Konza Prairie, bison that die on site are not removed. As a result, these carcasses create unique local disturbances (Figure 7) that are the focus of studies to assess their effects on soil nutrients and vegetation responses in tallgrass prairie.

When an individual bison dies, copious quantities of fluids (with high nitrogen concentration) are released during decomposition. Adult bison can weigh more than 800 kg, and these carcasses typically kill underlying and adjacent plants, creating a denuded zone of 4–6 m² (Figure 7). Although the fluids that are initially released are toxic to vegetation, these sites eventually become zones of high fertility. For example, soil cores extracted from the center of carcass sites on Konza Prairie 3 years after death had inorganic nitrogen concentrations that were two to three times higher than the surrounding prairie. This nutrient enrichment may extend up to 2.5 m away from the original carcass site and results in patches dominated initially by early successional species. The aboveground primary production in these patches is two to three times higher than in undisturbed prairie.

Although disturbances created by bison carcasses are sporadic and localized on Konza Prairie, they provide nutrient pulses that exceed all other natural processes, even urine and fecal deposits. Overall, we can only speculate about historical rates

of bison mortality. Given the enormous size of the bison population before their widespread slaughter in the 1800s, annual mortality was probably high. High death rates would have been especially common during droughts, when there would be the potential for large numbers of carcasses to occur across the landscape. Even though predators and scavengers may have consumed and relocated many of these carcasses, decomposition of the remaining and partial carcasses would still have resulted in patches of locally high nutrient concentration. Thus, although it was variable, bison mortality would have led to a continual cycle of disturbance and recovery of these patches in presettlement grasslands.

Are bison keystone species?

The net effects of selective bison grazing activities at the landscape, patch, and individual plant level include shifts in plant species composition, alterations of the physical and chemical environment, and increased spatial and temporal heterogeneity in vegetation structure, soil resource availability, and a variety of ecosystem processes (Figures 4, 5, and 6). Before bison reintroduction at Konza Prairie, the long-term burning experiments produced clear patterns of response in the vegetation. As fire frequency increased, the dominance of C₄ grasses increased, and the cover of C₃ grasses, forbs, and woody species decreased (Figure 4; Gibson and Hulbert 1987). Overall, plant species diversity declined as fire frequency increased in ungrazed tallgrass prairie (Collins et al. 1995).

These patterns in community structure, which had developed over 20 years of burning treatments at Konza Prairie, are being rapidly and dramatically altered by the grazing activity of the reintroduced bison. In particular, grazing by bison has lowered the abundance of the dominant C₄ grasses, increased the abundance of the subdominant C₃ grasses and forbs, and markedly increased plant species diversity (by 23%), richness (by 38%), and community heterogeneity (by 13%) relative to ungrazed sites, even under annual burning conditions (Hartnett et al. 1996, Collins and Steinauer 1998, Collins et al. 1998).

Because of the multiple and dramatic effects of bison on this landscape, we believe that bison are keystone species in the tallgrass prairie. Other authors have noted the potential of large grazing mammals to act as "keystone herbivores" capable of maintaining open grassland vegetation that would otherwise undergo succession to shrubland or woodland (Owen-Smith 1987). Indeed, the disappearance of a grazing megafauna at the end of the Pleistocene may have played a major role in the widespread transition from steppe to tundra at that time (Zimov et al. 1995). However, the concept of keystone species has been controversial since its inception (Power et al. 1996). One of the problems with this concept has been the variable interpretation of criteria by which species are determined to be keystone. Power et al. (1996) consider a keystone species to be "one whose impact on its community or ecosystem is large, and disproportionately large relative to its abundance." To make this definition operational, these authors proposed a measure of community importance (CI) to be used as an index of the strength of the impact of a given species:

$$CI = [(t_N - t_D)/t_N][1/p_i]$$

where t_N is a quantitative measure of a trait (e.g., diversity) in an intact community, t_D is the measure of the trait when species i has been deleted, and p_i is the proportional abundance (biomass) of species i before it was deleted. CI values "much greater than 1" indicate that a species is keystone. We estimate bison biomass at Konza Prairie to be approximately 11–12 g·m² (Collins and Steinauer 1998), which is approximately 1% of the total vegetative biomass. On Konza Prairie, diversity is significantly higher (10–33%) on grazed sites than ungrazed sites (Hartnett et al. 1996), and these values yield a range of CIs from 6 to 25. For this reason and others, we consider bison to be keystone species in tallgrass prairie ecosystems.

Are bison and cattle functional equivalents in tallgrass prairie?

The historical presence of immense herds of large ungulates in Great

Plains grasslands is undisputed (McHugh 1972), and we have emphasized the keystone role that bison played in determining the structure and function of tallgrass prairies at multiple spatial and temporal scales. With the replacement of native bison by domesticated cattle in the remaining grasslands, an obvious issue is the degree of similarity between these two ungulates with respect to their effects on tallgrass prairie. In other words, can bison and cattle be considered ecological equivalents?

There have been several previous attempts to answer this question, but the results have been equivocal at best (Plumb and Dodd 1993, Hartnett et al. 1997). The primary barrier to resolving this issue rests with a lack of comparative studies in which management is held constant and the type of grazer is varied. Such studies have recently been initiated at Konza Prairie. Results after 3 years indicate that the abundance and richness of annual forbs, and the spatial heterogeneity of biomass and cover, are higher in sites with bison than in sites with cattle. No dramatic differences have been detected, however, between cattle- and bison-grazed sites in cover of the dominant *C₄* grass, *A. gerardii*, or the dominant forb, *Ambrosia psilostachya*; total plant species richness is also not dramatically different (E. Gene Towne and David C. Hartnett, unpublished data).

Results at Konza Prairie are consistent with previous assessments (e.g., Schwartz and Ellis [1981], Van Vuren and Bray [1983], and Plumb and Dodd [1993] in mixed and short-grass prairie), which noted that both bison and cattle are generalist herbivores that graze preferentially on graminoids. Nevertheless, some differences in the foraging patterns of bison and cattle have been documented that may have long-term implications for grasslands. For example, bison have a higher proportion of graminoids in their diet than do cattle; consequently, forb and browse species are more common in cattle diets (Van Vuren and Bray 1983, Hartnett et al. 1997). Also, bison spend less time grazing than cattle and more time in nonfeeding activities (Plumb and Dodd 1993), and bison strongly prefer open grassland areas for grazing, whereas cattle use

wooded and grassland habitats opportunistically (Hartnett et al. 1997).

Studies that have focused exclusively on cattle generally concur that their grazing activities increase spatial heterogeneity and enhance plant species diversity, so long as stocking density is not too high (Collins 1987, Hartnett et al. 1996). Because bison grazing in tallgrass prairie has a similar effect, one could conclude that either herbivore can alter resource availability and heterogeneity and reduce the cover of the dominant grasses sufficiently to enhance the success of the subdominant species. Perhaps of greater importance than differences in foraging patterns between bison and cattle, however, are the number of nongrazing activities, such as wallowing and horning (i.e., rubbing on trees) that are associated exclusively with bison (Coppedge and Shaw 1997, Hartnett et al. 1997). These activities, when combined with the spatial redistribution of nutrients and selective consumption of the dominant grasses, may further increase plant species richness and resource heterogeneity, particularly at the landscape scale.

Nevertheless, it is likely that because bison and cattle are functionally similar as large grass-feeding herbivores, management strategies (stocking intensity and duration) will have a greater influence on the degree of ecological equivalency achieved than inherent differences in these ungulates (Hartnett et al. 1997). Clearly, the degree of overlap in diet and foraging patterns is greater between bison and cattle than between cattle and other historically important native herbivores (Hartnett et al. 1997), such as antelope (*Antilocapra americana*), deer (*Odocoileus virginianus*), and elk (*Cervus canadensis*). Indeed, the loss of antelope and elk from the tallgrass prairie, coupled with dramatic increases in deer populations, presents additional challenges for managing these ecosystems.

Conservation implications

Conserving small and moderate-sized tracts of once-vast biomes, such as the tallgrass prairie, presents a unique set of problems that are distinct from those associated with spatially re-

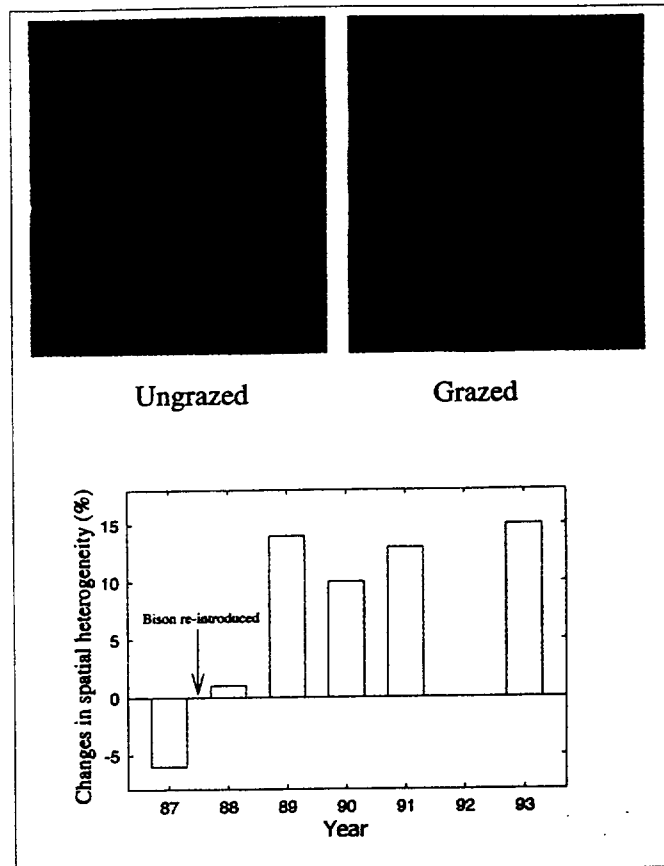
stricted ecosystems because many of the defining forces that historically were important in structuring these systems occurred at spatial scales that no longer exist. For example, in pre-1900s grasslands, fires were not plot-level or even watershed-level events but operated at spatial scales encompassing thousands of hectares. This large spatial scale resulted in potentially high fire frequencies throughout the tallgrass prairie because any point of ignition in this "inland sea of grass" could affect grasslands hundreds of kilometers distant.

Today, the fragmentation of Great Plains grasslands is recognized as a key factor in reducing the frequency of fire, which in turn contributes to species loss (Leach and Givnish 1996). Indeed, the primary management strategy for small prairie preserves, which are most prone to invasion by woody vegetation and exotic species, is to burn them as frequently as possible to suppress invasion by undesirable plants (Leach and Givnish 1996). Unfortunately, frequent (annual or biannual) spring fire maintains dominance by C_4 grasses but reduces plant species diversity relative to grasslands that are burned infrequently. One alternative is to conduct burns at different times of the year (Howe 1994), but summer fires, for example, may not prevent invasion or reduce the abundance of woody vegetation (Adams et al. 1982). In addition, burning in late summer may be difficult because of other considerations, including reduced ability to control the fire under dry, windy conditions. Not only are prairies threatened by fragmentation and invasion by undesirable species, but grasslands throughout the Great Plains are now affected by increased atmospheric nitrogen deposition (Wedin and Tilman 1996). Thus, remnant grasslands are subjected to a variety of anthropogenic factors that can reduce the diversity of native prairie species.

The spatial and temporal impacts of bison grazing activities caused by the historically large and nomadic herds are also best characterized as landscape-level forces. These too are difficult to replicate in today's fragmented grassland remnants. Yet just as some of the ecological characteristics of natural fires can be reintro-

duced to grasslands through prescribed fire, the key elements of bison grazing activities can and should be incorporated into conservation and restoration strategies for remnant prairies (Steuter 1997). One approach to accomplish this goal is the substitution of cattle for bison. Plumb and Dodd (1993) argued that the choice of whether to use cattle or bison as a management tool in grasslands is scale and context dependent. Clearly, reintroducing bison may not be appropriate for small prairie remnants with public access and low economic resources. But cattle, managed for their ecological rather than their economic value, may be suitable in such cases.

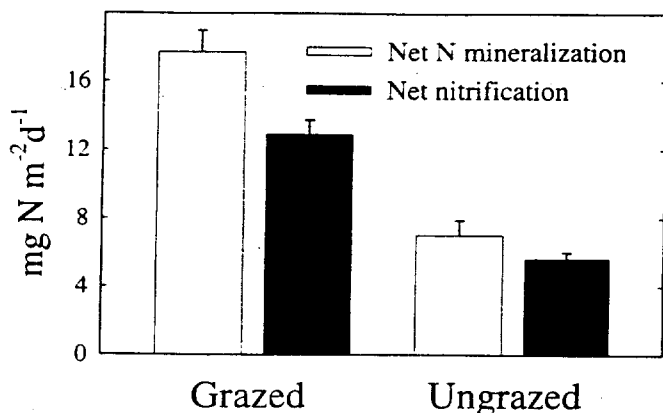
Figure 5. Landscape-level changes in spatial heterogeneity in tallgrass prairie induced by bison grazing activities. False-color composite of Thematic Mapper (TM) data from an area on Konza Prairie grazed by bison (upper left) and from a nearby area protected from grazing (upper right). Both sites were burned and have similar soil types, aspect, and slopes. Red colors represent areas of high productivity, and blue colors correspond to areas of low productivity or bare ground. (lower panel) Percentage difference in spatial heterogeneity of biomass (estimated from remotely sensed spectral reflectance data) between areas grazed by bison and adjacent ungrazed areas on Konza Prairie. Before bison reintroduction, watersheds scheduled to remain ungrazed appeared to have greater spatial heterogeneity than those scheduled to be grazed (negative values in 1987). After the reintroduction of bison in 1988, spatial heterogeneity in the grazed watersheds increased substantially. Spatial heterogeneity was assessed using the TEXTURE algorithm, which involves passing a moving 3×3 pixel window through the images and determining the differences between the minimum and maximum values for each subset of pixels (Briggs and Nellis 1991). Pixels represent derived Normalized Difference Vegetation Index (NDVI) values from TM data (30 m^2 spatial resolution) from 1988 to 1991 and from 1993 (TM data were not available for 1992). Previous studies have confirmed that the use of the TEXTURE algorithm with NDVI data is useful for estimating patterns of spatial heterogeneity in tallgrass prairie (Nellis and Briggs 1989, Briggs and Nellis 1991).



duced to grasslands through prescribed fire, the key elements of bison grazing activities can and should be incorporated into conservation and restoration strategies for remnant prairies (Steuter 1997). One approach to accomplish this goal is the substitution of cattle for bison. Plumb and Dodd (1993) argued that the choice of whether to use cattle or bison as a management tool in grasslands is scale and context dependent. Clearly, reintroducing bison may not be appropriate for small prairie remnants with public access and low economic resources. But cattle, managed for their ecological rather than their economic value, may be suitable in such cases.

Alternatively, mowing can be used to reduce the dominance of the tall grasses and to enhance species richness (Gibson et al. 1993, Collins and Steinauer 1998). Results from a long-term experiment at Konza Prairie incorporating annual fire, nitrogen addition, and mowing (Collins et al. 1998) indicated that on annually burned and fertilized treatment plots, productivity of the grasses was higher, and plant species diversity lower, than in control plots. However, on burned, fertilized plots that were mowed (with removal of the foliage; a rough substitute for grazing), plant species diversity was restored to levels similar to control plots (Collins and Steinauer 1998).

Figure 6. Net nitrogen mineralization and net nitrification rates in grazed and ungrazed areas of Konza Prairie. Measurements were made in situ for a 1-month period in June 1996 and May 1997 using a modified buried soil core technique (Raison et al. 1987). Replicate study plots were located on upland areas of adjacent grazed and ungrazed annually burned watersheds. Values are means $\pm$ 1 SE and are significantly different ($P < 0.05$, $n = 120$ per grazing treatment).



A combination of frequent spring fire to maintain populations of the desirable C_4 prairie grasses, decrease nitrogen availability (Blair 1997), and suppress growth of weedy annuals and woody vegetation, coupled with mowing portions of the site to reduce the competitive dominance of C_4 grasses, can enhance the abundance of forbs and maintain high plant species diversity in small remnant prairies. Ultimately, management designed to increase the spatial heterogeneity of resources in a manner analogous to that imposed by ungulate activities is essential if sig-

nificant and sustainable biotic diversity in tallgrass prairie is a goal.

Conclusions

Despite less than a decade of research at Konza Prairie on bison-tallgrass prairie interactions, the keystone role that bison must have historically played in this grassland is clear. Moreover, much as fire is now recognized as an essential component of tallgrass prairie management (because without fire this grassland disappears), the need for reintroducing the forces of large un-

gulate herbivory to this grassland is evident. Indeed, it is the interaction of ungulate grazing activities and fire, operating in a shifting mosaic across the landscape, that is key to conserving and restoring the biotic integrity of the remaining tracts of tallgrass prairie.

Before bison were reintroduced to Konza Prairie, Knapp and Seastedt (1986) speculated that bison grazing and fire could act in similar ways by reducing the accumulation of detritus in this system. It is primarily the blanketing effect of the accumulation of dead plant material above ground that limits productivity in undisturbed tallgrass prairie. Like fire, bison grazing reduces above-ground standing dead biomass. But it is now clear that the unique spatial and temporal complexities of bison grazing activities (Figure 5) are critical to the successful maintenance of biotic diversity in this grassland. This grazing-induced heterogeneity contrasts sharply with the spatial homogeneity induced by fire in an ungrazed landscape (Figure 6).

Tallgrass prairie, by virtue of its inherently variable climatic, grazing, and fire regimes, is an ecosystem that requires long-term study to document patterns and quantify processes (Knapp et al. 1998b). Through the partnership of The Nature Conservancy, the National Science Foundation's LTER program, and Kansas State University, ongoing studies at this site will continue to explore the ecological interactions of fire and grazing in the tallgrass prairie landscape. Such research is timely because conservation and management issues have intensified in the remaining tracts of this once-vast biome, particularly in response to predicted alterations in global climate and land-use changes. Interdisciplinary ecological research, such as that ongoing at Konza Prairie, will provide the basic information necessary for designing optimal conservation, restoration, and management strategies in this and other grasslands.

Acknowledgments

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Figure 7. Bison carcass approximately 9 months after death in burned tallgrass prairie. In this spring (May) photo, vegetation is completely lacking within the area in which the animal died. A zone of high fertility exists around the edge of this disturbance, and within 1–2 years the site will be dominated by early successional (annual) species.

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Age Group	Percentage
18-24	22%
25-34	18%
35-44	15%
45-54	12%
55-64	10%
65-74	8%
75-84	6%
85+	4%

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PREDATOR ACTIVITY RELATED TO LANDSCAPE FEATURES IN NORTHERN IOWA

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Abstract: We studied mammalian predator activity in relation to patches of grassland habitat in the agricultural landscape of northern Iowa to understand the potential interactions with ground-nesting birds, including waterfowl and ring-necked pheasant (*Phasianus colchicus*). We quantified presence and movement direction of striped skunk (*Mephitis mephitis*), raccoon (*Procyon lotor*), and red fox (*Vulpes vulpes*) using unbaited track stations placed along the edges of 100-ha blocks of grassland and at other locations throughout the surrounding landscape. We used logistic regression with repeated measures and Akaike weights to develop predictive models of predator presence as a function of landscape variables including distance from a grassland block, shape of grassland edges, and presence of woodlands, farmsteads, and wetlands. Predators were detected at track stations in the landscape near (≤ 500 m) grassland blocks 33.5% of the time, more frequently than at stations immediately adjacent to edges of blocks (22.6%), and much more frequently than at stations distant (> 500 m) from blocks (13.6%). Striped skunk presence at a station decreased as distance from grassland patches increased and was positively related to the number of farmsteads; raccoon presence was positively related to presence of woody cover; and red fox presence increased with greater area of pastureland and greater isolation from farmsteads, and decreased with increasing amount of strip habitat in the landscape. Predicted predator presence at locations where duck nests were found ≤ 500 m from blocks of grassland (23.1%) was within 1 SE of the Mayfield nest mortality rate, whereas predicted presence at isolated nest locations (12.0%) was greater than observed nest mortality. Track stations indicated that predators moved into and out of grassland patches at corners of blocks (80% of the time) much more frequently than when they traveled along the straight sides of blocks (7%). If presence of predators is directly related to predation rate, our models predict that risk to nesting birds would be greatest in patches near large grassland blocks where corridors, corners, and smaller patches focus predator activity. We envision that wildlife biologists could use models of predator activity to predict the potential influence of landscape configuration on predation risk to nesting birds.

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Key words: Akaike weights, corn belt, habitat fragmentation, Iowa, isolation, *Mephitis mephitis*, predation, *Procyon lotor*, raccoon, red fox, striped skunk, track stations, *Vulpes vulpes*.

In many parts of the highly altered agricultural landscape of the Corn Belt of the United States, perennial habitat has been reduced to a small fraction of the original extent. For example, in northern Iowa, more than 75% of land use is row-crop agriculture and the remaining perennial grassland, woodland, and wetland habitats exist in patches varying from a few to many hundreds of hectares linked by narrow strips of habitat along roads and streams. Habitat loss can be accompanied by increased landscape fragmentation, including decrease in patch size, increased patch isolation, and increase in habitat edge (Fahrig 1997). The loss and fragmentation of habitat are considered the most important underlying causes of declines in success of nesting waterfowl (Beauchamp et al. 1996) and other upland-nesting birds. Medium-sized carnivores are the major cause of nest losses

of waterfowl (Greenwood et al. 1987), pheasant (Clark et al. 1999), and ground-nesting passerines (Burger et al. 1994) in these landscapes.

Predators such as the red fox (hereafter, fox), raccoon, and striped skunk (hereafter, skunk) often are numerically abundant in these agricultural landscapes because their generalist food and habitat requirements have enabled them to adapt easily to the altered landscape composition and configuration (Andren et al. 1985). However, the relationships between these predators and ground-nesting birds are influenced as much by functional use of spaces in the landscape as they are by numerical responses (McLaughlin and Roughgarden 1993). The behavioral ecology of predator functional response and use of the landscape is important to determining the overall predation effects (Ims 1995, Lima and Zollner 1996). Much of the predation on nests is thought to be opportunistic (Vickery et al. 1992, Andren 1995), so understanding how landscape features influence predator activity has substantial practical implications for managing predators and

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nesting birds. Although evidence of predator activity frequently is inferred from studies of nesting birds, few studies have directly quantified the influence of landscape composition and configuration on predator presence or directly related predator activity to nesting success.

Predators are believed to move and forage in response to specific landscape features such as edges of habitat (Andren 1995, Dijak and Thompson 2000), or along internal features of patches such as streams (Heske 1995) and wetland edges (Phillips 2001) where increased diversity and availability of prey (Andren et al. 1985) or other characteristics that focus behavior (Sargeant 1972, Sargeant et al. 1987) may exist. Previous studies have identified various landscape composition variables such as farms (Lariviere and Messier 1998), woodland (Pedlar et al. 1997, Dijak and Thompson 2000), grassland (Clark et al. 1999, Greenwood et al. 1999), wetland (Greenwood et al. 1999, Phillips 2001), and pastureland (Sargeant 1972, Sargeant et al. 1987, Pedlar et al. 1997, Phillips 2001) that may influence presence of generalist predators. However, after habitat is lost, the configuration rather than composition of the remaining patches may become more important to predator activity. Juxtaposition of patches may be important if patches are smaller than the home range of a species or animals may move more when fragmentation scatters habitat patches (Ims 1995). If patches are small and isolated from predator activity centers they may be visited relatively infrequently. Strip habitat such as road ditches, streams and waterways (Heske 1995), and fence lines (Pedlar et al. 1997) may act as corridors between habitat patches (Ims 1995). Finally, the characteristics of edges of patches, including the shape, may influence how predators use the edges of patches as travel lanes. Corridors and corners have been predicted to funnel activity into a patch (Ims 1995).

In this study, we assessed evidence of activity of 3 common carnivores and determined how landscape composition and configuration variables were quantitatively related to predator activity and movements. Our approach was to (a) determine the most important landscape variables influencing the level of predator activity using track stations, (b) select models for predicting predator activity given landscape variables, (c) examine the effect edge shape has on predator movements, and (d) provide evidence that the models have explanatory value in understanding duck nesting success in grasslands of northern Iowa.

STUDY AREA

We conducted our study within the Eagle Lake Wetland Complex, a project area of the North American Wetland Conservation Act, located in the Iowa Prairie Pothole Region in Hancock and Winnebago counties in northern Iowa, USA. The 127-km² study area contains a complex of Wildlife Management Areas (WMA), Waterfowl Production Areas (WPA), Conservation Reserve Program (CRP) lands, and agricultural fields (row cropland, hayland, pastureland). The Iowa Department of Natural Resources (IDNR) manages nearly 700 ha of upland and 800 ha of wetlands in the study area including the lands owned by the U.S. Fish and Wildlife Service (USFWS). In these agricultural landscapes, perennial grasslands generally are in large squared, rectangular, or L-shaped blocks, often in multiples of 16 ha (Clark et al. 1999:982). Other grassland habitats are in much smaller patches, especially in linear configuration along roads, drainage ditches, and natural streams.

METHODS

Predator Activity

We collected data from the beginning of May through mid-July during the summers of 1999 and 2000. Presence of predator tracks identified to species was used to determine predator activity at sample units within habitats that might be used by both nesting birds and predators. We modified the track-survey technique used by Sargeant et al. (1993) and Sovada et al. (1995) so that sample units could be randomly distributed across the landscape. Sample units were allocated along the grassland–row-cropland edges of road ditches, drainage ditches, and around the edges of large blocks of grassland.

A sample unit consisted of 2 sub-units, 1 placed in the first few rows of row cropland adjacent to the grassland edge and the other placed 2 m into the grassland habitat. Each sub-unit consisted of 3 1-m² track stations separated by 3 m with sub-units parallel to the grassland–row-cropland edge. The multiple track stations allowed us to sample a large tracking area without extensive disturbance to the habitat and enabled us to better assess movement direction of predators.

Each station consisted of finely raked soil with a 3.5-cm white disk placed at its center. The sharp contrast between the disk and soil acted as a novel stimulus (Animal and Plant Health Inspection Service 1998) to attract the attention of pass-

ing predators to the center of the track station where they could leave a more detectable track. The disk did not contain scent or bait that would provide a reward, which would condition predators to search the area. When soil conditions were poor, mineral oil was applied to moisten the soil to improve track registration (M. A. Sovada, Northern Prairie Wildlife Research Center, personal communication). A numerical rating of track station condition was recorded to control and test for differences in the ability to detect and identify predator tracks (Kuehl 2001).

Sample units were checked after 2 nights of exposure. Similar studies using baited track stations used 1- (Heske 1995, Marini et al. 1995, Winter 2000), 2- (Dijak and Thompson 2000), and 7-day (Pedlar et al. 1997) exposure periods. We selected 2 exposure nights as a compromise between opportunity for predator response and reduction of weather disturbances.

Habitat and Landscape Variables

Land use and landscape variables were determined using low-altitude aerial photography for the study area and surrounding landscape. Geographical Information System (GIS) software was used to map and quantify landscape characteristics. Habitat was classified into 1 of 9 cover types: (1) row cropland, (2) strip grassland (terrace, fence line), (3) drainage ditch, (4) grassland block (WMA, CRP, WPA), (5) hayland and pastureland, (6) water, (7) woodland (including shelterbelts surrounding farmsteads), (8) roads, and (9) farmsteads. Classifications were verified by ground observations.

Relating Predator Activity to Landscape Variables

Sample unit locations were selected randomly from strata that reflected our primary interest in how predator activity might vary with the landscape variables, especially with the distance away from a large block of perennial grassland habitat. We defined 3 strata in the landscape with regard to their isolation from these grassland blocks: locations that were adjacent to the edge (hereafter, Edge) of a grassland block, locations that were ≤ 500 m from a block of grassland (hereafter, Near), and locations that were > 500 m from a block of grassland (hereafter, Far). We used the GIS to allocate sample units within the Edge stratum among 3 types of edges around the block: straight edges along the straight sides of grassland blocks ($n = 13$), at the convex corners ($n =$

11), and at the concave corners ($n = 13$) along the edges of blocks of grassland. For example, at the edge of an L-shaped block of grassland, 5 convex corner locations and 1 concave corner could be sampled. We also selected sample units from all possible 9-m sections of gravel road ditch ($n = 10$) and drainage ditch ($n = 5$) in the Near stratum. We selected sample units from all possible 9-m sections of gravel road ditch ($n = 12$) and drainage ditch ($n = 6$) in the Far stratum.

We used the GIS to measure a priori selected landscape variables within a 500-m radius buffer around sample units. This buffer distance was based on the home-range sizes of the predators of interest, especially fox (Sargeant et al. 1987), raccoon (Glueck et al. 1988), and skunk (Greenwood et al. 1985). The radius also is reasonable considering the home-range sizes of nesting ducks (Gilmer et al. 1975) and pheasants (Clark et al. 1999).

On Near and Far sample units, the natural logarithm of the distance (m) to grassland block (Dgrass), farmstead (Dfarm), and wooded habitat (Dwood), the area (ha) of wooded habitat (Awood), agricultural grasslands (pastureland and hayland; Apast), and managed grasslands (CRP, WMA, WPA; Agrass), the length of strip habitat (road ditches and fences combined; Lstrip), and the number of farms (Nfarm) were measured as predictor variables. When modeling predator activity in the Edge stratum, we dropped variables describing distance to grassland block and farmstead, area of grassland, and length of strip habitat. We replaced these variables with variables that reflected characteristics of the grassland blocks, including edge density of the block (Edgrass), the perimeter of wetland edge (Pwet), number of wetlands in the block (Nwet), and shape of the block (categorized as straight side, concave corner, or convex corner) of grassland edge (Shape). All distance measurements were log-transformed to better meet assumptions of normality. We converted length measurements to 100-m units so that they were scaled to area measurements.

Statistical Analysis

We used multiple logistic regression with repeated measures on sample units to model the presence of predator activity as a function of landscape variables. To model the effect of varying distance away from grassland blocks, we combined sample units from Near and Far strata into a grouping we called Distant from grassland

blocks (all units where distance to block of grassland > 0). We modeled the predator activity data from the Edge stratum separately (distance to block of grassland = 0). The raw response variable (p) was the presence of at least 1 predator track at a sample unit. Responses were modeled on the logit scale, $Y_{\text{species}} = \log(p/1-p) = f(\text{landscape variables})$.

We reduced the number of candidate landscape variables using univariate tests and correlation analyses. After preliminary analyses, we selected 8 variables that differed among locations with respect to predator presence and that were not highly correlated. Absolute values of Pearson correlation coefficients ranged from 0.03 to 0.64 among these 8 variables. We considered only linear models of the variables without interactions to retain simplicity and to avoid constructing more model combinations than we could resolve with the data. After exploratory analyses, ≤ 25 candidate model combinations of the 8 variables were considered for each predator species.

These candidate models were compared using Akaike's Information Criterion values, corrected for small sample size (AIC_c ; Burnham and Anderson 1998:51). Akaike's Information Criterion is designed to select the best-fit model without over fitting the data with too many parameters. Goodness-of-fit statistics and an index of overdispersion ($\hat{c} = \chi^2/\text{df}$) were calculated from a global model (Burnham and Anderson 1998). Models were ranked using ΔAIC_c values. We calculated Akaike weights (Burnham and Anderson 1998:124, Eq. 4.2) from the ΔAIC_c to assess the relative likelihood of each model and importance of each variable (Burnham and Anderson 1998:141). We considered that models with $\Delta AIC_c < 2$ all fit the data well (between 2 and 7 models for individual predator species). Models within 2 ΔAIC_c were weighted and normalized so that we could calculate weighted average parameter estimates ($\hat{\beta}$) (Burnham and Anderson 1998:133, Eq. 4.6) and associated standard errors (Burnham and Anderson 1998:135, Eq. 4.9) of variables remaining in the models. Each estimated parameter β_i is interpreted as usual for logistic regression, i.e., a unit increase in an explanatory variable results in an e^{β_i} increase in the odds ratio.

We validated the utility of our modeling approach by using the best-fit model to predict predator activity from landscape variables within a 500-m buffer around 20 locations randomly selected from a larger data set of nest locations of radiomarked mallards (*Anas platyrhynchos*) within

the study area (R. Koford and G. Dodici, Iowa Cooperative Fish and Wildlife Research Unit, unpublished data). Estimated probabilities of predator presence were compared to observed risk of nest failure. We back-transformed from the logit scale to estimate the probability of predator presence by calculating $\text{Pr}(p) = 1/(1 + e^{-Y_{\text{species}}})$. We converted observed daily nest survival estimates ($\hat{S}_d$) to 2-day mortality estimates ($1 - \hat{S}_d^2$) and compared the latter to predator presence during intervals when the nest was active. Half of the nests in this sample were ≤ 500 m and half were > 500 m away from a block of grassland. We did not compare estimated predator presence and nest failure rate for Edges of blocks of grassland because very few nests were located in this stratum.

Predator movement direction was assessed from individual tracks and the predominant trail on sample units. Sample units where the direction of predator movement could not be determined were excluded from movement analyses. The proportion of predator movement perpendicular (into or out of the grassland habitat) was compared and contrasted to parallel movement on sample units. We examined sample unit type (road ditch, drainage ditch, block side, convex corner, concave corner) and location along the edge of a block of grassland (straight side or corner) to determine whether movements of predator species were affected by these features.

RESULTS

Predator activity differed significantly among Edge, Near, and Far sample unit locations ($\chi^2 = 23.94$, $\text{df} = 2$, $P < 0.001$). Sample unit locations near grassland blocks had the highest combined predator activity, whereas units at the edges of blocks and far from blocks showed increasingly less activity (Fig. 1).

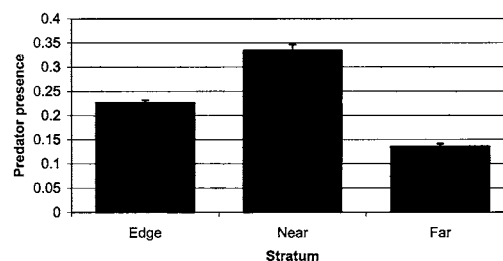


Fig. 1. Predator presence ($\pm$ SE) estimated by track counts on sample units located at the Edges, Near (≤ 500 m) and Far (> 500 m) from blocks of grassland in northern Iowa during May through Jul, 1999 and 2000.

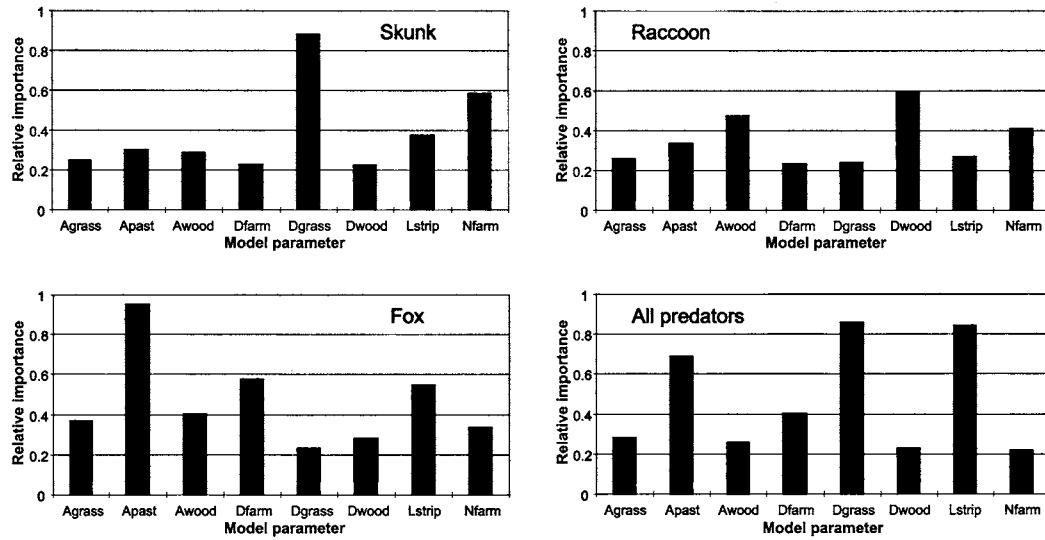


Fig. 2. Relative importance of landscape variables for predicting activity of striped skunk, raccoon, red fox, and all predators on isolated sample units in northern Iowa, May–Jul, 1999 and 2000. Abbreviations of model parameters: Agrass = area of grassland, Apast = area of pasture, Awood = area of woodland, Dfarm = distance to farm, Dgrass = distance to grassland block, Dwood = distance to woodland, Lstrip = length of strip habitat, Nfarm = number of farms.

Sample Units Distant from Grassland Blocks

Of the possible 595 sample unit-nights, skunk tracks were present at 45, fox tracks were present at 32, raccoon tracks were present at 24, domestic dog tracks were present at 4, and no units were visited by domestic cat. On 42 occasions, visible tracks of these large predators were observed but specific identification was not reliable so we included the response only in measures of total predator activity. We did not attempt to interpret presence as a direct measure of abundance because each predator species could react differently to the sample unit.

Skunk.—Distance from a sample unit to a block of grassland and number of farmsteads within the buffered radius were the most important variables influencing skunk activity. Based on variable importance, distance to a block of grassland was 1.5 times more important than the number of farms and 2.5 to 4 times more important than other variables in the global model for explaining skunk activity (Fig. 2). The goodness-of-fit statistics for the skunk global model (Pearson $\chi^2 = 581.75$, $df = 586$, $P = 0.542$) indicated a good fit to the data and no evidence of overdispersion ($\hat{c} = 0.993$). Each of the best-fit models ($\Delta AIC_c < 2$) for skunk activity included distance to a block of grassland, whereas other variables in the best-fit models included number of farms, area of pas-

tureland, and length of strip habitat. Akaike weights indicated twice the support for a model that included both distance to a block of grassland and number of farms compared to the model that also included length of strip habitat (Table 1) or the model that only included distance to a block of grassland ($w_i = 0.179$). Using the average parameter estimates (Table 2), the

Table 1. Akaike Information Criterion corrected for small sample sizes and model weights for the 2 best-fit models for striped skunk, raccoon, red fox, and all predators on distant sample units in northern Iowa, May–Jul, 1999 and 2000.

Species	Parameters included in model	Model Statistics		
		AIC _c	ΔAIC_c	w_i
Striped skunk	Dgrass, Nfarm	308.625	0.000	0.353
	Dgrass, Nfarm, Lstrip	309.937	1.313	0.183
Raccoon	Dwood	195.045	0.000	0.260
	Nfarm, Dwood	195.516	0.472	0.206
Red fox	Dfarm, Apast, Lstrip	240.101	0.000	0.251
	Dfarm, Apast	240.656	0.555	0.190
All predators	Dgrass, Apast, Lstrip	605.586	0.000	0.369
	Dgrass, Dfarm, Apast, Lstrip	605.607	0.021	0.365

^a Abbreviations of model parameters: Apast = area of pasture, Dfarm = distance to farm, Dgrass = distance to grassland block, Dwood = distance to woodland, Lstrip = length of strip habitat, Nfarm = number of farms.

Table 2. Averaged parameter estimates ($\bar{\beta}$, SE) for landscape variables included in the best-fit activity models for striped skunk, raccoon, red fox, and all predators combined on sample units Distant from blocks of grassland in northern Iowa, May–Jul, 1999 and 2000.

Landscape variable	Striped skunk		Raccoon		Red fox		All predators	
	$\bar{\beta}$	SE	$\bar{\beta}$	SE	$\bar{\beta}$	SE	$\bar{\beta}$	SE
Agrass				0.015	0.000			
Apast	0.023	0.001			0.149	0.001	0.055	0.001
Awood			0.534	0.010	-0.353	0.026		
Dfarm					0.551	0.029	0.227	0.018
Dgrass	-0.260	0.003					-0.179	0.002
Dwood			-0.816	0.028				
Lstrip	-0.018	0.001	-0.013	0.001	-0.040	0.001	-0.019	0.001
Nfarm	0.334	0.041	-0.344	0.017	0.242	0.010		

^a Abbreviations of model parameters: Agrass = area of grassland, Apast = area of pasture, Awood = area of woodland, Dfarm = distance to farm, Dgrass = distance to grassland block, Dwood = distance to woodland, Lstrip = length of strip habitat, Nfarm = number of farms.

best-fit model for skunk activity was $Y_{\text{skunk}} = -1.195 - 0.260(\text{Dgrass}) + 0.334(\text{Nfarm})$.

Raccoon.—Relative importance of landscape variables influencing raccoon activity was less distinct than for skunk, but distance to woodland and area of woody cover were more important than other variables in the global model (Fig. 2). For the raccoon global model, the goodness-of-fit statistics (Pearson $\chi^2 = 551.22$, $df = 586$, $P = 0.846$) indicated a good fit to the data and no evidence of overdispersion ($\hat{c} = 0.941$). Variables that occurred in the best-fit models ($\Delta\text{AIC}_c < 2$) for raccoon activity included number of farms, distance to woody cover, area of woodland, area of pastureland, and length of strip habitat. Although area of woodland was nearly as important as distance to woodland, Akaike weights show nearly twice the support for the model including only distance to woodland ($w_i = 0.260$; Table 1) when compared with the model that contained only the area of woodland ($w_i = 0.149$). Including the variable for the number of farms did not improve the model fit. Using the average parameter estimates (Table 2), the best-fit model for raccoon activity was $Y_{\text{coon}} = 0.423 - 0.816(\text{Dwood})$.

Fox.—Area of pastureland was the single most important variable influencing fox activity, but distance to the nearest farmstead and length of strip habitat also were important for explaining activity (Fig. 2). The fox global model goodness-of-fit statistics (Pearson $\chi^2 = 601.13$, $df = 586$, $P = 0.324$) indicated a good fit to the data and no evidence of overdispersion ($\hat{c} = 1.026$). Each of the best-fit models ($\Delta\text{AIC}_c < 2$) for fox activity included the area of pastureland, while other variables in the models included number of farms, distance to farmstead, area of grassland, area of

woodland, and length-of-strip habitat. Akaike weights supported the addition of the length-of-strip variable to the model that only included area of pastureland and distance to the nearest farmstead (Table 1). Using the average parameter estimates (Table 2), the best-fit model for fox activity was $Y_{\text{fox}} = -5.316 + 0.551(\text{Dfarm}) + 0.149(\text{Apast}) - 0.040(\text{Lstrip})$.

All Predators.—Distance to a block of grassland, length of strip habitat, and area of pastureland were more important than other variables in explaining the activity of all predators (Fig. 2). When all predators were combined, the goodness-of-fit statistics for the global model (Pearson $\chi^2 = 586.25$, $df = 586$, $P = 0.489$) indicated a good fit to the data and no evidence of overdispersion ($\hat{c} = 1.001$). Each of the best-fit models ($\Delta\text{AIC}_c < 2$) for predator activity included distance to grassland block and length of strip habitat. Best-fit models also included distance to nearest farm and area of pastureland. Akaike weights indicated that the addition of the distance to farm variable to the best-fit 3-variable model actually had reduced support (Table 1). Using the average parameter estimates (Table 2), the best-fit model for predator activity was $Y_{\text{predator}} = -0.245 - 0.179(\text{Edgrass}) + 0.055(\text{Apast}) - 0.019(\text{Lstrip})$.

Model Predictions.—Models predicted an average 2-day probability of predator presence at observed duck nest locations Near blocks of grassland that matched the observed nest mortality rate very closely (Table 3). Predicted presence of predators at Far nest locations was lower, but the predicted presence was about 2 times the observed nest mortality rate (Table 3). Estimated probability of presence at duck nests located Near blocks of grassland of skunk ($t = 3.52$, $df = 12$, $P =$

Table 3. Estimated 2-day nest mortality ($\hat{S}_d^2$, SE) and predicted probability of predator presence within 2 days ($\hat{p}$, SE) at duck nest locations Near (≤ 500 m) and Far (> 500 m) from a block of grassland in northern Iowa, May–Jul, 1999 and 2000.

Nest location	Nest mortality ^a		Predator species							
			All predators		Striped skunk		Raccoon		Red fox	
	$\hat{S}_d^2$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE	$\hat{p}$	SE
Near	0.203	0.06	0.231	0.032	0.127	0.015	0.019	0.003	0.139	0.073
Far	0.061	0.022	0.120	0.000	0.068	0.007	0.009	0.001	0.033	0.006

^a R. Koford and G. Dodici, Iowa Cooperative Fish and Wildlife Research Unit, unpublished data.

0.004), of raccoon ($t = 3.79$, $df = 11$, $P = 0.003$), and of all predators combined ($t = 3.44$, $df = 9$, $P = 0.007$) was greater than the probability of predator presence at Far nest locations (Table 3). The estimated probability of fox presence was numerically greater, but more variable, on nests Near blocks of grassland than on Far locations ($t = 1.45$, $df = 9$, $P = 0.18$).

Sample Units at Edges of Grassland Blocks

Of the possible 681 sample unit-nights, skunk tracks were present at 38, fox tracks were present at 45, raccoon tracks were present at 37, domestic dog tracks were present at 3, mink (*Mustela vison*) or weasel (*Mustela* spp.) tracks were present at 3, opossum (*Didelphis marsupialis*) tracks were present at 1, and none were visited by domestic cat. On 39 occasions, visible tracks could not be iden-

tified to any 1 of these species, but are included in estimates of total predator activity.

Skunk.—The most important variable influencing skunk activity was the number of wetlands in the surrounding habitat. Based on variable importance, the number of wetlands was 2 to nearly 4 times more important than other variables in the general model for explaining skunk activity (Fig. 3). The goodness-of-fit statistics for the skunk global model (Pearson $\chi^2 = 673.39$, $df = 672$, $P = 0.478$) indicated a good fit to the data and no evidence of overdispersion ($\hat{c} = 1.00$). Each of the best-fit models ($\Delta AIC_c < 2$) for skunk activity around block edges included the number of wetlands, and Akaike weights provided additional support that a single parameter model including the number of wetlands was the most appropriate model (Table 4). Using the average

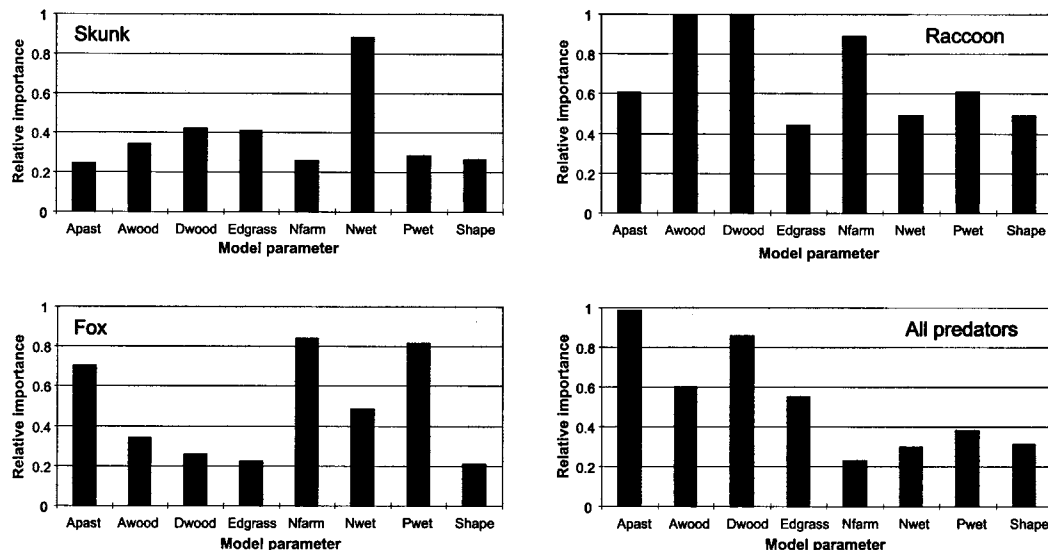


Fig. 3. Relative importance of landscape variables for predicting activity of striped skunk, raccoon, red fox, and all predators on block edge sample units in northern Iowa, May–Jul, 1999 and 2000. Abbreviations of model parameters: Apast = area of pasture, Awood = area of woodland, Dwood = distance to woodland, Edgrass = edge density of grassland, Nwet = number of wetlands, Pwet = perimeter of wetland, Shape = shape of the block (categorized as straight side, concave corner, or convex corner) of grassland edge.

Table 4. Akaike Information Criterion (AIC_c) corrected for small sample sizes and model weights for 2 best-fit striped skunk and all predator presence models for sample units along the edge of blocks of grassland in northern Iowa, May–Jun, 1999 and 2000.

Species	Parameters included in model ^a	AIC_c	ΔAIC_c	w_i
Striped skunk	Nwet	280.837	0.000	0.208
	Nwet, Dwood	281.227	0.390	0.171
All predators	Dwood, Awood,			
	Apast, Edgrass	708.554	0.000	0.590
	Dwood, Awood, Apast	709.280	0.726	0.410

^a Abbreviations of model parameters: Apast = area of pasture, Awood = area of woodland, Dwood = distance to woodland, Edgrass = edge density of grassland, Nwet = number of wetlands.

parameter estimates (Table 5), the best-fit model for skunk activity along the edge of blocks of grassland was $Y_{\text{skunk}} = -1.213 + 0.139(\text{Nwet})$.

Raccoon.—Landscape variables influencing raccoon activity were more closely related and more unpredictable than for skunk, but number of farmsteads, distance to woodland, and area of woodland had higher variable importance indices than other variables in the model (Fig. 3). Variable importance suggests that number of farmsteads, distance to woodland, and area of woodland were 1.5 to >2 times more important than other variables in explaining raccoon activity. However, the goodness-of-fit statistics for the general raccoon model (Pearson $\chi^2 = 1154.69$, $df = 672$, $P < 0.001$) indicated a poor fit to the data with no evidence of overdispersion ($\hat{c} = 1.72$). Due to the poor fit of the general model, a predictive model was not calculated.

Fox.—Number of farmsteads, perimeter of wet-

land edge and, to a lesser extent, area of pastureland were the most important variables influencing red fox activity along edges of blocks of grassland (Fig. 3). Number of wetlands was slightly more important than the remaining variables. Number of farmsteads, perimeter of wetland edge, and area of pastureland were nearly 1.5 times more important than the number of wetlands and 2 times more important than all other variables in the model. However, the goodness-of-fit statistics for the general fox model (Pearson $\chi^2 = 924.86$, $df = 672$, $P < 0.001$) indicated a poor fit to the data, with little evidence of overdispersion ($\hat{c} = 1.37$). Due to the poor fit of the general model, a predictive model for fox activity was not calculated.

All Predators.—When all predators were combined, area of pastureland and distance to woodland were the most important variables in the general model (Fig. 3). The goodness-of-fit statistics for the global model (Pearson $\chi^2 = 701.77$, $df = 672$, $P = 0.207$) indicated a good fit to the data and no evidence of overdispersion ($\hat{c} = 1.04$). Only 2 models fit the data adequately ($\Delta AIC_c < 2$), and each included distance to woodland, area of woodland, and area of pastureland variables (Table 4). The model that included edge density of grassland had nearly 1.5 times the support as the model without that variable. Using the average parameter estimates (Table 5), the best-fit model for block edge predator activity is $Y_{\text{predator}} = 0.971 - 0.457(\text{Dwood}) - 0.047(\text{Awood}) - 0.093(\text{Apast}) - 5.920(\text{Edgrass})$.

Movement Direction

Predator movement direction along the edge of the grassland patch, either perpendicular or parallel to the edge of the row-crop field, differed significantly among road ditch, drainage ditch, block straight side, convex corner, and concave corner samples ($\chi^2 = 65.381$, $df = 4$, $P < 0.001$). Nearly half of the observed difference resulted from the increased proportion of perpendicular movements by predators into and out of grasslands at convex and concave corners (Cell $\chi^2 = 11.48$ and 17.97 , respectively). Only 15% of predator movement direction along straight edges (road ditch, drainage ditch, block side) was perpendicular to the grassland habitat, whereas perpendicular movements accounted for more than 74% and 80% along convex and concave edges, respectively, depending on species (Table 6).

DISCUSSION

Use of simple unbaited track stations was a useful sampling device to identify the local predator

Table 5. Averaged parameter estimates ($\bar{\beta}$, SE) for landscape variables included in the best-fit activity models for striped skunk and all predators combined on block edge sample units in northern Iowa, USA, May–Jul, 1999 and 2000.

Landscape variable ^a	Predator species			
	Striped skunk		All predators	
	$\bar{\beta}$	SE	$\bar{\beta}$	SE
Apast	-0.011	0.021	-0.093	0.001
Awood	0.070	0.002	-0.047	0.002
Dwood	-0.247	0.016	-0.457	0.615
Edgrass	-6.984	19.853	-5.920	2.576
Nwet	0.139	0.015		
Pwet	0.0001	0.0003		

^a Abbreviations of model parameters: Apast = area of pasture, Awood = area of woodland, Dwood = distance to woodland, Edgrass = edge density of grassland, Nwet = number of wetlands, Pwet = perimeter of wetland.

Table 6. Mean proportion (p, SE) of movement perpendicular to the grassland–row cropland edge by predators on sample units where tracks were identified in northern Iowa, USA, May–Jul, 1999 and 2000.

Species	Road ditch			Drainage ditch			Straight side of block			Convex corner of block			Concave corner of block		
	n	p	SE	n	p	SE	n	p	SE	n	p	SE	n	p	SE
Striped skunk	37	0.0270	0.0270	8	0.0000	0.0000	9	0.0000	0.0000	13	0.8462	0.1042	15	0.9333	0.0667
Raccoon	16	0.0000	0.0000	8	0.0000	0.0000	8	0.1250	0.1250	19	0.7368	0.1038	10	0.9000	0.1000
Red fox	25	0.1200	0.0663	6	0.0000	0.0000	23	0.1304	0.0718	17	0.7647	0.1060	5	0.8000	0.2000
All predators	97	0.0515	0.0226	29	0.0690	0.0479	44	0.0682	0.0384	53	0.7358	0.0611	41	0.8780	0.0517

community (J. L. Drossel and C. A. Ribic, Wisconsin Cooperative Wildlife Research Unit, personal communication) and to assess predator activity near grassland habitats where birds nest (Sovada et al. 1995). As expected, predator presence in these agricultural landscapes was greatest near blocks of grassland, but presence was much lower near small, isolated habitat patches distant from these large blocks. The greatest detected presence of predators was at habitats such as small patches and corridors near grassland blocks and not necessarily at the immediate edge of a block. Our results on predator presence correspond well with many studies of success of ground-nesting birds. In landscapes with large amounts of grassland habitat, effects of predators on ground-nesting birds are diluted (Greenwood et al. 1995, Sovada et al. 2000). Nest success generally increases with patch size (Horn 2000, Sovada et al. 2000). However, when there is very little grassland and nesting habitat is in small isolated patches, success in such patches can be above average (Clark et al. 1999) or vary considerably among patches (Horn 2000).

In combination, the predator and nesting studies suggest that patches and corridors that concentrate activity around large blocks of grassland may be places in the landscape where nesting birds may be particularly exposed to predators. Considering the relative importance of time spent in foraging versus nonforaging activities (Stephens and Krebs 1986), spending time visiting isolated patches or searching the centers of large blocks of grassland may not be as profitable as foraging in moderately sized patches near blocks of grassland that attract nesting birds or other prey.

Our findings also are consistent with the habitat requirements of the common predators we studied. Skunks prefer to forage along agricultural field edges (Verts 1967) surrounding grasslands (Greenwood et al. 1999) and wetlands (Phillips 2001). When distance from these preferred foraging habitats increased, skunk activity

decreased. Skunks commonly use farmsteads as den sites (Lariviere and Messier 1998), and so we observed a positive influence of the number of farms on skunk activity. Raccoon activity is consistently greater near woody habitat (Pedlar et al. 1997, Dijak and Thompson 2000), so for this species, the distance to woody cover is a measure of isolation from their preferred habitat. Foxes are more mobile predators with larger home ranges that prefer large blocks of perennial grassland habitat and pasturelands for foraging (Sargeant 1972, Sargeant et al. 1987, Phillips 2001). Foxes also appeared to avoid farmsteads where human disturbance would be common.

Our data on predator presence are consistent with many results on success of ground-nesting birds. In landscapes with large amounts of grassland habitat, effects of predators on ground-nesting birds are diluted (Greenwood et al. 1995, Sovada et al. 2000). When there is very little grassland and nesting habitat is in small isolated patches, success in such patches can be above average (Clark et al. 1999) or vary considerably among patches (Horn 2000). Our models did not predict predator presence at the edges of blocks of grassland as effectively as they did in the larger landscape context. However, like predator activity, waterfowl nest success is not consistently related to distance from edges of blocks of grassland (Pasitschniak-Arts et al. 1998). Nonetheless, the positive influence that area of pastureland and woodland had on overall predator activity suggests that these blocks are important as focus areas of denning and foraging (Sargeant 1972, Sargeant et al. 1987, Pedlar et al. 1997).

Predators used corners to enter and exit grassland habitat, supporting previous findings (Ims 1995) that corners may funnel activity. The increased fox activity along straight grassland edges supports the idea that these features can be used as travel lanes (Andren 1995). The larger size of foxes correlates with greater movement distances, and these long edges may be an impor-

tant component influencing home range configuration and interactions with prey populations.

The close relationship between estimated predator presence and nest mortality rates supports the validity and utility of the predator model predictions. However, the importance of predator community cannot be overlooked when using these models. For example, if foxes are the primary predator affecting duck nest success, the model that explicitly addresses fox activity may be more useful than 1 that addresses all predators collectively.

MANAGEMENT IMPLICATIONS

By understanding the predators' view of the landscape, wildlife biologists can incorporate a larger-scale view into management plans that might influence the success of ground-nesting birds. Our research supports the importance of core habitat for nesting and further emphasizes that corridors and moderately sized patches of habitat near large blocks are foci of predator activity. Clark et al. (1999) found that grassland patches should be >15.6 ha to have adequate core area to improve nesting success of pheasants in these landscapes, although larger grassland blocks are suggested for waterfowl (Reynolds 2000, Sovada et al. 2000). However, in the highly impacted agricultural landscapes of the Corn Belt where a dilution effect is not as likely a management option, isolated grassland patches, roadsides, conservation buffers, and the characteristics of patch shape play a role in managing landscape because of the effect on predator behavior. More-focused management of cover within patches, exclusion of predators, or even expensive eradication may still play a role, but we contend that such efforts will not be as effective in the long run as will approaches based on the large-scale landscape perspective.

We propose that wildlife biologists could utilize models like those that we constructed to link landscape features within a GIS to predator presence and then reasonably compare predicted predator presence among landscape configurations. Managers could then plan restoration efforts and choose among land-use policies that would account for the potential influence of predators on nesting birds.

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Southern Great Plains Boomer



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Grasslands Ecosystems, Endangered Species, and Sustainable Ranching in the Mexico-U.S. Borderlands: Conference Proceedings

Ecosistemas de Pastizales, Especies en Peligro y Ganadería Sostenible en Tierras Fronterizas de México-Estados Unidos: Conferencia Transcripciones



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Abstract

The semi-arid grasslands in the Mexico-United States border region are relatively intact and provide one of the best opportunities in North America to preserve and nurture an extensive series of grassland ecosystems. The conference was organized to increase appreciation for the importance of the remaining semi-arid grasslands and to create a platform for expanding the integration of natural and social sciences among individuals and organizations. The conference was attended by ranchers, environmentalists, academics, and agency personnel from both nations. Main topics include grassland ecology and biodiversity, management and conservation, and sustainable borderland ranching. Endangered species management, especially of black-tailed prairie dogs (*Cynomys ludovicianus*), was an important topic. Oral presentations were in English or Spanish, with simultaneous translations, and the papers have been printed in both languages. The conference revealed the ties between ecological processes and environmental conditions in the Borderland grasslands and the cultural and economic priorities of the human communities who depend on them. This recognition should enable interested people and groups to work together to achieve satisfactory solutions to the challenges of the future.

Keywords: semi-arid grasslands, endangered species, sustainable ranching, Mexico-U.S. borderlands

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**Grasslands Ecosystems, Endangered Species, and
Sustainable Ranching in the Mexico-U.S. Borderlands:
Conference Proceedings**

**Ecosistemas de Pastizales, Especies en Peligro y
Ganadería Sostenible en Tierras Fronterizas de
México-Estados Unidos: Conferencia Transcripciones**

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J.W. Kieckhefer Foundation
Animas Foundation
Malpai Borderlands Group
Sonoran Institute
Udall Center for the Study of Public Policy
USDA Forest Service, Rocky Mountain Research Station,
Southwestern Borderlands Ecosystem Management Project

En nombre de *Ecosistemas de Pastizales, Especies en Peligro y Ganadería Sostenible en Tierras Fronterizas de México-Estados Unidos*, el comité organizador extiende un sincero agradecimiento a las siguientes prestigiadas organizaciones por su generoso apoyo para la organización de este evento:

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Sonoran Institute
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USDA Forest Service, Rocky Mountain Research Station,
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Attendees included ranchers from both sides of the border.
Los participantes incluyeron rancheros de ambos lados de la frontera.



Young attendees during a herpetology talk.
Jóvenes participantes durante una ponencia sobre herpetología.



Ray Turner in the questions and answers session.
Ray Turner en la sesión de preguntas y respuestas.



Mary Hershdofer, Xavier Basurto and Bill McDonald at the registration table.
Mary Hershdofer, Xavier Basurto y Bill McDonald en la mesa de registro.



Welcome to the conference by Mac Donaldson.
Bienvenida a la conferencia por Mac Donaldson.



The translation booth.
La cabina de traducción.

Introduction

Introducción

Towards Place-Based Borderlands Grassland Conservation

Xavier Basurto *University of Arizona*

Diana Hadley *Arizona State Museum*

When European explorers first observed the vast grasslands of the American continent, they viewed a series of interconnected, intact grassland ecosystems flourishing with an enormous diversity of flora and an abundance of wildlife. The term “sea of grass” appears frequently in descriptions of the vast prairie grasslands that extended from Canada to central Mexico. Many writers stated that the variety of wildlife species and their numbers “staggered the imagination.” Relying on the thriving grasslands, the plains teemed with bison, pronghorn, deer, bighorn sheep, badgers, fox, prairie dogs, wolves and grizzlies, eagles, hawks, a vast array of grassland birds, such as prairie chickens and burrowing owls, as well as the ubiquitous grasshopper.

Today, the situation is vastly different. Temperate grasslands have the lowest rate of protection of all the Earth’s biomes and are recognized as among the most endangered ecosystems on Earth. In the Midwestern United States, tallgrass prairie, mixed-grass prairie, and shortgrass prairie are among the most severely altered and diminished landscapes on the continent. Only in recent years have a few small patches of the Midwest’s remnant prairies received protection.

The semi-arid grasslands of the sparsely populated Borderlands region have fared a bit better than those of the Midwest. Neglect has engendered some degree of preservation, and thousands of square miles of native grasslands are still intact, even if not in the best condition. Today, the Borderlands region provides one of our best opportunities to preserve and nurture an extensive series of grassland ecosystems.

The conference, “Grassland Ecosystems, Endangered Species, and Sustainable Ranching in the Mexico-United States Borderlands,” held in Nuevas Casas Grandes, Chihuahua, in 2001, had multiple purposes. As conference organizers, our first objective was to increase appreciation for the importance of the remaining semi-arid grassland ecosystems along the border. Second, we wanted to create a platform for expanding integration between the natural sciences and the social and economic structures that provide for human subsistence in these grasslands. Conference goals were consistent with the objectives established by Michael Soulé, when

he introduced the concepts of conservation biology into mainstream science. With a base in conservation biology, the format and structure of the conference provided for increased attention to the needs of the human communities that rely on grasslands, in recognition that the success of biological conservation depends on its acceptance, compatibility, and integration into social, economic, and cultural systems.

The Casas Grandes conference was a continuation of the on-going discussion of the values and conservation of semi-arid grasslands that began in 1996 at the grasslands conference in Tucson sponsored by the Audubon Research Ranch Foundation and other organizations. As the first bi-national conference on grasslands conservation, the 2001 “Grassland Ecosystems, Endangered Species, and Sustainable Ranching in the Mexico-United States Borderlands” conference added an exciting, international mix of interests, bringing together researchers, natural resources managers, and local users (ranchers, *ejidatarios* and tourism businesses) from both sides of the border. The meeting took place in the center of the Borderland grasslands, at a location where many divergent views of appropriate uses of grasslands exist. Representatives of the divergent views were able to discuss issues of concern on their home ground. One group of discussions pointed to the need for better integration between community goals and research efforts. Other discussions shed light on various aspects of grassland ecology and methods for maintaining biological diversity without hampering economic development.

The most important message that emerged from the conference was cultural. The conference revealed the ties between the ecological processes and environmental conditions of the Borderland grasslands and the cultures and economies of the human communities whose subsistence depends on them. Recognition of these ties will enable all those concerned with the uses and/or preservation of grasslands to find a common ground for solutions to the challenges of the future.

The conference organizers decided to publish the proceedings of this experience, because we believe that the papers as well as the informal opinions expressed by participants may provide useful guidelines for future

meetings, research, or grassland management. The proceedings reflect the bi-national, multidisciplinary, and inclusive nature of the conference and depart from the standard form of such publications. Papers are presented in the original language, Spanish or English, with a summary translated into the second language. In addition to academic articles, the proceedings include transcriptions of informal talks given at the conference and reflect the informal, non-academic nature of these presentations. Our goal is to make this publication available to the widest audience possible and to the full range of persons interested in the ecology, values, and uses of the Borderland ecosystems. The articles and talks published in these proceedings reflect the opinions of the authors or speakers, and in no way reflect the opinions of the U.S. Forest Service, which has so generously agreed to publish them.

Finally, we wish to acknowledge a number of individuals who throughout the conference and publication process provided us with invaluable help and comments. Mr. Norman Bebon (U.S. Customs Service), Ms. Patricia Przbyl (U.S. Immigration and Naturalization Service) and their staffs provided all the necessary support to enable us to conduct a “bi-national field trip” and cross the border at the Berrendo, Chihuahua/Antelope Wells, New Mexico crossing. Ms. Louise Peterson drove us to the Gray Ranch after waiting patiently for us for hours at

the border. The professional translating skills of Angelina C. Covarrubias and Carlos Portillo made it possible to have a truly bilingual meeting. Ms. Imelda Dávila and her staff at the Hotel Hacienda were always helpful and flexible in accommodating our sometimes unusual needs. Members of the Ejido San Pedro prepared a delicious lunch for all the participants, served it at the San Pedro Research Station, and graciously invited us into their homes. To all of them, our sincere thanks.

Special thanks also to Mac Donaldson, Vista Michael, Linda Kennedy, Bill Branan and Owen McCaffrey of the Research Ranch Foundation board of directors and the Audubon Whittell Research Ranch staff. For their dynamism and enthusiastic support during the conference, we are sincerely indebted to our conference assistants: Jerrod Butcher, Juan Caicedo, Samia Carrillo, Alex Conley, Rocio Covarrubias, Jennie Duberstein, Dan Ginter, Mary Hershdorfer, Ana Davidson, Erika Marce, Lourdes Perches, Marcela López and Eduardo Ruiz. We are grateful for the editorial skills of Tiffany Ash, Ricardo and Rocio Covarrubias, Brooke Gebow, María Eugenia Guillermo, Diego Valdés, and Emily Will. Finally, we wish to express our gratitude to Gerald Gottfried and Carl Edminster and the U.S. Forest Service for support and interest in the publication of these proceedings.

It was a great pleasure to work with all of you. Thanks for the opportunity.

Xavier Basurto and Diana Hadley
Conference Organizers

Hacia la Conservación de Pastizales en Tierras Fronterizas

Xavier Basurto *University of Arizona*

Diana Hadley *Arizona State Museum*

Cuando los exploradores Europeos observaron por vez primera los vastos pastizales del continente Americano, vieron una serie de ecosistemas de pastizal intactos, interconectados, florecientes, con una enorme diversidad de flora y una abundante fauna silvestre. El término “Mar de Pastos” aparece con frecuencia en descripciones de los vastos pastizales de pradera que se extendían desde Canadá hasta el centro de México. Muchos escritores manifestaron que la variedad de especies de fauna silvestre y sus densidades “hacían dar vuelta la imaginación”. Debido a la prosperidad de los pastizales, los valles estaban llenos de bisontes, berrendos, venados, cimarrones, tejones, zorras, perritos llaneros, lobos y osos pardos, águilas, halcones, gran cantidad de aves de los pastizales como las gallinas llaneras y tecolotes zancos, así como los omnipresentes saltamontes.

Hoy en día, la situación es muy diferente. Los pastizales templados tienen el índice de protección más bajo de todos los biomas de la Tierra y están reconocidos como los ecosistemas más amenazados del planeta. En el occidente medio de los Estados Unidos, las praderas de pastos altos, pastos mixtos y pastos bajos, están entre los sistemas más severamente alterados y restringidos en el continente. Únicamente en años recientes, algunas áreas pequeñas de los restos de las praderas de la región central, han recibido protección.

Los pastizales semiáridos de las tierras esparcidamente pobladas de la región fronteriza han tenido un mejor fin que las del medio-oeste. El abandono ha generado cierto grado de preservación y miles de kilómetros cuadrados de pastizales nativos están todavía intactos. En la actualidad, la región fronteriza proporciona una de nuestras mejores oportunidades para preservar y promover el crecimiento de una serie extensiva de ecosistemas de pastizal.

La conferencia “Ecosistemas de Pastizales, Especies en Peligro y Ganadería Sostenible en Tierras Fronterizas de México-Estados Unidos” realizada en Nuevo Casas Grandes, Chihuahua en 2001, tuvo múltiples propósitos. Como organizadores de la conferencia, nuestro primer objetivo fue incrementar la apreciación sobre los ecosistemas de pastizales semiáridos que aún persisten a lo largo de la frontera. Segundo, quisimos crear una plataforma que facilite la integración entre las ciencias naturales y

las estructuras económicas y sociales que proporcionan subsistencia a los humanos en esos pastizales. Las metas de la conferencia fueron consistentes con los objetivos establecidos por Michael Soulé, cuando introdujo los conceptos de la biología de la conservación a las principales corrientes científicas. Con base en la biología de la conservación, el formato y estructura de la conferencia proporcionaron una mayor atención a las necesidades de las comunidades humanas que se relacionan con los pastizales, reconociendo que el éxito de la conservación depende de su aceptación, compatibilidad e integración con sistemas sociales, económicos y culturales.

La conferencia de Casas Grandes fue la continuación de una discusión, que sobre los valores y la conservación de los pastizales semiáridos, comenzó en 1996 con la conferencia de pastizales en Tucson patrocinada por la Audubon Research Ranch Foundation y otras organizaciones. Como la primera conferencia binacional sobre la conservación de pastizales, la conferencia “Ecosistemas de Pastizales, Especies en Peligro y Ganadería Sostenible en Tierras Fronterizas de México-Estados Unidos” de 2001, añadió una excitante mezcla internacional de intereses, uniendo a investigadores, administradores de recursos naturales y usuarios locales (ganaderos, ejidatarios y representantes de turismo) de ambos lados de la frontera. La reunión se realizó en el centro de los pastizales fronterizos, en un lugar donde existen muchas perspectivas diferentes sobre los usos adecuados de los pastizales. Representantes de diferentes perspectivas pudieron discutir cuestiones de interés en su tierra. Algunas discusiones se enfocaron en la necesidad de una mejor integración entre las metas de la comunidad y los esfuerzos de investigación. Otras discusiones iluminaron varios aspectos de la ecología de los pastizales y los métodos para mantener la diversidad biológica sin dificultar el desarrollo económico.

El mensaje más importante que surgió de la conferencia fue de ámbito cultural.

La conferencia reveló los lazos entre los procesos ecológicos y las condiciones ambientales de las comunidades humanas cuya subsistencia depende de ellos. El reconocimiento de estos lazos permitirá a todos los interesados en el uso y la conservación de los pastizales,

encontrar un punto en común para las soluciones a los retos del futuro.

Los organizadores de la conferencia decidieron publicar las memorias de esta experiencia, porque creemos que los trabajos al igual que las opiniones informales expresadas por los participantes pueden brindar lineamientos útiles para las reuniones, la investigación y el manejo de pastizales en el futuro. Las memorias reflejan la naturaleza binacional, multidisciplinaria y global de la conferencia y parten de la forma estándar de dichas publicaciones. Los trabajos se presentan en su idioma original, español o inglés, con un resumen traducido al segundo idioma. Además de los artículos académicos, las memorias incluyen la transcripción de pláticas informales presentadas en la conferencia y reflejan la naturaleza informal y no academica de estas ponencias. Nuestra meta es hacer disponible esta publicación al mayor público posible y al mayor rango de personas interesadas en la ecología, los valores y los usos de los ecosistemas fronterizos. Los artículos y las pláticas publicadas en estas memorias reflejan las opiniones de los autores y oradores, y de ninguna manera reflejan las opiniones del Servicio Forestal de los EE.UU., que con generosidad aceptó publicarlas.

Finalmente, deseamos agradecer a un número de individuos que a lo largo de toda la conferencia y el proceso de publicación nos brindaron su valiosa ayuda y comentarios. El Sr. Norman Bebon (Servicio Aduanal de los EE.UU.), la Sra. Patricia Przbyl (Servicio de Inmigración y Naturalización de los EE.UU.) y su personal brindaron todo el apoyo necesario para permitirnos realizar una “salida de campo binacional” y cruzar la

frontera en Berrendo, Chihuahua – Antelope Wells, Nuevo México. La Sra. Louise Peterson nos condujo al Gray Ranch después de esperarnos pacientemente por horas en la frontera. Las habilidades profesionales de traducción de Angelina C. Covarrubias y Carlos Portillo hicieron posible una verdadera reunión bilingüe. La Sra. Imelda Dávila y su personal del Hotel Hacienda siempre se mostraron serviciales y flexibles a complacer nuestras necesidades, en ocasiones, poco comunes. Los miembros del ejido San Pedro prepararon un delicioso almuerzo para todos los participantes, servida en la Estación de Investigación San Pedro, además muy gentilmente nos invitaron a sus hogares. A todos ellos, nuestro más sincero agradecimiento.

Agradecemos especialmente a Mac Donaldson, Vista Michael, Linda Kennedy, Bill Branan y Owen McCaffrey del consejo directivo del Research Ranch Foundation y al personal del Audubon Whittell Research Ranch. Por su dinamismo y ayuda entusiasta durante la conferencia, estamos sinceramente agradecidos con nuestros asistentes: Jerrod Butcher, Juan Caicedo, Samia Carrillo, Alex Conley, Rocío Covarrubias, Jennie Duberstein, Dan Ginter, Mary Hershdorfer, Ana Davidson, Erika Marce, Lourdes Perches, Macela López y Eduardo Ruiz. Agradecemos las habilidades editoriales de Tiffany Ash, Ricardo y Rocío Covarrubias, Brooke Gebow, María Eugenia Guillermo, Diego Valdés y Emily Will. Finalmente, deseamos expresar nuestro agradecimiento a Gerald Gottfried y Carl Edminster y al Servicio Forestal de los EE.UU. por su apoyo e interés en la publicación de estas memorias.

Fue un gran placer trabajar con todos ustedes. Gracias por la oportunidad de hacerlo.

Xavier Basurto y Diana Hadley,
Organizadores de la Conferencia

Welcome

Mac Donaldson *Empire Ranch*

Ladies and Gentlemen:

On behalf of the Audubon Research Ranch, welcome to this conference concerning the Black-Tailed Prairie Dog.

This conference, a continuation of the Grasslands Ecosystem Session in Tucson, Arizona, in 1996 is to further the knowledge and understanding of these grasslands that we live in, and an effort to share these unique biotic communities with others.

The Black-Tailed Prairie Dog is found from Canada to Mexico and is one member of the animal kingdom that's presence has been greatly reduced through European impact.

Often misunderstood and easily eliminated, this rodent is representative of a once flourishing community that was integral to our biodiverse plains and prairies.

I hope that the health of these lands will continue to improve and that the knowledge gained and spread by this conference will enhance our presence upon earth.

Bienvenida

Mac Donaldson *Rancho Empire*

Damas y Caballeros:

A nombre del Audubon Research Ranch les doy la bienvenida a esta Conferencia Binacional titulada Ecosistemas de Pastizal, Especies en Peligro y Ganadería Sustentable en la Frontera México-Estados Unidos, que aborda ampliamente el tema del perrito llanero de Cola Negra.

Esta conferencia, una continuación de la Sesión de Ecosistemas de Pastizal en Tucson, Arizona en 1996, tiene el propósito de ampliar nuestro conocimiento y entendimiento de estos pastizales en los que vivimos,

y representa también un esfuerzo por compartir estas singulares comunidades bióticas con los demás.

El Perrito llanero de cola negra se encuentra desde Canadá hasta México y es un miembro del reino animal cuya presencia se ha reducido considerablemente a causa del impacto de la colonización Europea.

Con frecuencia incomprendido y fácilmente eliminado, este roedor es representativo de una comunidad antaño floreciente que era parte integral de la biodiversidad de nuestras llanuras y praderas.

Espero que la salud de estas tierras siga mejorando y que el conocimiento obtenido y difundido durante esta conferencia complete nuestra presencia en el mundo.

Section I

Grassland Ecology and Biodiversity

Ecología y Biodiversidad Pastizale

Grassland Ecology and Diversity

(invited paper)

Laurie B. Abbott *Department of Animal and Range Sciences, New Mexico State University*

Grasslands of the Chihuahuan Desert region are ecologically and economically important. These grasslands are valued for their rangeland, wildlife, watershed, and recreation resources. Biological diversity also raises the value of grassland communities. The potential for multiple uses within the region increases as the diversity of the resource base increases. In order to sustainably manage for biological diversity, it is important to understand the factors that influence the ability of organisms to coexist within a given area. The following discussion focuses on the main factors that influence the diversity of Chihuahuan Desert grassland communities.

The factors that influence diversity fall into five major categories: species characteristics, biotic interactions, resource availability, environmental heterogeneity, and disturbance (Harper 1977, Huston 1994). None of these categories is mutually exclusive, but they frequently interact to influence the distribution and abundance of organisms on the landscape. I will first describe each of these factors individually, and then discuss how the interactions of these factors may influence species diversity within communities.

Species characteristics include morphological, physiological, reproductive, and life history characteristics. They comprise the essential physical and behavioral aspects of organisms. Plant morphology may be described generally in terms of growth form, above- and below-ground structures, and size. Physiological differences are broadly categorized in terms of metabolic requirements and tolerances to environmental conditions. Reproductive and life history traits include lifespan, age of first reproduction, longevity of the reproductive period, flowering and fruiting phenology, seed dispersal, dormancy, and germination requirements. These components are interrelated and act in combination on the ecology of the organism. For example, resource acquisition, carbohydrate allocation, and growth are physiological functions, but these functions depend on morphological structures for uptake, transport, and growth. Similarly, reproduction usually commences after plants reach a minimum size, allocation of carbohydrates to reproductive structures influences developmental phenology, and seed morphology affects seed dispersal. These linkages between form and function

are fundamental to the relationship of organisms to their environment.

Biotic interactions are the suite of connections between organisms within a community. Interactions may occur between member of the same or different species, and the outcome of these interactions may be positive, negative, or neutral for the participating organisms. Competition, defined as reciprocal negative interaction between two organisms, has traditionally been considered as one of the most important processes structuring communities (Connell 1990). The strength of competitive effects is influenced by the resource-acquisition abilities of individual organisms, the limited resources for which the organisms are competing, and the relative abundances of competing organisms.

Herbivory is another important form of biotic interaction in grasslands. The effects of herbivory are influenced by characteristics of both the herbivores and the vegetation. The kinds and amounts of vegetation harvested by herbivores vary with differences in selectivity, that depend on food preferences and ability to harvest. In turn, the response of plants depends on their ability to either tolerate or avoid herbivory.

Other important biotic interactions include facilitation and mutualism. Facilitation occurs when one organism alters the environment such that it becomes more favorable for a second organism. Mutualism results in reciprocal positive interactions—when both organisms benefit. In the pollination example, the plant benefits from the transfer of pollen between flowers, and the pollinator benefits from food gathered at the time of pollination.

The availability of resources influences the distribution and abundance of both plants and animals. Key resources for plants are light, nutrients, water, oxygen, carbon dioxide, and space. Animals require adequate food, water, and cover to carry out activities necessary to persist and thrive. The resource requirements vary by species. Furthermore, animal social behaviors range from solitary to highly gregarious. Thus, the availability of other individuals of the same species differentially influences the ability of species to mate, rear offspring, forage, and hunt.

Environmental heterogeneity commonly dictates the spatial and temporal availability of resources. Variable availability of resources exists due to differences in

landforms, geologic materials, and climate. These factors interact with biotic organisms over time to influence soil development. Soils characteristics such as texture, depth, water-holding capacity, pH, cation exchange capacity, and temperature are important determinants of the distribution and abundance of plants, which in turn influence the availability of suitable habitat for both domestic animals and wildlife. Temperature and precipitation typically vary both spatially and temporally. In addition to the total amount of precipitation that falls at a location, the characteristic frequency and intensity of precipitation events is of particular importance.

Disturbances result in relatively sudden mortality or biomass loss within a community (White and Pickett 1985). The number of organisms killed may vary from less than one (in the case of some plants) to all the members of a community. Disturbances vary in frequency, intensity, type, spatial extent, and seasons in which they occur. Disturbance regimes are the suite of these disturbance components that characteristically influence a site. Disturbances may originate naturally or through the activities of humans. Disturbances common in Chihuahuan Desert Grasslands include herbivory, fire, drought, invasive species introductions, and land-use change, but extreme cold events, disease, floods, and landslides may also occur.

Species characteristics, biotic interactions, resource availability, environmental heterogeneity, and disturbance are not independent processes or factors within communities and ecosystems. Multiple interactions of species and processes are instrumental in creating and maintaining diversity, as illustrated in the following examples.

To some degree, interactions between organisms are defined by their morphological and physiological characteristics. For example, many grass species tolerate grazing because their apical meristems (buds or growing points) are protected or are low to the ground, and thus new tillers can grow from these protected buds after removal of top-growth. Similarly, an herbivore's perception of plant palatability is affected by the presence or absence of protective morphological features such as spines and awns, or by relative differences in biochemical constituents such as protein, carbohydrates, and secondary compounds.

Resource availability and environmental heterogeneity are closely associated. For example, the availability of water is a function of soil texture, structure, and depth, in addition to position within the landscape. Nutrient availability is similarly influenced by soil texture; cation-exchange capacity and water-holding capacity of clay-rich soils are typically greater than sandy soils. Organic matter also influences water and nutrient status of soils, thus the availability of these physical resources

is affected by the organisms that once inhabited that landscape. Living things can also alter temperature regimes, intercept precipitation, reduce evaporation, or increase soil moisture loss through transpiration.

Disturbances structure communities primarily because they suddenly change mortality rates, affecting population sizes and age distributions of populations relative to each other. Species response to different types of disturbances is often a function of morphological, physiological, and reproductive traits. For example, thick bark or buried meristematic tissue (buds) may protect plants from damage due to fire or severe cold. Short-lived species are favored by frequent disturbances, and long-lived species should dominate in communities where the frequency of disturbances is very low. Species diversity should be optimized when intermediate levels of disturbance occur (Connell 1978). The distribution of organisms is influenced by the interaction of resource availability, environmental heterogeneity, and species characteristics, and these factors influence the spatial dimension of some disturbances. For example, patchy distribution of herbaceous plants affects the impact of fire through the continuity of fine fuels, and selective grazing may result in patches that are more heavily impacted by herbivores. The patches themselves vary in substrate and available resources, and may in turn be colonized by different sets of species. Thus, disturbances that result in patchy mosaics of habitat promote coexistence through local influx and loss of species (Harper 1977).

Finally, spatial and temporal scales must be considered in any discussion of biological diversity. The spatial scales of resource and environmental changes are important determinants of which organisms occur on which sites. Biotic interactions, vital processes, and resource availability may happen on short time scales (from seconds to days) as well as longer time scales, incorporating seasons, years, and decades.

In conclusion, the diversity of Chihuahuan Desert Grasslands results from the interactions of multiple factors. Understanding the relationships of these factors provides some measure of insight to land managers interested in maintaining and manipulating these richly diverse lands and the organisms that inhabit them.

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Ecología y Diversidad de Pastizales

(resumen)

Laurie B. Abbott *Departamento de Ciencia Animal y de Pastizales, Universidad Estatal de Nuevo México*

Los pastizales de la región del Desierto Chihuahuense son ecológica y económicamente importantes. Esos pastizales son de gran valor debido a sus recursos ganaderos, faunísticos, hidrológicos y recreativos, así como a su diversidad biológica. El potencial de usos múltiples dentro de la región aumenta conforme la diversidad de los recursos se incrementa. Para administrar en forma sustentable la diversidad biológica, es importante entender los factores que influyen en la habilidad de los organismos para coexistir dentro de un área determinada. La siguiente discusión se enfoca en los factores principales que influyen en la diversidad de las comunidades de los pastizales del Desierto Chihuahuense.

Los factores que influyen en la diversidad se agrupan en cinco categorías: características de la especie, interacciones bióticas, disponibilidad de recursos, heterogeneidad ambiental, y perturbación (Harper 1977, Huston 1994). Ninguna de estas categorías es mutuamente excluyente, sino que interactúan con frecuencia para influir en la distribución y abundancia de los organismos en el paisaje.

Las características de las especies incluyen rasgos morfológicos, fisiológicos, reproductivos, y de antecedentes vitales. Ellos abarcan los aspectos físicos y del comportamiento que son esenciales en los organismos. La morfología de las plantas generalmente se describe en términos de formas de crecimiento, estructuras subterráneas y aéreas, y tamaño. Las diferencias fisiológicas se categorizan según el requerimiento metabólico y la tolerancia a las condiciones ambientales. Las características reproductivas, y de antecedentes vitales incluyen el ciclo de vida, edad de la primera experiencia reproductiva, longevidad del periodo reproductivo, fenología de la floración y la fructificación, dispersión de semillas, dormancia y requerimientos para la germinación. Estos componentes están interrelacionados y actúan en forma combinada sobre la ecología del organismo. Por ejemplo, la adquisición de recursos, la asignación de carbohidratos y el crecimiento son funciones fisiológicas, pero estas funciones dependen de las estructuras morfológicas para tomar los recursos, trasportarlos y crecer. Esas relaciones entre forma y función son fundamentales para la interrelación de los organismos con su medio ambiente.

Las interacciones bióticas son el conjunto de interacciones entre los organismos de una comunidad. Estas pueden darse entre miembros de la misma especie o de

diferentes especies, y el resultado de las interacciones entre los individuos participantes puede ser positivo, negativo o neutro. La competencia, definida como una interacción recíproca negativa entre dos organismos, ha sido considerada como uno de los procesos más importantes en la estructuración de las comunidades (Connell, 1990). La intensidad de los efectos competitivos esta influenciada por las habilidades de los organismos para adquirir los recursos, los escasos recursos por los que compiten los organismos y las abundancias relativas de los organismos competidores.

La herbivoría es otra forma importante de interacción biótica en los pastizales. Los efectos de la herbivoría están influenciados por las características de los herbívoros y la vegetación. Las clases y cantidades de vegetación consumida por los herbívoros varía con las diferencias en selectividad, la cual depende de las preferencias alimenticias y la habilidad para cosechar. A su vez, la respuesta de las plantas depende de su habilidad para tolerar o evitar la herbivoría.

Otras interacciones bióticas importantes incluyen la facilitación y el mutualismo. La facilitación ocurre cuando un organismo altera el ambiente de tal forma que lo hace favorable para un segundo organismo. El mutualismo resulta de interacciones recíprocas positivas, en las que ambos organismos interactuantes, se benefician. En la polinización, por ejemplo, la planta se beneficia al ser transportado su polen hacia otras flores, mientras que el polinizador se beneficia con el néctar obtenido en el tiempo de la polinización.

La disponibilidad de recursos influye en la distribución y abundancia de plantas y animales. Los recursos clave para las plantas son la luz, nutrimentos, agua, oxígeno, dióxido de carbono y espacio. Los animales requieren en forma adecuada de alimento, agua y cobertura para realizar las actividades necesarias para subsistir y producir frutos. La necesidad de recursos varía entre las especies. Además, las conductas sociales en los animales varía desde organismos solitarios hasta altamente gregarios. Así, la presencia de otros individuos de la misma especie influye en forma diferencial en la habilidad de la especie para aparearse, producir progenie, alimentarse y depredar.

La heterogeneidad ambiental generalmente determina la disponibilidad espacial y temporal de los recursos.

Existe variación en la disponibilidad de recursos debido a diferencias en el paisaje, materiales geológicos y el clima. Estos factores interactúan a través del tiempo con los organismos vivos para influir en el desarrollo del suelo. Las características del suelo tales como la textura, profundidad, capacidad de retención de agua, pH, capacidad de intercambio catiónico y temperatura, son determinantes importantes en la distribución y abundancia de las plantas, las cuales a su vez influyen en la disponibilidad de hábitats adecuados para la fauna doméstica y silvestre. La temperatura y la precipitación típicamente varían tanto espacial como temporalmente. En adición a la cantidad total de precipitación que cae en una localidad, es de particular importancia la frecuencia e intensidad característica de los eventos lluviosos.

Las perturbaciones son procesos que tienen como resultado una mortalidad o una pérdida de biomasa repentina dentro de una comunidad (White and Pickett, 1985). El número de organismos muertos puede variar de menos de uno (en el caso de algunas plantas) hasta todos los miembros de la comunidad. Las perturbaciones varían en frecuencia, intensidad, tipo, extensión espacial y temporadas en las que ocurren. Estas pueden originarse naturalmente o a través de las actividades humanas. Las perturbaciones comunes en los pastizales del Desierto Chihuahuense incluyen la herbivoría, el fuego, sequías, introducción de especies invasoras y el cambio en el uso del suelo, aunque también pueden ocurrir eventos de heladas extremas, enfermedades, inundaciones y derrumbes de tierras.

Las características de las especies, las interacciones bióticas, la disponibilidad de recursos, la heterogeneidad ambiental y la perturbación no son procesos o factores independientes dentro de las comunidades y ecosistemas. Las interacciones múltiples de las especies y procesos, son esenciales para crear y mantener la diversidad, como se ilustra en los siguientes ejemplos.

Hasta cierto grado, las interacciones entre los organismos están definidas por sus características morfológicas y fisiológicas. Por ejemplo, muchas especies de gramíneas toleran el pastoreo debido a que sus meristemos apicales (yemas o puntos de crecimiento) están protegidos o crecen por debajo del suelo y de esta forma nuevos brotes pueden crecer de estas yemas protegidas después de que las partes aéreas son removidas. Similarmente, la percepción de un herbívoro sobre la palatabilidad de una planta es afectada por la presencia o ausencia de estructuras morfológicas protectoras tales como espinas o aristas o por diferencias relativas en los componentes bioquímicos tales como proteínas, carbohidratos y compuestos secundarios.

La disponibilidad de recursos y la heterogeneidad ambiental están muy asociadas. Por ejemplo, la disponibilidad de agua está en función de la textura, estructura

y profundidad del suelo, además de la ubicación en el paisaje. De igual forma, la disponibilidad de nutrientes está influenciada por la textura del suelo; la capacidad de intercambio catiónico y la capacidad de retención de agua es regularmente mayor en los suelos arcillosos que en los arenosos. La materia orgánica influye también en el *status* de agua y nutrientes de los suelos y, asimismo, la disponibilidad de esos recursos físicos es afectada por los organismos que alguna vez habitaron en el paisaje. Los elementos vivos pueden también alterar los regímenes de temperatura, interceptar la precipitación, reducir la evaporación o incrementar la pérdida de humedad del suelo a través de la transpiración.

Las perturbaciones estructuran a las comunidades principalmente porque cambian en forma repentina las tasas de mortalidad, afectando los tamaños y distribución de edades en las poblaciones. La respuesta de las especies a diferentes tipos de perturbaciones es a menudo una función de procesos morfológicos, fisiológicos y reproductivos. Por ejemplo, una corteza gruesa o los tejidos meristemáticos ocultos (yemas) pueden proteger a las plantas de ser dañadas por el fuego o por heladas severas.

Las especies de ciclo corto son favorecidas por las perturbaciones frecuentes, en tanto que las de ciclo largo dominan en comunidades donde la frecuencia de perturbaciones es muy baja. La diversidad de especies se optimiza cuando ocurren niveles moderados de perturbación (Connell, 1978). La distribución de organismos está influenciada por la interacción de la disponibilidad de recursos, la heterogeneidad ambiental y las características de las especies y estos factores influyen en la dimensión espacial de algunas perturbaciones. Por ejemplo, la distribución en manchones de plantas herbáceas afecta el impacto del fuego en la continuidad de materiales finos incendiables y, asimismo, un pastoreo selectivo puede darse en manchones que son más fuertemente impactados por los herbívoros. Los manchones mismos varían con el sustrato y la disponibilidad de recursos y pueden, a su vez, ser colonizados por diferentes grupos de especies. Así, las perturbaciones que resultan en mosaicos de hábitats, promueven la coexistencia a través de un ingreso y pérdida de especies a nivel local (Harper, 1977).

Finalmente, las escalas espaciales y temporales deben considerarse en cualquier discusión sobre diversidad biológica. Las escalas espaciales y los cambios ambientales son determinantes de los organismos que habitan en determinados sitios. Las interacciones bióticas, los procesos vitales y la disponibilidad de recursos pueden ocurrir en escalas de tiempo cortas (de segundos a días) así como escalas de tiempo largas, comprendiendo estaciones, años y décadas.

En conclusión, la diversidad de los pastizales del Desierto Chihuahuense es el resultado de las

interacciones de múltiples factores. El entendimiento de las interrelaciones de esos factores proporciona una medida de conocimiento profundo para los manejadores de pastizales interesados en la conservación y manipulación de esas tierras ricas en diversidad y de los organismos que las habitan.

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Status and Distribution of Chihuahuan Desert Grasslands in the United States and Mexico

(invited paper)

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Grasslands comprise a small part of the Chihuahuan Desert but are vital to the biological diversity of the ecoregion. Characteristic grasses of the Chihuahuan Desert are tobosa (*Pleuraphis mutica*) and black grama (*Bouteloua eriopoda*) but other common species include alakali sacaton (*Sporobolus airoides*), big alkali sacaton (*S. wrightii*), mesa dropseed (*S. flexuosus*), blue grama (*B. gracilis*), sideoats grama (*B. curtipendula*), hairy grama (*B. hirsuta*), slender grama (*B. filiformis*), chino grama (*B. brevista*), spruce top grama (*B. chondrosioides*), bush muhly (*Muhlenbergia porteri*), several three awns (*Aristida* spp.), and fluff grass (*Dasyochloa pulchella*) (Johnson 1974, Dinerstein et al. 2000). Many of the sites discussed in this paper and in greater detail in Dinerstein et al. (2000), contain large, contiguous tracts of grassland that support critical ecological processes, numerous endemic species and high plant and animal diversity.

Chihuahuan Desert grasslands were formerly characterized by extensive areas of tobosa and black grama with blue grama dominating at higher elevations. However, grassland areas throughout the Chihuahuan Desert are undergoing large-scale transformation from grass-dominated to shrub-dominated systems (Buffington and Herbel 1965, Weltzin et al 1997). The encroachment of native shrubs, including honey mesquite (*Prosopis glandulosa*), creosote (*Larrea tridentata*), and ephedra (*Ephedra* spp.), into former open grassland have been attributed to a variety of factors including climate change, over grazing, fire suppression, distribution of shrub seeds by domestic livestock, and removal of native herbivores (Herbel et al. 1972, Nielson 1986, Schlesinger et al. 1990). Such desertification typically results in the formation of coppice dunes, reduced grass cover, and increased heterogeneity in resource distribution (Nielson 1986), seriously compromising the integrity of the system.

A review of information collected from experts at the 1997 Biological Assessment Workshop of the Chihuahuan Desert indicates that there are still many high quality grasslands within the ecoregion. World Wildlife Fund (WWF) and others hosted this workshop to identify

high biodiversity sites in the Chihuahuan Desert, defined by WWF (Dinerstein et al. 2000) as covering 629,000 km² (Figure 1). Of the 61 terrestrial sites nominated by experts at the workshop, 14 of these areas are characterized fully or partly by significant amounts of grassland. In this paper we have estimated the amount of grassland in each of these 14 priority conservation sites (Table 1) based on the workshop results and our field experience.

Extant grasslands comprise just 10% of the entire ecoregion. However, they cover nearly 6,000,000 hectares, 23% of the 268,000 km² area of the workshop's 61 priority conservation sites. If the full complement of species, habitats, and processes of the Chihuahuan Desert are to be conserved, grassland management and protection strategies must be developed. This paper summarizes some of the findings of that workshop specifically related to the distribution and status of Chihuahuan Desert grasslands. Figure 1, adapted from Dinerstein et al. (2000), presents is a map of the Chihuahuan Desert with numbered priority sites for conservation. Numbered sites that represent grasslands correspond to the site descriptions in this paper discussed below.

Priority Grassland Sites within the Chihuahuan Desert

Appleton-Whittell Research Ranch Sanctuary and Canelo Hills (1.08)—The grasslands within this 62-km² region are located in southeast Arizona and are a mixture of private, federal, and state lands. These grasslands are dominated by blue and hairy grama and big alkali sacaton. The 20,149-ha Audubon research ranch is located within this area. These grasslands have not been grazed since 1969.

Big Hatchet–Alamo Hueco Mountains (1.22)—This area is located in southwest New Mexico along the U.S./Mexico border, owned and managed by the Bureau of Land Management. It contains low, mid, and high elevation grasslands. Degraded low-elevation grasslands now consist of creosote and fluff grass. Mid-elevation grasslands contain grama grasses, tobosa interspersed with

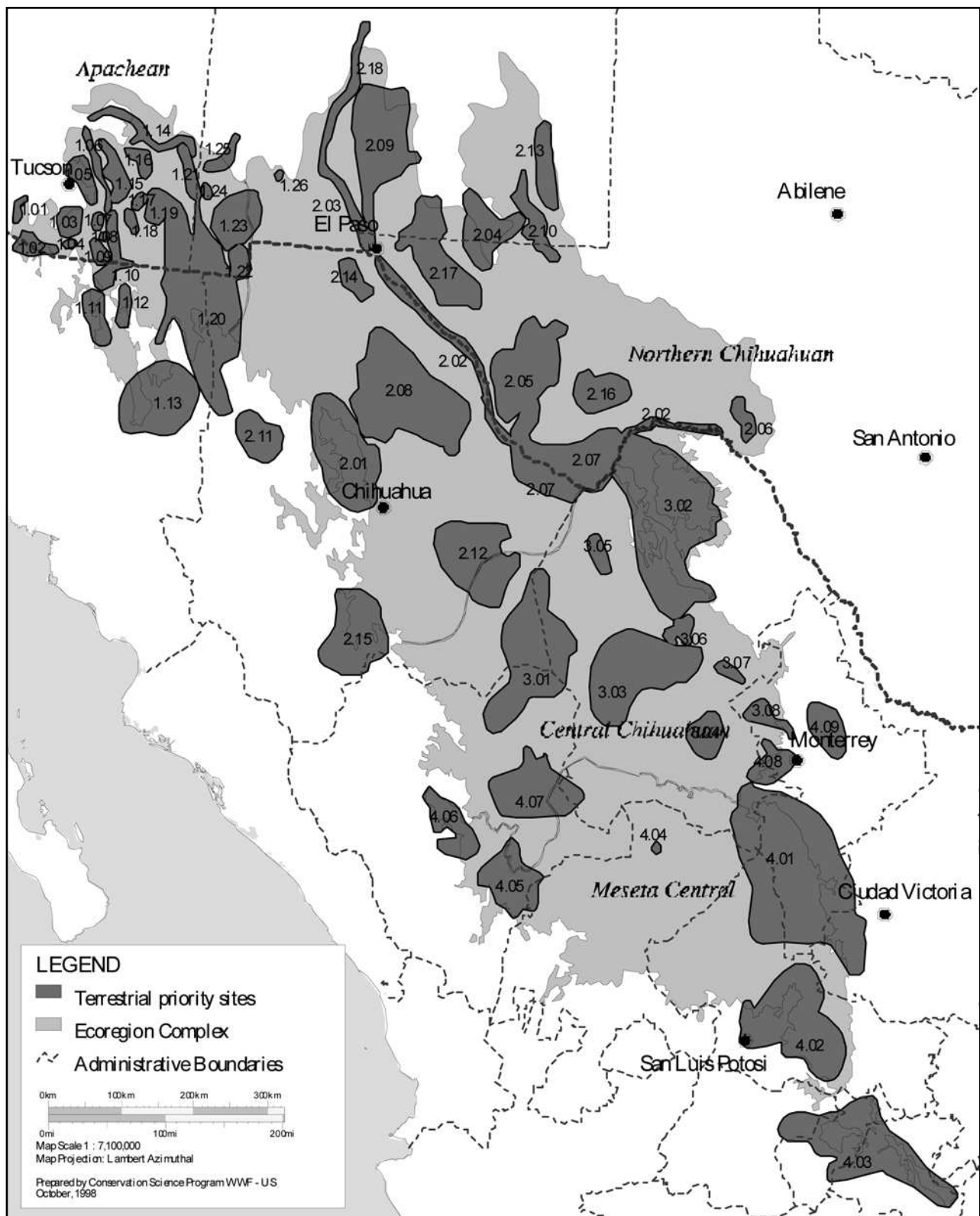


Figure 1. Priority sites for conservation in the Chihuahuan Desert identified by the World Wildlife Fund.

Table 1. Priority Grassland Sites for Conservation in the Chihuahuan Desert.

Map #	Priority Site Name	Total Area of Site in Km ²	% Grassland	Total Area Grassland in Km ²
1.08	Appleton-Whittell	62	100	62
1.19	Sulphur Springs Valley	621	65	403
1.20	Chiricahua-Peloncillo-Sierra Madre Complex	19,156	50	9,578
1.22	Big Hatchets-Alamo Hueco Complex	1,022	60	613
1.24	Lordsburg Playa	209	70	146
2.01	Sierra del Nido	9,827	40	3,390
2.05	Davis-Chinati Mts.	8,643	50	4,321
2.08	Chihuahuan Grasslands	15,889	80	12,711
2.09	Tularosa Basin	10,101	50	5,050
2.12	La Perla	9,069	80	7,255
2.13	Mescalero Dunes	2,297	60	1,378
2.16	Marathon Basin	3,130	80	2,504
4.01	Altiplano Mexicano Nordoriental	60,000	20	12,000
		140,026		59,411

mesquite shrublands. High-elevation lands primarily support grama grasses interspersed with beargrass (*Nolina microcarpa*), silktassel (*Garrya wrightii*), whitethorn acacia (*Acacia constricta*), Palmer agave (*Agave palm-eri*), and other grass species such as *Muhlenbergia* sp., sprangletop (*Diplachne dubia*), and threeawns (*Aristida* sp.). Within this area 40,250 ha are managed as an Area of Critical Environmental Concern (ACEC).

Sulphur Springs Valley Grassland (1.19) – This is a 621 km² area in southeast Arizona that is private and state owned. The eastern portion of the valley contains high quality semi-desert grama grasslands. The western portion of the valley is degraded and now heavily shrub encroached. Lehman's love grass, an aggressive exotic, has invaded much of the grasslands in this area. High numbers of sandhill cranes winter here as do mountain plovers.

Chiricahua-Peloncillo-Sierra Madre Complex (1.20) – This vast area (19,156 km²) along the United States/Mexico border is a mixture of private and federal ownership. The grasslands of the Animas Valley of southwest New Mexico extend south into northern Chihuahua, Mexico. Dominant grassland species include blue grama, black grama, tobosa, and big alkalai staccato. This grassland area has been recognized for its importance to biological diversity. It contains one of the largest remaining black-tailed prairie dog complexes in North America and the only complex in Mexico.

Lordsburg Playa (1.24) – This 209-km² area in western New Mexico consists of private, state, and federal lands. The closed basin with seasonal playas is surrounded by now degraded semi-desert grasslands. It is a saline habitat and dominated by alkali sacaton and endemic Griffiths' saltbush (*A. torreyi griffithsii*) and other saltbush species. It is an important migratory stopover site for shorebirds including many grassland-adapted species, such as long-billed curlew.

Sierra del Nido (2.01) – The grasslands in this site comprise about 40% of the area and are Plains and Great Basin community types. The area is a mixture of ejido lands, Mennonite colonies, and private ranches. Portions of this area are heavily agricultural and fragmented, but extensive tracts of grass remain. This area contains important higher elevation grama grasslands for migratory and overwintering grassland passerines and the white-sided jackrabbit (*Lepus calottis*).

Davis-Chinati Mountains Complex (2.05) – The grasslands within this site cover a high mesa that spans between the two mountain ranges and are known as the Marfa Grasslands. Blue and sideoats grama are dominant species. The area is home to a large herd of pronghorn antelope, and until the early 1990s hosted a breeding population of mountain plover. High numbers of grassland birds winter here as well as breeding populations of western meadowlarks, lesser nighthawks, and Cassin's sparrow.

The North-Central Chihuahua Grasslands (2.08) – This is a large area (15,889 km²), generally considered high quality intact grasslands. This is probably the best example of Chihuahuan Desert grasslands remaining, dominated primarily by blue and black grama, large swales of tobosa and areas of sacaton. Land ownership is a mixture of ejido and private ranches. In general, private ranches have lower intensity grazing and a rotational system while ejido lands are heavily and continuously grazed. This area is important for migratory and resident grassland birds including the aplomado falcon (*Falco femoralis*). It is also important for pronghorn antelope (*Antilocapra americana*), white-sided jackrabbit, and the kit fox (*Vulpes macrotis*).

Tularosa Basin (2.09) – This priority site contains the Organ, Franklin, and San Andres Mountains, the northern Jornada, and the Tularosa Basin as well. A number of large patches of grassland persist within the Tularosa

Basin, in particular lowland grasslands of mesa dropseed, big alkali sacaton, tobosa, and grama grasses interspersed with scrublands. This basin is entirely federally owned (U.S. Department of Defense and U.S. National Park Service) and has not been grazed by livestock for 50 years. It is home to many sensitive grassland species and aquatic species associated with seasonal playas. The northern Jornada supports semi-desert grasslands west of the San Andres Mountains. The elevation is slightly higher than the Tularosa basin. This area is dominated by blue grama and sacaton but also contains black, hairy, and sideoats grama and New Mexico needle grass (*Stipa neomexicana*). Banana and soaptree yucca are also interspersed throughout the region.

La Perla (2.12) – While many portions of this 9,069-km² tract of grassland and Chihuahuan Desert scrub are highly degraded and dominated by seasonal playas, some portions are intact and are dominated by grama grasses, tobosa, and sacaton. The southern Chihuahua area is important for breeding and overwintering grassland birds and white sided jackrabbit. It is one of just two areas in Mexico with populations of pronghorn antelope

Mescalero Sands (2.13) – This area on the eastern edge of the Chihuahuan Desert is dominated by plains grasses such as sand bluestem (*Andropogon hallii*) and little bluestem (*Schizachyrium scoparium*). As a transition from desert to plains it contains several endemic species, such as the sand dune lizard (*Sceloporus graciosus arenicolous*), and two crickets, *Ammobamentes mescalero* and *Stenopelmatus mescalero*. This area of sandy soils and large dunes is managed primarily by the U.S. Bureau of Land Management.

Marathon Basin (2.16) – The high quality grasslands of this basin in West Texas are home to scattered prairie dog colonies and are important for breeding populations of burrowing owls.

Sierra Blanca (2.17) – This extensive tract of land in southeast New Mexico and west Texas falls under a combination of private, state, and federal ownership. There are few roads and settlements within this semi-desert grassland primarily composed of blue, black, and sideoats grama, tobosa, curly mesquitegrass, three-awns, soap-tree yucca, cholla (*Opuntia imbricata*), mesquite, and creosote bush. This site contains large intact grasslands including Fort Bliss' McGregor range, a high quality, ungrazed grama grassland. Grassland condition throughout this region ranges from excellent to poor (grassland areas with heavy shrub encroachment). Within the area known as Otero Mesa, black-tailed prairie dogs and pronghorn antelope occur.

Altiplano Mexicano Nordoriental (4.01) – This extremely large conservation site is located in northeast Mexico at the southeast edge of the Chihuahuan Desert. The western valley of this region is dominated by

gypsum grasslands, mainly grama grasses, fluff grass, sacaton, and three awns. Mainly under ejido ownership, this land has been fragmented by extensive agriculture and degraded by overgrazing. The western valley is home to the Mexican prairie dog (*Cynomys mexicanus*), an endangered species endemic to the region. Most remaining open grasslands in this area are occupied by the Mexican prairie dog. This range of this species has contracted significantly, and the majority of the population is now found in the states of Coahuila and Nuevo Leon. Remaining colonies are highly fragmented. This area is also home to a disjunct breeding population of mountain plovers (*Charadrius montanus*) and many sensitive species of grassland birds including Botteri's sparrows (*Aimophila botterii*) and the endemic Worthen's sparrow (*Spizella wortheni*). This region also contains many endemic grass species.

Acknowledgments

The majority of the information presented in this paper was obtained from "Ecoregion-Based Conservation in the Chihuahuan Desert: A Biological Assessment," a product of a priority setting workshop for the Chihuahuan Desert Ecoregion hosted by the World Wildlife Fund and others in 1997. We thank all of the participants, whose extensive knowledge of the Chihuahuan Desert made the workshop a success and the publication an important reference.

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Evaluación del Estado y Distribución de los Pastizales del Desierto Chihuahuense en los Estados Unidos y México

(resumen)

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Jennifer Atchley Montoya *World Wildlife Fund, Chihuahuan Desert Ecoregion*

Los pastizales del Desierto Chihuahuense comprenden una pequeña parte del Desierto Chihuahuense pero son esenciales para la diversidad biológica de la ecoregión. Muchos de los sitios que se discuten en este trabajo y en mayor detalle en Dinerstein et al. (2000), contienen segmentos de pastizal grandes y contiguos que dan soporte a procesos ecológicos críticos, tienen alto endemismo y sustentan una alta diversidad de plantas y animales.

Gran parte de las áreas de pastizal a través del Desierto Chihuahuense están sufriendo una transformación a gran escala, de un sistema dominado por gramíneas a un sistema dominado por arbustos (Buffington and Herbel 1965, Weltzin et al. 1997). Un gran número de factores han influido en el avance de arbustos nativos en áreas de pastizal abierto. Esos factores incluyen cambio climático, sobrepastoreo, supresión de incendios naturales, distribución de semillas de arbustos por el ganado y la remoción de herbívoros nativos (Herbel et al. 1972, Nielson 1986, Schlesinger et al. 1990). Este proceso de desertificación que resulta en formación de dunas, reducción de la cobertura por gramíneas e incremento en la heterogeneidad de la distribución de recursos (Nielson 1986), compromete seriamente la integridad del sistema.

Aún persisten áreas extensas de pastizal a través del Desierto Chihuahuense, con los pastizales más intactos localizados en Chihuahua, México. También hay pastizales semidesérticos que permanecen intactos en México y Estados Unidos, en áreas de mayor precipitación. De acuerdo a la World Wildlife Fund (WWF) existen sitios de alta diversidad en el Desierto Chihuahuense que abarcan 629,000 km² (Figura 1). De 61 sitios nominados por expertos, 14 están caracterizados total o parcialmente por ser pastizales (Tabla 1).

Sitios de pastizal prioritarios dentro del Desierto Chihuahuense

Rancho y Santuario de Investigación Appleton-Whittell y Canelo Hills (1.08) – Los pastizales dentro de esta

región de 62 km² se localizan en el sureste de Arizona. Se componen de tierras privadas, federales y estatales que no se han usado para pastoreo desde 1969.

Big Hatchet-Montañas Alamo Hueco (1.22) – Esta región se localiza en el suroeste de Nuevo México, a lo largo de la frontera con México. Contiene pastizales a baja, media y alta elevación. Dentro del área, 40,250 hectáreas se administran como un Área de Interés Ambiental Crítico (Area of Critical Environmental Concern - ACEC).

Pastizal del Valle de Sulphur Springs (1.19) – Esta área de 621 km² en el sureste de Arizona es propiedad privada y estatal. El este del valle contiene pastizal semidesértico de alta calidad, mientras el oeste está degradado e invadido por arbusto.

Complejo Chiricahua-Peloncillo-Sierra Madre (1.20) – Esta es un área vasta a lo largo de la frontera entre México y los Estados Unidos que mezcla tierras privadas y federales, y contiene importantes pastizales desérticos relativamente intactos. Ha sido reconocida por su importancia a la diversidad biológica y contiene uno de los últimos complejos grandes de perros llaneros de cola negra en Norteamérica y el único complejo en México. Esta región contiene la segunda diversidad biológica más alta en todo México.

Lordsburg Playa (1.24) – Esta área de 209 km² en el oeste de Nuevo México consiste de tierras privadas, estatales y federales. El área es una cuenca cerrada, con playas temporales, rodeada por pastizales semidesérticos degradados. Es un sitio importante para aves costeras migratorias.

Sierra del Nido (2.01) – Este Pastizal se localiza en la punta noroeste de la Ecoregión del Desierto Chihuahuense y constituye una mezcla de ejidos, colonias Menonitas y ranchos privados. Los pastizales de tipo Pradera y Gran Cuenca comprenden aproximadamente 40% del área. Además contiene pastizales a mayor altura importantes para aves migratorias e invernales.

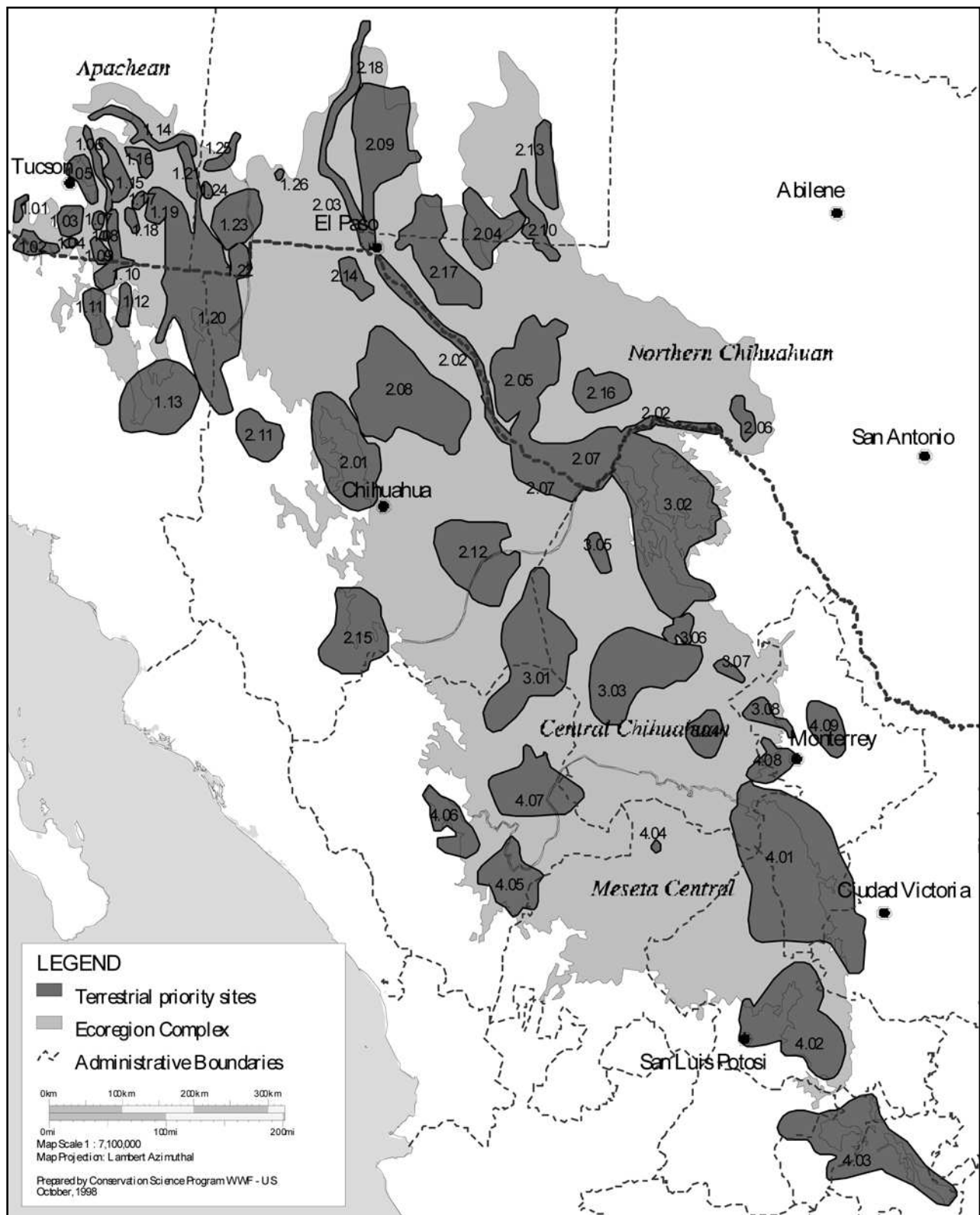


Figura 1. Sitios prioritarios para la conservación en el Desierto Chihuahuense identificados por World Wildlife Fund.

Tabla 1. Sitios de pastizal prioritarios para la conservación en el Desierto Chihuahuense.

Map #	Priority Site Name	Total Area of Site in Km ²	% Grassland	Total Area Grassland in Km ²
1.08	Appleton-Whittell	62	100	62
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2.13	Mescalero Dunes	2,297	60	1,378
2.16	Marathon Basin	3,130	80	2,504
4.01	Altiplano Mexicano Nordoriental	60,000	20	12,000
		140,026		59,411

Complejo Montañoso Davis- Chinati (2.05) – Los pastizales dentro de este sitio cubren un mesa alta que se extiende entre dos macizos montañosos conocidos como los Pastizales Marfa. Esta área es refugio de diversas especies de mamíferos y aves.

Pastizales del Norte-Centro de Chihuahua (2.08) – Esta es un área grande de pastizal intacto de alta calidad, y quizá el mejor ejemplo de pastizal del Desierto Chihuahuense. La tierra es una mezcla de ejidos y ranchos privados. Estos últimos practican pastoreo de baja intensidad y un sistema rotatorio. El área es importante para aves de pastizal migratorias y residentes.

Cuenca de Tularosa (2.09) – Esta región mide 10,000 km². Contiene los mejores pastizales en la cuenca de Tularosa y la Jornada norte. La cuenca es propiedad federal y no se ha usado para pastizaje en 50 años. Sustenta muchas especies de pastizal y acuáticas. La Jornada norte sustenta pastizales semidesérticos a una elevación ligeramente más alta que la cuenca de Tularosa.

La Perla (2.12) – Área de 9,069 km² de pastizal y arbusto chihuahuense, de propiedad privada y ejidal. Contiene un segmento de pastizal relativamente intacto en el sur de Chihuahua y el norte de Durango. Es importante para aves de pastizal en gestación o migrando por invierno, liebres y antílopes.

Dunas Mescalero (2.13) – Esta área de suelos arenosos y grandes dunas es manejada principalmente por el U.S. Bureau of Land Management.

Cuenca de Maratón (2.16) – Esta área de 2,130 km² de pastizales en el oeste de Texas es propiedad de the Nature Conservancy. El área contiene pastizales intactos y constituye un importante hábitat de invierno para aves de pastizal migratorias.

Sierra Blanca (2.17) – Esta área de 7,418 km² es una combinación de tierras privadas, federales y estatales, y es principalmente semidesértica. Las condiciones del pastizaje en esta región van de excelente a deficiente.

Altiplano Mexicano Nordoriental (4.01) – Esta área de 60,000 km² se localiza en el noreste de México. El área se compone principalmente de ejidos que la han fragmentado mediante agricultura extensiva y la han degradado mediante pastoreo excesivo. El valle occidental es hogar del perro llanero mexicano, una especie en peligro, endémica a la región. El área también es hogar para muchas especies de aves de pastizal, y contiene muchas especies endémicas de pasto.

Agradecimientos

La mayor parte de la información presentada en este trabajo fue obtenida de “Ecoregion-Based Conservation in the Chihuahuan Desert: A Biological Assessment,” un producto emanado de un taller prioritario para la Ecoregion Desierto Chihuahuense promovido por la World Wildlife Fund y otros en 1997. Agradecemos a todos los participantes cuyos extensivos conocimientos sobre el Desierto Chihuahuense hicieron que el taller fuera exitoso y la publicación una referencia importante.

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Fire Ecology and Management in Grasslands of the American Southwest

(invited paper)

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Many ecologists have indicated that fire is as important as wind or precipitation in shaping North American ecosystems. There is little question that fire is prevalent in grasslands and that it contributes to the structure and function of such systems in the Southwest. In this paper I outline pre-settlement fire regimes, then describe post-settlement regimes and vegetation response to fire. I conclude by describing the potential for applying fire to these systems, many of which have not experienced fire for many years. This overview draws heavily from Wright and Bailey (1982) and McPherson and Weltzin (2000).

Humphrey (1958) reviewed historical accounts dating back to 1528 and concluded that fire was prevalent and widespread in Southwestern grasslands at the time of, and shortly after, Anglo settlement. Wright and Bailey's (1982) book summarizes the considerable indirect evidence and agrees with Humphrey's assessment. Evidence from adjacent ecosystems, for example, fire scars on tree rings from ponderosa pine forests upslope from Southwestern grasslands, also supports this interpretation. The cumulative indirect and direct evidence indicates an average fire-return interval of about 5-15 years, depending on site characteristics. Frequency probably was directly related to site productivity, such that increased available soil moisture and nitrogen input contributed to increased incidence of fire. Thus, sites with more frequent fires also had higher precipitation and nitrogen inputs, such that relatively frequent fires did not pose a threat to site productivity in the absence of large herbivores.

Fine fuel accumulation probably was the primary constraint on fire spread in grassland systems before Anglo settlement, rather than ignition sources. In Southwestern grasslands, fuel moisture drops annually during an extended dry period that coincides with plentiful lightning at the leading edge of the summer monsoon. After Anglo settlement, fire spread became limited by availability of fine fuel as livestock removed grass. A national policy of fire suppression also depressed fire frequency in these systems. Today fire spread remains limited by the paucity of fine fuel, as mediated by livestock grazing, in most of the region's grasslands.

Fire effects on vegetation have been summarized in several recent publications (notably, McPherson and Weltzin 2000). With woody plants, there is a highly variable response that is species- and site-specific. Even within a species and site, response depends on growth stage and size of woody plants. Response of herbaceous plants tends to be strongly dependent on post-fire precipitation; if post-fire precipitation is high, herbaceous response will be quite rapid. If post-fire precipitation is average or below average, herbs may not achieve pre-burn productivity until above-average precipitation returns; this recovery may require several years.

These generalizations are tempered by many exceptions and the fact that nearly all of the research on fire ecology in Southwestern grassland ecosystems was conducted over 30 years ago. As such, most of this research lacks modern experimental design and analysis. In addition, the physical and biological environments characterizing these systems have changed within the last few decades. Finally, there have been dramatic changes in socio-economic goals and objectives in these systems. I briefly describe some of these changes to illustrate the point that the world has changed markedly from the one that researchers described in the 1950s, 1960s, and 1970s.

From a strictly physical standpoint, we are observing increases in global and regional temperatures. Since the industrial revolution we have witnessed profound, and recently exponential, increases in temperature variation. We are beginning to see changes in timing of frost, high temperatures, low temperatures, precipitation seasons, and other extreme events, and these certainly will have ramifications for ecosystem structure and function. So, in addition to well-described direct effects of changes in atmospheric chemistry on C_3 versus C_4 plants (i.e., increased atmospheric CO_2 concentrations tend to favor the former at the expense of the latter), we also observe indirect effects that are mediated through changes in climate (McPherson and Weltzin 2000).

Increased fragmentation has characterized Southwestern ecosystems. Grasslands, particularly in the southwestern United States, are "ground zero" for human development. The grasslands lie immediately below

protected Forest Service land, but at a sufficiently high elevation that they experience relatively mild climates, thus representing a prime target for human occupation. Urban development and the associated fragmentation undoubtedly have large consequences for these systems, particularly with respect to hydrology and fire, but these impacts remain poorly documented.

Livestock numbers have decreased substantially in the last century, down to about 20% of estimates for the early 1900s. These decreases in large herbivores within the last 100 years still represent considerably more livestock than were present before Anglo settlement. In addition, negative impacts of livestock on site productivity may persist for several decades.

The increase in abundance of nonnative grasses represents another biological change in these systems. In southeastern Arizona, the dominant nonnative plant is *Eragrostis lehmanniana* (Lehmann lovegrass). Diversity of herbaceous species declines with increased abundance of lovegrass (McPherson et al. 2002). Unfortunately, we do not understand causality in this case; we don't know if lovegrass is invading areas of low diversity, or if lovegrass is causing these declines in diversity. In any event, Southwestern grasslands now contain plenty of lovegrass, buffel grass, and many other species that were not present at the time of Anglo settlement. These "new players" have created systems that are different from the systems that were present in the pre-settlement era and also different from the systems that were studied in the 1950s through the mid-1970s, when most of the research on fire ecology was conducted.

The spread of nonnative plants over the last three to five decades has helped to overcome the fine-fuel constraint on fire. These grasses produce more biomass than native grasses, especially during dry years; the biomass is highly lignified, so it decomposes relatively slowly (McPherson 1997 and references therein). It is available as fuel for a longer period of the year than most native grasses, and, as a result, the increased fuel associated with these nonnative grasses contributes to increased fire spread, since fuel is the most dominant constraint in these systems. The dominant nonnative grasses respond favorably to fire, which contributes to this positive feedback cycle among the presence of these grasses, accumulation of fuel, spread of fire, and spread of the grasses.

Perhaps more important than these changes in environmental conditions is a change in perspective. Goals and objectives have changed throughout most of the world, including Southwestern grasslands. For example, the advent of the Society for Conservation Biology in the United States about 15 years ago is evidence of changing values. Our goals have grown beyond consumptive uses, meat and leather, for example, and are typified by the mission statement of the Society for Conservation

Biology, which reads, in part, to "help develop the scientific and technical means for the protection, maintenance and restoration of life on this planet." As a society, we are also interested in biological diversity, as many of the speakers have suggested at this symposium.

Our objectives do not necessarily include the re-creation of historical conditions. For one thing, we have a very poor understanding of what these conditions were. For another, these systems have changed so profoundly that I think it is impossible to try to restore pre-settlement conditions. In addition, our goals do not include grassland "health" and grassland "integrity," because those are undefined, undefinable, and unmeasurable ideas. We need to focus on goals and objectives that can be evaluated, can be measured, and can be repeated over time.

With respect to bringing fire back into these systems, we must have clearly defined goals before we act. Fire is clearly not a panacea—it can be beneficial, depending on specific objectives. Its absence from these systems is disturbing for many of us, but that does not call for broad scale re-introduction of fire without consideration of fire effects, season, and frequency.

It is especially important that we pay greater attention to seasonality than we have in the past. Most managers who have the nerve to re-introduce fire take this step only during periods that fire can be controlled relatively easily. In Southwestern grasslands, this strategy translates to many fires during March and April, a time inconsistent with historical fire regimes. Most fires in this region probably occurred in late June or early July, coincident with the onset of the southwestern monsoon. What are the implications of applying spring fires for species that have evolved in the presence of periodic summer fires? We really don't know, but we shouldn't assume that they are benign.

Finally, it is clear that we should be paying great attention to monitoring efforts. "Adaptive management" has become the law of the land among resource-management agencies in the United States. Yet we cannot adapt management without monitoring. In the absence of information derived from monitoring, we simply don't know what to adapt *to* or how to adapt to it. Acquisition of relevant information should facilitate progress toward pro-active management that targets productive, diverse grasslands in this region.

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Ecología de Fuego y Manejo de Pastizales en el Sudoeste Norteamericano

(resumen)

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Para muchos ecologistas, el fuego es tan importante como el viento o la precipitación en la formación de los ecosistemas en Norteamérica, y ciertamente es importante para la estructura y función de los pastizales del sudoeste Norteamericano.

Se ha investigado y concluido que el fuego prevalecía y abarcaba áreas extensas al momento de la colonización europea, y aún poco tiempo después. El fuego era un fenómeno importante en estos sistemas de pastizal. Existe evidencia directa de esto en sistemas adyacentes a los pastizales. La evidencia acumulativa directa e indirecta indica un intervalo promedio de incendio de 5 a 15 años, dependiendo de las características del sitio. Esta frecuencia probablemente se relacionaba con la productividad del sitio, de tal forma que mayor humedad de suelos y mayor suministro de nitrógeno resultarían en una mayor incidencia de fuego.

Antes de la colonización europea, la incidencia de fuego era limitada por la disponibilidad de combustibles finos y no por la abundancia de fuentes de ignición. Los incendios en el sudoeste de los Estados Unidos cesaron al llegar grandes cantidades de ganado con la colonización. La disminución de combustibles finos y la supresión activa de incendios redujeron dramáticamente la frecuencia de los incendios. Las consecuencias de este cambio en frecuencia y de la reintroducción del fuego en estos sistemas son inciertas.

La introducción de especies de pasto no nativas en las últimas décadas ha servido para aumentar el combustible disponible para los incendios, estas especies producen más biomasa que se descompone más lentamente, haciéndola disponible como combustible durante más tiempo. Esto sugiere un ciclo de retroalimentación positiva, porque el pasto no nativo responde favorablemente al fuego.

La respuesta de la vegetación al fuego es altamente variable y dependiente al lugar y especie en particular. En plantas maderables, esta depende de la etapa de crecimiento de la planta, mientras que en herbáceos, depende de la cantidad de precipitación después de un incendio. Si la precipitación es alta la respuesta será bastante rápida. Pero cuando la precipitación es promedio o abajo del promedio, puede ser que los herbáceos no recuperen la productividad que tenían antes del incendio

hasta que llueva abundantemente de nuevo, y eso puede tardar varios años.

Sin embargo, estas generalizaciones presentan muchas excepciones porque la mayoría de estas investigaciones se hicieron hace más de 30 años. Además, el ambiente físico y biológico que caracteriza a estos sistemas ha cambiado en las últimas décadas.

Desde una perspectiva física, el mundo ha cambiado dramáticamente. Las temperaturas globales y regionales aumentan, además de la variación en temperaturas. También hay cambios en heladas, altas y bajas temperaturas, temporalidad de la precipitación y otros eventos extremos, que probablemente tendrán ramificaciones en la estructura y función del ecosistema.

La cantidad de ganado ha disminuido significativamente en el último siglo, a un 20% del ganado que había en la región a principios de 1900. Muchos sistemas han cambiado en los últimos 100 años en términos de herbívoros grandes, pero no existía ganado antes de la colonización. Los efectos negativos del ganado en la productividad del sitio pueden persistir por varias décadas.

El aumento en la abundancia de especies de pasto no nativas representa otro cambio biológico en estos sistemas. Estas nuevas especies han creado sistemas diferentes de los que existían antes de la colonización, y de los que se estudiaron desde la década de los 50 hasta mediados de los 70.

Los cambios en perspectiva son quizá más importantes que los cambios en las condiciones ambientales. La creación de la Sociedad para la Biología de Conservación en los Estados Unidos es evidencia de que nuestros objetivos van más allá de los usos de consumo. Como sociedad, nos interesa la diversidad biológica.

Estos objetivos no incluyen la recreación de condiciones históricas, porque existe muy poca información de las mismas, y porque los sistemas han cambiado con tal profundidad que resultaría imposible reproducir las condiciones anteriores a la colonización. Es necesario que los objetivos de enfoque puedan evaluarse, medirse y repetirse con el tiempo. Esto se aplica a la reintroducción de fuego en estos sistemas, porque el objetivo debe ser claro antes de aplicar el fuego, considerando efectos, temporada y frecuencia.

Es especialmente importante considerar la temporalidad. En la actualidad se usa el fuego en períodos de fácil control. En los pastizales del sudoeste, sucede en marzo y abril, lo que no concuerda con los regímenes de fuego históricos. La mayoría de los incendios en esta región ocurrían a finales de junio y principios de julio, al inicio del monzón sudoccidental. Desconocemos las implicaciones de la aplicación de incendios primaverales en especies que evolucionaron con incendios periódicos en verano.

Finalmente, está claro que debemos poner mayor énfasis en los esfuerzos de monitoreo. El “manejo adaptativo” se ha convertido en el credo de las agencias de manejo de recursos en los Estados Unidos, pero no podemos adaptar el manejo sin la información derivada del monitoreo.

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Vertebrate Diversity In Northwestern Chihuahua, Mexico

(summary)

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Biodiversity loss is one of the most severe global environmental problems. Among other factors, it is fostered by the destruction and fragmentation of natural ecosystems. The Chihuahuan prairies merit no exception; a great number of its associated species are endangered by habitat fragmentation or deterioration. The prairie dog (*Cynomys* spp) illustrates this situation. Prairie dogs are rodents that form extensive colonies in northwest Mexico. Historically this species occupied extensive grassland areas. However, its current geographic distribution is only 2 percent of its original range. Prairie dogs are keystone species for the North American prairies and their presence induces habitat diversity, which increases regional environmental heterogeneity and promotes the establishment of a greater number of animal and plant species in the surroundings.

Mexico has one of the largest populations of black-tailed prairie dogs (*Cynomys ludovicianus*) in North America. This colony, which extends over an area of 20,000 hectares, is known as the Janos–Casas Grandes complex and is located in the municipality of Janos, Chihuahua, 75 kilometers south of the border between the United States and Mexico. This region includes

habitats characteristic of grasslands and the Sierra Madre. Prairie-dog colonies and contiguous areas maintain a richly diverse fauna that includes 300 species of vertebrates. Of these, seven are amphibians; 28, reptiles; 218, birds; and 47, mammals. Our inventory includes a considerable group of species that have obtained protective status under the Mexican government. These include the green toad (*Bufo debilis*), Texas horned lizard (*Phrynosoma cornutum*), golden eagle (*Aquila crissaltes*), bald eagle (*Haliaeetus leucocephalus*), porcupine (*Erethizon dorsatum*), black bear (*Ursus americanus*), badger (*Taxidea taxus*), bison (*Bison bison*), and the kit fox (*Vulpes macrotis*).

The goal of this research project is to build a base for establishing a biosphere reserve that would conserve regional biodiversity and preserve the native ecosystem. Such a reserve would facilitate increased professional training opportunities in conservation biology and ecology, as well as improve socioeconomic conditions for the local people. Furthermore, this proposal is of great relevance because it would allow for the conservation of a poorly represented biome in Mexico's National System of Protected Areas.

Diversidad de Vertebrados del Noroeste de Chihuahua, México

(artículo invitado)

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Uno de los problemas ambientales globales más severos es la pérdida de la diversidad biológica, propiciada, entre otros factores por la destrucción y fragmentación de los ecosistemas naturales. Las praderas de Chihuahua no escapan a esta situación, por lo que gran número de especies asociadas a este ecosistema se encuentran amenazadas debido a la fragmentación y el deterioro del hábitat. Un claro ejemplo de esto son los perros llaneros (*Cynomys* spp), roedores que forman grandes colonias en el noroeste de México. Históricamente esta especie ocupó extensas áreas de pastizales naturales, sin embargo, su distribución geográfica actual se ha visto reducida a un 2% del área original. Los perros llaneros son especies clave ecológicamente en las praderas de Norteamérica, su presencia induce una mayor diversidad de hábitats, lo que incrementa la heterogeneidad ambiental regional y promueve el establecimiento de un mayor número de especies animales y vegetales a su alrededor.

En México se encuentra una de las poblaciones más grandes de perros llaneros de cola negra (*Cynomys ludovicianus*) que persiste en Norteamérica (20,000 ha). Esta colonia conocida como Complejo Janos Casas-Grandes se localiza en el Municipio de Janos, Chihuahua a 75 km al sur de la frontera entre México y Estados Unidos,

e incluyen áreas representativas de los pastizales y de la Sierra Madre. El área ocupada por las colonias de perros llaneros y áreas contiguas mantienen una fauna muy diversa, que incluye 300 especies de vertebrados de las cuales 7 son anfibios, 28 reptiles, 218 aves y 47 mamíferos. Nuestro inventario incluye a un grupo considerable de especies que se encuentran en alguna categoría de conservación, según el gobierno de México, como el sapo *Bufo debilis*, el sapo cornudo (*Phrynosoma cornutum*), el águila real (*Aquila crisaetos*), el águila de cabeza blanca (*Haliaeetus leucocephalus*), el puercoespín (*Erethizon dorsatum*), oso negro (*Ursus americanus*), tlalcoyote (*Taxidea taxus*), bisonte (*Bison bison*) y LA zorra norteña (*Vulpes macrotis*).

La meta de esta investigación es la de establecer una reserva de la biosfera que permita la conservación de la biodiversidad regional y así preservar un ecosistema nativo. Además representa un área propicia para incrementar la oportunidad de entrenamiento profesional en ecología y biología de la conservación, así como para mejorar las condiciones socioeconómicas de los pobladores locales. Esta propuesta cobra mayor relevancia ya que su establecimiento permitiría la conservación de un bioma muy poco representado en el Sistema Nacional de Áreas Protegidas.

Diversity of Amphibians and Reptiles Associated With Grasslands of Janos–Casas Grandes, Chihuahua, Mexico

(summary)

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Prairie-dog (*Cynomys ludovicianus*) colonies in northwest Chihuahua, Mexico, have been of great significance not only in initiating protection programs for the species but also in learning about the biological diversity (flora and fauna) of the natural grasslands of Janos–Casas Grandes, Chihuahua. Therefore a study of the herpetological fauna within the prairie-dog colonies and surrounding areas was launched more than two years ago in what is known as the Janos–Casas Grandes complex. The area is located 75 kilometers south of the Mexico–U.S. border in the municipality of Janos, Chihuahua. Within prairie-dog towns, the dominant vegetation is natural grassland, while mesquite (*Prosopis* spp.) prevails in the surrounding areas. More than 300 species of vertebrates have been identified.

To conduct an inventory of the herpetological fauna of the area, a plot-trap system arranged in quadrants and without a drift-fence was implemented. Nine traps were installed in each quadrant, placed 30 meters from one another; with this arrangement, 16 different sites in each environment were studied. Thus eight were located in mesquite (72 traps) and eight in grasslands, including the only grasslands where it is known that prairie dogs were exterminated approximately 10 years ago. Specimens collected at these sites were identified and marked, and meristic data were measured before the animals were released. In addition, population data are also being collected about other herpetological species inhabiting the area. Audiovisual transects are conducted for two or three hours inside and outside the quadrants to complement the information gathered in the trap system. Thirty species of herpetofauna were identified in prairie-dog colonies. Of these, six were amphibians and 24, were reptiles.

However it is believed that the diversity may be even greater because other species have been recorded near the study area. Snakes are the best-represented group, with 14 species, followed by lizards with eight. In most cases the herpetofauna use the prairie-dogs' burrows as shelters against heat or extreme cold. They also likely hibernate in these burrows. Seven species of reptiles associated with small shrubs and pocket-rat (*Dipodomys* spp.) burrows were recorded in grasslands without prairie dogs. In mesquite areas, 15 species of herpetofauna were found. Of these, three are amphibians and 12 are reptiles, but the mix differs from that of grasslands—while 24 species were exclusive to grasslands, only seven were to mesquite areas. It is now known that the Janos–Casas Grandes area maintains 39 species of herpetofauna, 80 percent more than expected.

Of this area's known herpetofauna, knowledge of rattlesnakes (*Crotalus* spp.) is of particular interest as they maintain outstandingly abundant populations in the area, especially in grasslands. Although few incidents of people being bitten by snakes have taken place, more reports have been made about snakebites of cattle and horses. Therefore it is important to carefully study the five species that inhabit this area; they are: *Crotalus atrox*, *C. lepidus*, *C. molossus*, *C. scutulatus*, and *C. viridis*.

The herpetofaunistic diversity of prairie-dog colonies in northeastern Chihuahua is notably high compared to other prairie-dog colonies in North America. Our purpose is to highlight this fact in order to promote conservation of grasslands, currently seriously threatened by land-use changes, demographic growth, and increasing encroachment by agriculture. As well, Mexico's National System of Protected Areas under serves this environment.

La Diversidad de Anfibios y Reptiles Asociada a los Pastizales de Janos-Casas Grandes, Chihuahua, México

(artículo invitado)

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La presencia de las colonias de perros de la pradera (*Cynomys ludovicianus*) en el Noroeste de Chihuahua, México ha sido de gran importancia no sólo para iniciar programas de protección de esta especie, sino para conocer la diversidad biológica (flora y fauna) de los pastizales naturales de Janos-Casas Grandes, Chihuahua. Por tal motivo, desde hace más de dos años se inició formalmente el estudio de la herpetofauna dentro y en los alrededores de las colonias de perros llaneros en lo que se conoce como el Complejo Janos-Casas Grandes. El área se localiza en el Municipio de Janos, Chihuahua a 75 km al sur de la frontera entre México y Estados Unidos. Dentro de las colonias la vegetación dominante es el pastizal natural y en los alrededores predomina el matorral de mesquite (*Prosopis* spp.). En las colonias de perros llaneros se han identificado hasta el momento más de 300 especies de vertebrados.

Para llevar a cabo el inventario de las especies de herpetozoos de la zona implementamos un sistema de cuadrantes de trampas de caída en arreglo de cuadrícula o gradilla sin cerco de desvío (drift-fence). En cada cuadrante se instalaron 9 trampas a una distancia de 30 metros una de otra, con este arreglo estudiamos 16 diferentes sitios de cada ambiente, es decir 8 sitios de pastizal, 8 de mesquite (72 trampas) y del único pastizal en el cual sabemos que los perros de la pradera fueron exterminados hace aproximadamente 10 años. Los ejemplares recolectados en estos sistemas se identifican y de cada uno se toman datos merísticos, se marcan y luego se liberan. Con estos datos estamos obteniendo además datos poblacionales de las especies de herpetozoos que habitan en esta zona. Además se realizan transectos audiovisuales diurnos y nocturnos de 2 a 3 horas de duración dentro y fuera de los cuadrantes para complementar el sistema de trampas. En las colonias de perros llaneros hemos registrado 30 especies de herpetozoos, de los cuales 6 son anfibios y 24 son reptiles, sin embargo, consideramos que esta diversidad aún puede aumentar debido a que sabemos de otras especies que se han registrado muy cerca

del área de estudio. El grupo mejor representado es el de las serpientes con 14 especies, seguido por las lagartijas con 8. Nos hemos percatado de que en la mayoría de los casos los herpetozoos utilizan las madrigueras de perros llaneros como refugio durante el calor o frío extremos, es altamente probable que estiven y/o hibernen dentro de estas madrigueras. En el pastizal sin perros de la pradera hemos registrado 7 especies de reptiles asociados generalmente a arbustos de pequeño tamaño y a madrigueras de rata canguro (*Dipodomys* spp.). En las áreas de mesquite hemos encontrado 15 especies de herpetozoos de los cuales 3 son anfibios y 12 son reptiles pero la composición es diferente a la de los pastizales, encontrando 24 especies exclusivas del pastizal y 7 exclusivas del mesquite. Hasta ahora sabemos que el área de Janos-Casas Grandes mantiene una diversidad de 39 especies de herpetozoos (poco más del 80% de la diversidad esperada).

De la herpetofauna conocida en la zona resulta particularmente interesante el conocimiento sobre las serpientes de cascabel (*Crotalus* spp.) que mantienen poblaciones notablemente abundantes en esta zona y particularmente en los pastizales. Aún cuando tenemos conocimiento de que existen pocos accidentes de personas por mordedura de serpiente sí hemos tenido noticias de animales (vacas y caballos) afectados, por lo tanto creemos indispensable estudiar con más cuidado las especies de serpientes de cascabel que habitan en esta zona y que son cinco: *Crotalus atrox*, *C. lepidus*, *C. molossus*, *C. scutulatus*, y *C. viridis*.

La diversidad herpetofaunística en las colonias de perros llaneros del noroeste de Chihuahua es notablemente alta, comparada con otras colonias de perros llaneros en Norteamérica. Nuestra intención es resaltar este hecho para promover la conservación del ambiente de pastizal natural que se encuentra seriamente amenazado por el cambio del uso de suelo, la presión demográfica y el acelerado avance de la agricultura y sobre todo tomando en cuenta que este ambiente está poco representado en el Sistema de Áreas Naturales Protegidas de México.

The Importance of Maintaining Carnivores in Wildlands

(transcription)

Dave Foreman *The Wildlands Project*

I'd like to talk a little bit about another important disturbance regime in much of the western United States and Mexico. We've talked some about the importance of fire. Another one is the importance of natural hydrological cycles. But an often-overlooked important ecological disturbance regime is predation. Research around the world and in many habitats has found the importance of large carnivores in top-down regulation of ecosystems.

Jim Estes, studying sea otters off the coast of California some 20 years ago, found that when the sea otters had been trapped out over 100 years ago, their habitat, the kelp forest, often called "the redwood forest of the Pacific Ocean," disappeared. The reason for this was that, without the sea otter to control the sea urchin, sea urchin populations exploded and grazed away the kelp forest, losing not only the kelp forest but also the many other species dependent on it. Since California sea otters have been reintroduced in the Pacific Ocean, the kelp forest and other species have been coming back.

Yellowstone National Park lost all wolves and mountain lions in 1930. The park service trapped and shot them out. Elk populations in Yellowstone National Park grew very large. But even more importantly, elk behavior changed. The elk became lazy, lying in large herds in the meadows near the rivers, chewing their cuds, overgrazing. The area looked like one of the worst cow pastures around in some places. So bad was the elk overgrazing and overbrowsing that beavers could not reestablish themselves in Yellowstone National Park—the elk had browsed away the willows. But when wolves were reintroduced into Yellowstone less than ten years ago, suddenly the elk behavior changed radically. They were no longer big, fat, lazy "meadow potatoes." They were elk again. They were up running around, looking over their shoulders at the wolves. While the wolves have not caused the elk population to decrease, they have radically changed elk behavior. Now the overgrazed meadows are coming back. Willows are growing back up in streams and researchers believe that beavers are going to be able to recolonize streams in Yellowstone National Park.

The last example I want to give occurred in west Texas where coyotes had been experimentally trapped out of an area that had six species of burrowing rodents.

After the coyotes were trapped out, kangaroo rats were able to outcompete the other five species of burrowing rodents. This displacement is called competitive exclusion. Without the predation pressure of the coyotes on the kangaroo rats, the other species could not compete with the kangaroo rats.

Those are just a few examples from around the world of the importance of top-down regulation of ecosystems by large carnivores, how these ecosystems begin to unravel when large carnivores are removed, and how these ecosystems begin to regain integrity when the large carnivores are reintroduced.

Another importance of large carnivores for conservation is their umbrella effect. If you protect habitat adequate for a viable population of large carnivores, you are going to protect habitat for many other species as well, certainly not for all species, but for many. And a final important reason for protecting large carnivores is their effect on our behavior and on our attitudes. If there is anything human beings have too much of, it's arrogance. There is nothing quite like large carnivores to teach us humility.

I'd like to show how the Wildlands Project and other groups such as Sky Island Alliance and Naturalia are using these ideas of top-down regulation and conservation in this area on the U.S.–Mexico borderlands that we call the Sky Islands, the area that is the overlap between the Rocky Mountains and the Sierra Madre, between the Sonoran Desert and the Chihuahuan Desert. Michael Soule and Reed Moss, two of the leading conservation biologists in the world, propose a scientific conservation approach called "rewilding." Based on the important role of large carnivores in regulating ecosystems and on the need of large carnivores for large, secure habitat areas and the fact that in much of the world today there are no longer large-enough single protected areas, "rewilding" means we have to look at landscape linkages, or connectivity, between protected areas and other habitat.

Requirements for survival represent factors important to maintaining ecological health. Among these focal species are keystone species. Keystone species, like large carnivores, have a disproportionate effect on the ecosystem and other species relative to their actual numbers. Here in the Sky Islands region (Figure 1), the Mexican

SKY ISLANDS WILDLANDS NETWORK

A Proposed System of Conservation Lands

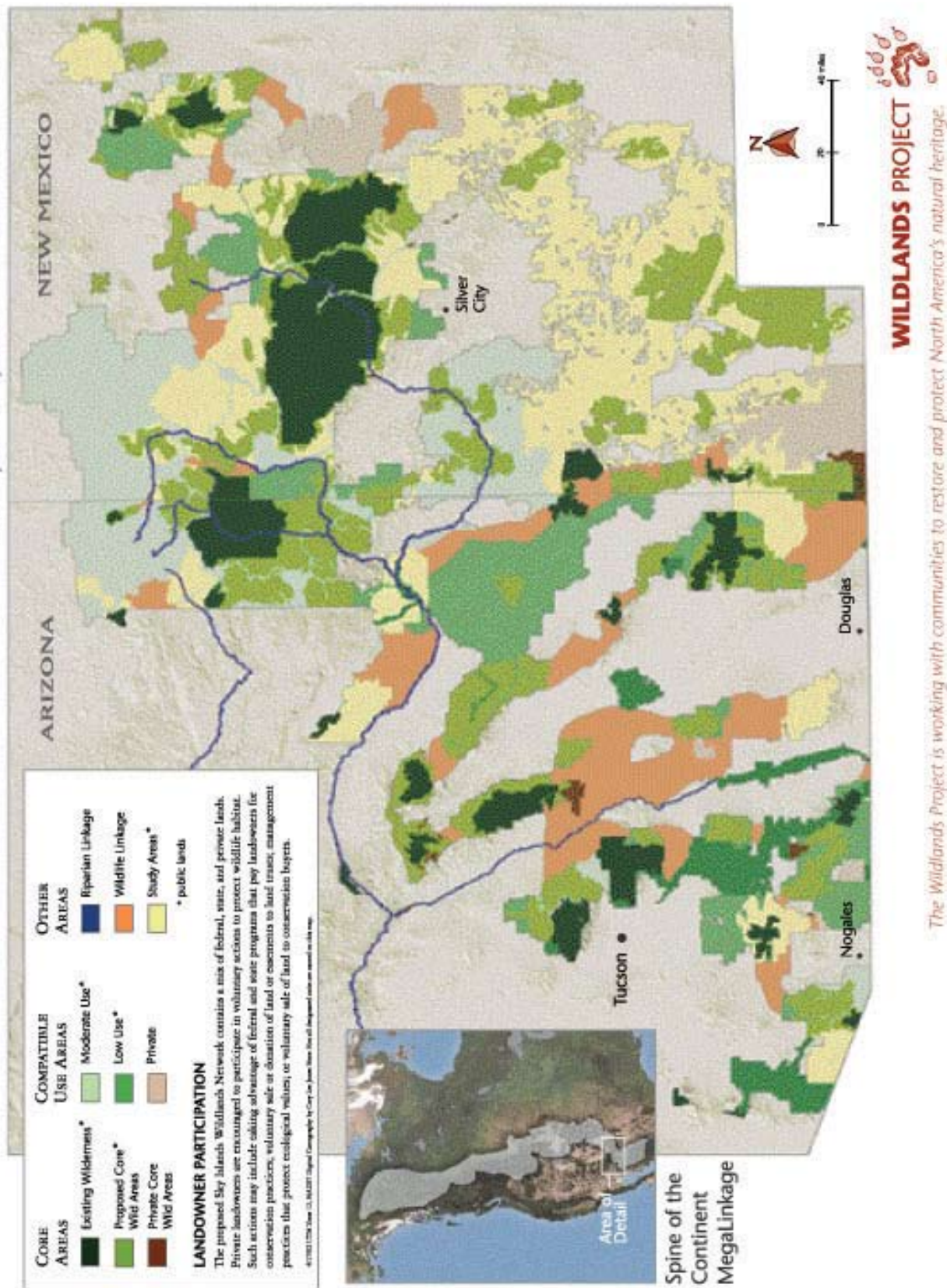


Figure 1. The Sky Islands Wildlands Network: A proposed system of conservation lands.

wolf was probably the most important keystone species. The loss of the Mexican wolf has caused changes in the landscape. Recently Mexican wolves have been reintroduced in southeastern Arizona and southwestern New Mexico. Carnivores like the Mexican wolf and the jaguar need large core areas and connectivity because they are vulnerable to persecution. The authors of *Continental Conservation*, the state-of-the-art book on science-based conservation, say that protected areas should be roadless or have limited access. This was shown with the reintroduction of Mexican wolves in the Apache-Sitgreaves National Forests. Large core areas can allow for more species, maintain natural disturbance regimes like fire, ensure population viability of sensitive species and enhance wilderness.

The Mexican wolves were originally released in an area of the Apache National Forest in Arizona that had many dirt roads through it. Almost immediately five were shot along-side dirt roads. Two others were run over. What needed to be done was to have reintroduced the Mexican wolf in the Gila wilderness area and the Aldo Leopold wilderness area in New Mexico, almost a million acres of roadless country, much of it ungrazed by domestic livestock. The Mexican wolf and other large carnivores need these roadless protected areas if they are going to survive.

The jaguar once ranged throughout New Mexico, Arizona, Texas, Louisiana, and Arkansas in the United States. It is one of the focal species in the Sky Islands Wildlands Network, and conservationists in the United States and Mexico are studying how we can get jaguar populations to disperse back into Arizona and New Mexico. So we have developed a recommendation for the jaguar as a focal species, conservation recommendations to help jaguars disperse from their northernmost breeding population in Sonora and begin to recolonize suitable areas in Arizona and New Mexico. Jaguar researchers tell us, for example, that among the preferred areas for jaguars in the United States are lower elevation river regions, such as the Blue River in southeastern Arizona. This area has a jeep trail through it, a dirt road through it. For jaguars' security, conservationists, with some support from a few local ranchers, are proposing that

some of these dirt roads be closed to provide a larger secure area.

The Gila and the Aldo Leopold wilderness areas are highly isolated. They are island protected areas and are not connected to one another. We know that many species need landscape linkage; they need to move across large areas. This ecosystem connectivity maintains ecosystem flows. It is essential for the population viability of wide-ranging species and it also enhances wilderness. Instead of the old model of isolated national parks, wildlife refuges or other protected areas, Reed Noss and others have proposed a new model where we look at the entire landscape, where we look at protected core areas, wildlife movement linkages between them, and also at compatible-use areas on private and public land around these protected areas, to look at the landscape as a whole and not only for conservation purposes, but also for how people can sustainably make a living on the landscape outside the core protected areas.

We have been finding that to connect areas in Arizona and New Mexico, looking at public lands is not enough. We have to look at well-managed private lands such as Guadalupe Canyon Ranch, owned by my friend Drum Hadley, and other large ranches owned by members of the Malpais Borderlands group, not to tell the landowners what to do with their land, but to acknowledge their exemplary management and to examine how their ranches and their grazing practices fit into larger conservation objectives. So instead of isolated protected areas, we have proposed a system of public and private lands to be managed as a whole, to try to put linkages back into landscape so that jaguars can disperse north into the United States and that ultimately Mexican wolves can disperse south into Sonora and Chihuahua as well (Figure 1). I think that all of us, landowners, ranchers, conservationists, hunters and wildlife biologists are all interested and all need to work out an approach to the entire landscape so that healthy communities, healthy families can coexist with healthy families and communities of jaguars, thick-billed parrots, Mexican wolves, prairie dogs and many other species, so that we truly can create conservation-oriented and sustainable land use for the 21st century.

La Importancia de Mantener Carnívoros en Áreas Silvestres

(resumen)

Dave Foreman *Proyecto Wildlands*

Según han demostrado estudios realizados alrededor del mundo, los carnívoros de gran tamaño regulan los ecosistemas por medio de su influencia en las cadenas alimenticias. Existen muchos ejemplos de la forma en que los ecosistemas se desequilibran al retirar a los carnívoros de gran tamaño y de cómo recobran su integridad al reintroducirllos.

Hace 100 años las nutrias de mar desaparecieron de la costa de California por caza indiscriminada. Con ellas desapareció también su hábitat: el bosque de algas marinas. Sin las nutrias, que se alimentan de erizos de mar, la población de erizos incrementó muchísimo y acabó con el bosque de algas. Sin embargo, desde que se reintrodujeron las nutrias, el bosque de algas y otras especies han regresado.

El parque nacional de Yellowstone perdió todos los lobos y pumas en 1930. Esto tuvo como resultado que las poblaciones de alce crecieran. En ausencia de sus depredadores naturales, los alces se hicieron perezosos, las praderas empezaron a mostrar los efectos del sobrepastoreo y los sauces del sobreramoneo, lo que afectó incluso a los castores. Cuando se reintrodujeron los lobos hace menos de 10 años, el comportamiento de los alces se revirtió, y lo mismo sucede gradualmente con el entorno natural.

En otro ejemplo, se extrajeron los coyotes de un área del oeste de Texas que contenía seis especies de roedores. Las ratas canguro dominaron y desplazaron a las otras cinco especies. A esto se le llama exclusión competitiva. Sin la presión por depredación de los coyotes sobre las ratas canguro, las otras especies no pudieron competir contra las ratas canguro.

La presencia de carnívoros grandes también es importante para esfuerzos de conservación de hábitats y ecosistemas, en lo que se conoce como “el efecto sombrilla”. Si se protege el hábitat de una población de carnívoros grandes, se protege también el hábitat de muchas otras especies. Michael Soule y Reed Noss, dos de los biólogos de conservación más respetados en el mundo, proponen un enfoque científico de conservación que se basa en entender el importante papel que juegan los carnívoros grandes en la regulación de los ecosistemas, en su necesidad de áreas de hábitat grandes

y seguras, y en la conectividad entre áreas protegidas y otros hábitats.

Las especies clave, como los carnívoros grandes, tienen fuertes efectos en el ecosistema y en otras especies. La pérdida del lobo mexicano en la región de montañosa del sureste de Arizona y el suroeste de Nuevo México (*Sky Islands*), ha causado cambios en el paisaje (Figura 1). Los carnívoros como el lobo mexicano y el jaguar necesitan grandes áreas núcleo que tengan conectividad entre ellas. Estas áreas núcleo permiten más especies, sustentan regímenes de alteración naturales como los incendios, aseguran la viabilidad poblacional de especies sensibles y realzan la naturaleza. Los autores de *Continental Conservation*, un libro de conservación fundamentada en ciencia, mencionan que las áreas protegidas deben carecer de caminos y tener acceso limitado. Esto se mostró con la reintroducción del lobo mexicano en el Bosque Nacional Apache (ver figuras anexas).

Originalmente se liberaron los lobos mexicanos en un área del Bosque Nacional Apache que tenía muchos caminos. Casi inmediatamente se cazaron cinco a lo largo de estas brechas, y otros dos fueron atropellados. Lo que debió hacerse era liberarlos en el área silvestre de Gila y en el área silvestre Aldo Leopold en Nuevo México, que constituyen casi un millón de acres sin caminos. El lobo mexicano y otros carnívoros grandes necesitan estas áreas protegidas sin caminos para sobrevivir.

El jaguar es una de las especies centrales en la Red Silvestre de las montañas del sudeste de Arizona (*Sky Islands*), y se está estudiando la forma de hacer que se disperse en Arizona y Nuevo México desde Sonora. Esta especie prefiere áreas de ríos de baja elevación como el Río Azul en el sudeste de Arizona. Esta área tiene un camino que la atraviesa. Para seguridad del jaguar, se ha propuesto que algunas de estas brechas se cierren.

Las áreas silvestres de Gila y Aldo Leopold están altamente aisladas. Son áreas protegidas y no están conectadas una con otra. Sabemos que muchas especies necesitan conectividad porque se mueven a través de grandes áreas. Esta conectividad entre ecosistemas mantiene el flujo dentro de los mismos, y es esencial para la viabilidad poblacional de especies de amplio movimiento. El nuevo modelo, propuesto por Reed

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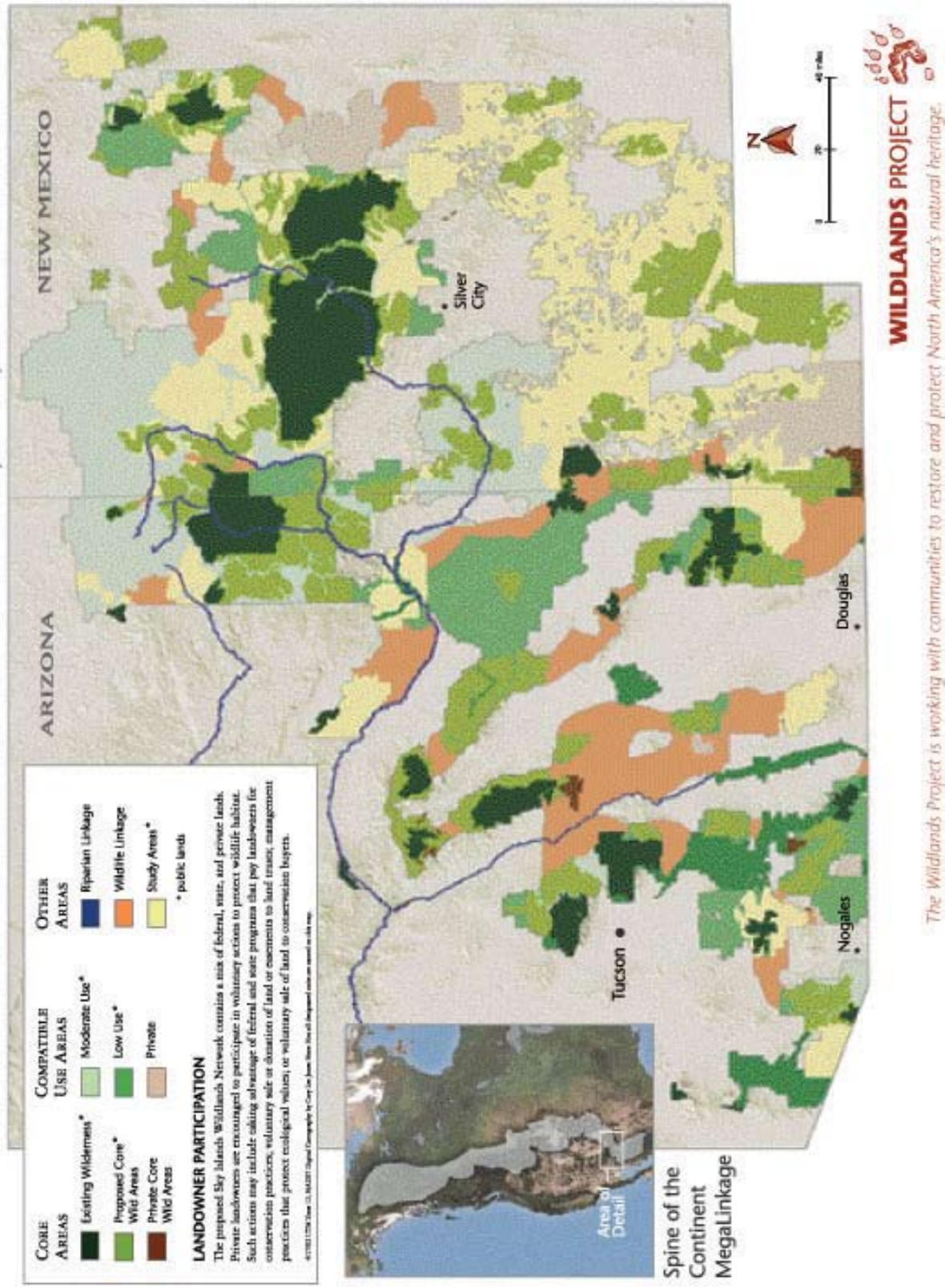


Figura 1. Red silvestre de montañas (Sky Islands): Un sistema propuesto para la conservación de tierras.

Noss y otros, examina las áreas núcleo protegidas y las conexiones de movimiento de fauna entre ellas, pero además examina el uso compatible de propiedad pública y privada alrededor de estas áreas protegidas.

Hemos encontrado que las tierras públicas no son suficientes para conectar áreas en Arizona y Nuevo México. Por lo tanto, es necesario mirar hacia la propiedad privada, para entender la forma en que esos ranchos y sus prácticas de pastoreo pueden ser compatibles con los objetivos globales de conservación, y así crear un marco de conservación y uso sustentable de la tierra para el siglo 21.

Section II

Management and Conservation

Conservación y Manejo

Grasslands of Mexico: A Perspective on Their Conservation

(summary)

Patricia Manzano *Agrupación Dodo*

Rurik List *Instituto de Ecología, Universidad Nacional Autónoma de México*

Grasslands are areas dominated by grasses and herbs with few or no trees. Grasslands receive too much rain for a desert environment and too little for a forest. Temperate North American grasslands, especially, have undergone changes on a continental level. Their high productivity and fertility, added to their level topography and lack of trees, make them ideal sites for farming and ranching. The transformation and loss of grasslands is causing the loss of species that depend on them, including grasslands birds, prairie dogs, and the black-footed ferret, the most endangered mammal of North America.

Researchers from the Institute of Ecology of the Autonomous University of Mexico (UNAM) began to study prairie dogs in 1994. During two years of living on an *ejido* (communally owned land) in Janos–Casas Grandes, the researchers familiarized themselves with the plants and animals living in that grasslands habitat, as well as with the problems affecting the zone and the needs of the population. The area includes mesquite, cholla and creosote scrublands, riparian areas and the ecotone between oak forest and foothills grassland. Mormons, Old Colony Mennonites, provincial *ejidatarios* (members of ejidos), and a growing urban population all use this area, destroying prairie-dog colonies, which has reduced overall wildlife.

In the last decade the area has received less rain, putting added pressure on the grasslands. The number of head of cattle in the summer pastures has remained level, despite decreased rainfall and available food. This has caused notable overgrazing, resulting in soil erosion and changes in vegetation composition. As a consequence of overgrazing and the loss of the prairie dogs, grasslands are being transformed into unproductive lands scrub, and inhabitants, especially young people, are leaving the area in search of better economic opportunities. Fortunately, in the past five years many Canadian, Mexican and U.S. organizations have taken great interest in the importance of grasslands, and are working on numerous projects focused on grasslands and their species.

Grasslands Conservation Workshops

In the last five years, diverse conferences, workshops, and forums have been held on the conservation and restoration of North American grasslands. They have covered issues such as endangered species and sustainable ranching along the U.S.–Mexico border, and bird conservation.

Conservation Projects in the Grasslands of Janos–Casas Grandes, Chihuahua

1. After being reintroduced into various places in the United States, the endangered black-footed ferret has been successfully reintroduced into the large prairie-dog colonies in Mexico's Janos–Casas Grandes area.
2. Power-line posts have been modified to avoid bird electrocutions in areas that have proven highly dangerous to bird populations.
3. The United States and Mexico are collaborating on a project to monitor ferruginous hawks with radio transmitters to learn where they reproduce.
4. Grassland birds are being monitored in order to compare data with areas in the Chihuahuan Desert.
5. The National Institute of Farming and Livestock Investigations has created uniform tools to measure grasslands health.
6. The impact of power lines on raptor populations is being monitored.
7. Agrupación Dodo and The Nature Conservancy are developing an educational teacher's guide on grasslands birds.
8. A new botanical garden has been created at the Cultures Museum of the North, in Casas Grandes, Chihuahua.

One of the most urgent challenges facing grasslands conservation is to raise awareness and consciousness

in the communities that inhabit them. Investigators, conservationists, landowners, local, state and federal governments, and inhabitants are all part of the grasslands conservation process. Many areas have achieved great progress due to the collaboration of diverse interest groups. We hope this will be the case for grasslands.

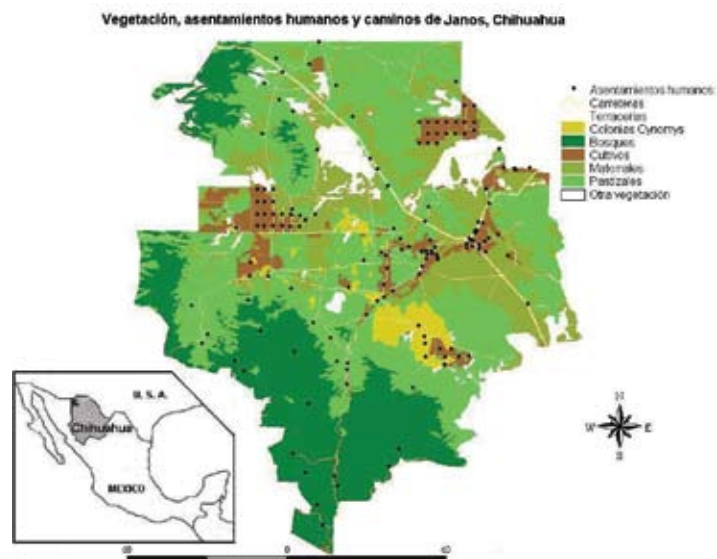


Figure 1. Vegetation, villages and roads of Janos, Chihuahua.

Los Pastizales del Norte de México: Una Perspectiva Para Su Conservación

(artículo invitado)

Patricia Manzano *Agrupación Dodo*

Rurik List *Instituto de Ecología, Universidad Nacional Autónoma de México*

Los pastizales son áreas dominadas por pastos y hierbas donde los árboles son escasos o están ausentes. Se encuentran en sitios donde llueve poco para ser bosques pero mucho para ser desiertos. Los pastizales templados son uno de los biomas que han sufrido una mayor transformación a nivel continental, debido a la alta productividad que le dan sus fértiles suelos, lo que aunado a su topografía plana y a su carencia de árboles, han hecho de los pastizales sitios ideales para el desarrollo de la agricultura y la ganadería.

La transformación y pérdida de pastizales está causando la pérdida de numerosas especies, como las aves de pastizal, que son el gremio de aves que más ha reducido sus poblaciones en las últimas décadas, o los perros llaneros que en un siglo redujeron el área que ocupaban en un 98%. La desaparición de los perros llaneros ha causado a su vez la reducción de las especies que dependen de ellos, como el hurón de patas negras, que es el mamífero mas amenazado de Norteamérica.

Fueron precisamente los perritos llaneros, los que nos llevaron a trabajar en los pastizales del norte de México desde 1994, como parte de un grupo de trabajo del Instituto de Ecología de la Universidad Nacional Autónoma de México, que realizaba las primeras listas de especies de animales y plantas que habitan la zona de Janos - Casas Grandes. Durante más de dos años vivimos en uno de los ejidos, lo cual nos permitió comprender muchos de los problemas que afectan esta zona y las necesidades de su población.

El área de Janos - Casas Grandes es un mosaico de vegetación, que además de los pastizales también incluye matorrales de mesquite, cholla y gobernadora, zonas riparias y el ecotono entre el bosque de encino y el pastizal de las laderas montañosas. Es también un mosaico cultural, donde se mezclan diferentes grupos como son los menonitas, mormones, ejidatarios provenientes de diferentes partes del país y una creciente población urbana.

Los menonitas vivieron una fuerte transformación cultural al aceptar el uso de vehículos automotores y electricidad, previamente prohibidos por sus tradiciones. Este hecho produjo un éxodo masivo de menonitas a

otros estados de México e incluso a otros países donde pudieran continuar con su antiguo modo de vida. En la actualidad una de las colonias menonitas es como un pueblo fantasma. Los que se quedaron han trabajado arduamente en desarrollar la agricultura en la región, ayudados por los subsidios a la electricidad que les permiten extraer el agua a precios bajos, a pesar de una veda a la creación de nuevos pozos, existente en la región. La mayor parte de estos cultivos se han hecho sobre pastizales, y en algunos casos sobre colonias de perritos llaneros, lo cual reduce las posibilidades de sobrevivencia a la fauna silvestre.

La última década ha llovido menos que el promedio anual, lo cual ha agregado una presión extra a los pastizales. Debido a que los índices de agostadero en la región son fijos independientemente de la intensidad de las lluvias, el número de cabezas de ganado se ha mantenido igual a pesar de haber menos alimento disponible. Esto a causado un notable sobrepastoreo, que a la vez ha resultado en la erosión del suelo y en cambios en la composición de la vegetación. A consecuencia del sobrepastoreo y de la pérdida de los perros llaneros, el pastizal se está transformando en un matorral, lo que origina la pérdida de las especies que dependen del pastizal para sobrevivir, pero también reduce el potencial económico de los habitantes locales. Existe una constante migración, sobre todo hacia los Estados Unidos, por parte de los habitantes jóvenes del área en busca de mejores perspectivas económicas.

Afortunadamente, en el último lustro la importancia de los pastizales ha despertado un gran interés en Norteamérica, y actualmente muchas organizaciones de Canadá, Estados Unidos y México trabajan en numerosos proyectos enfocados a la conservación de los pastizales y sus especies.

Talleres Para la Conservación de los Pastizales

En los últimos 5 años se han llevado a cabo diversas conferencias, talleres y foros que buscan la conservación y restauración de los pastizales de Norte América.

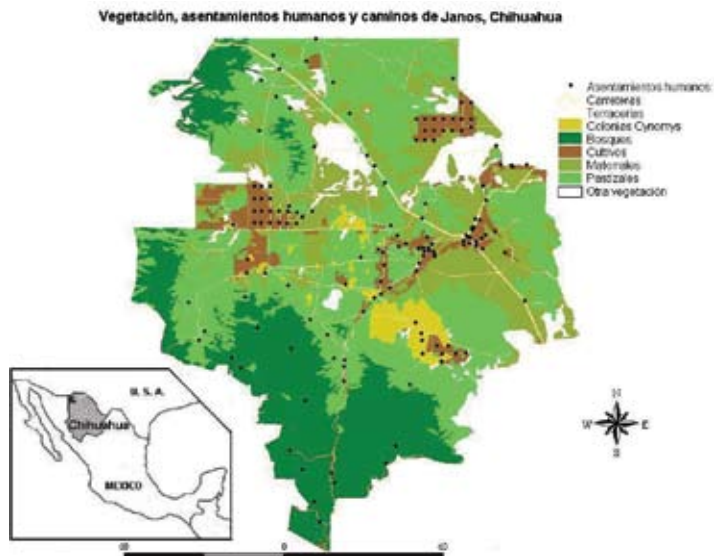


Figura 1. Vegetación, asentamientos humanos y caminos de Janos Chihuahua.

1) Conferencia sobre Ecosistemas de Pastizal, Especies en Peligro y Ganadería

Sustentable en la Frontera México - EE.UU. la cual logró reunir a expertos de los Estados Unidos y México, así como a propietarios de la tierra de Chihuahua, México. La conferencia fue un primer paso para lograr establecer una comunicación entre los expertos y las comunidades.

2) La Comisión de Cooperación Ambiental (CCA) ha realizado una serie de foros de consulta para elaborar estrategias de apoyo para la conservación de los pastizales. Se han llevado a cabo 3 reuniones (una en Nuevo Casas Grandes, Chihuahua, una en Mapimí, Durango, y recientemente una en la estación experimental La Campana, en Chihuahua, en colaboración con Iniciativa para la Conservación de las Aves de Norte América, NABCI por sus siglas en inglés). En estas ocasiones se reunió a especialistas en pastizales de Canadá, Estados Unidos y México. Los resultados de estas reuniones son la preparación de estrategias nacionales para la conservación de pastizales, la formación de un comité tri-nacional que trabajará para organizar esfuerzos de colaboración para la preservación de los pastizales de Norte América, y la formación de vínculos de colaboración entre personas de los tres países en proyectos conjuntos. Cabe destacar que el área de Janos-Casas Grandes ha sido elegida como una de las áreas importantes para la conservación de aves en donde se llevarán a cabo proyectos piloto de conservación.

3) Pronatura Noreste organizó un taller para la formación de una red de sitios para la conservación de las aves

del pastizal en el desierto chihuahuense. Un importante avance de este taller fue la formación de un grupo de trabajo sobre aves de pastizal, cuyo fin es homogenizar las metodologías de investigación y monitoreo, optimizar el uso de recursos, compartir la información y experiencia de las instituciones e individuos participantes así como la creación de una base de datos con la información existente.

Proyectos de conservación en los pastizales del área de Janos - Casas Grandes

1) La reintroducción del hurón de patas negras. El hurón de patas negras se considera el mamífero norteamericano mas amenazado de extinción. Estos animales fueron considerados extintos, pero en 1984 se encontró una pequeña colonia de hurones en Meteetsee, Wyoming. Los últimos individuos fueron capturados e incorporados a un programa de cría en cautiverio cuya finalidad era el hacer crecer la población lo suficiente como para poder reintroducir a los animales a su ambiente natural. En 1991 se llevó a cabo la primera reintroducción en una colonia de perros llaneros de Wyoming, desde entonces se han hecho reintroducciones en siete sitios de los Estados Unidos. Sin embargo las colonias de perros llaneros en este país no son lo suficientemente grandes como para poder sostener una población de hurones a largo plazo. El complejo de perros llaneros de Janos - Casas Grandes, en Chihuahua es el mayor de Norteamérica. Desde 1988 se comenzó a considerar la posibilidad de reintroducir los hurones de patas negras en Janos, proyecto que se hizo posible en el otoño del 2001, cuando personal del Instituto de Ecología UNAM y del Servicio de Pesca y Vida Silvestre de los Estados Unidos liberaron a los primeros hurones en la colonia de perros llaneros de mayor tamaño en el mundo, conocida como El Cuervo. A partir de entonces se han realizado 6 reintroducciones y se han liberado 161 individuos. Los monitoreos llevados a cabo han mostrado que los hurones se han adaptado bien al área, e incluso se han encontrado 9 hurones nacidos en libertad.

2) Electrocutación de aves en líneas eléctricas en Janos, Chihuahua. La electrocución de aves en líneas eléctricas es un problema que crece conforme crece la población humana y sus necesidades. En 1997 se detectaron las primeras aves electrocutadas en las líneas de energía de la zona de Janos, Chihuahua. A partir de ese momento se comenzaron a conjuntar una serie de esfuerzos dirigidos a solucionar el problema. Muchas organizaciones han colaborado para investigar, evaluar

y proponer soluciones para evitar que más aves mueran electrocutadas en los postes de energía eléctrica. En el año 2000 la Comisión Federal de Electricidad comenzó la modificación de algunas de las líneas peligrosas, esto mediante el remplazó de las crucetas metálicas por crucetas de madera. En marzo de 2001 se llevo a cabo el Primer Taller sobre Electrocutación de aves en México: hacia un diagnostico y perspectivas de solución. El resultado del taller fue la creación de un comité multidisciplinario que atenderá este problema, especialmente la identificación de acciones a corto, mediano y largo plazos, y la identificación de necesidades y oportunidades para investigación, comunicación, capacitación, financiamiento, modificación de estructuras en líneas de energía, legislación y cooperación internacional, especialmente con los Estados Unidos.

A principios del 2003 la Comisión Federal de Electricidad (CFE) ha remplazado las crucetas de las principales líneas que cruzan las colonias de perros llaneros, con lo cual se ha logrado una importante reducción en el riesgo de electrocución en Janos, sin embargo, aún existen estructuras peligrosas que deben ser modificadas. Este gran esfuerzo por parte de la CFE debe ser apoyado y en lo posible replicado en otras zonas del país.

- 3) Monitoreo de aguililla real (*Buteo regalis*). Proyecto conjunto E. U. A. y México para la colocación de radios de telemetría vía satélite a aves que invernán en Chihuahua con el fin de saber dónde se reproducen.
- 4) Monitoreo de aves de pastizal. Se homogeneizarán metodologías, lo cual permitirá la comparación de datos con otras áreas del Desierto Chihuahuense.
- 5) Homogenización de indicadores de salud de pastizales a cargo del Instituto Nacional de Investigaciones Agrícolas y Pecuarias, con el fin de tener herramientas sólidas que permitan diagnosticar el estado de un pastizal.

- 6) Evaluación de poblaciones de rapaces e impacto de líneas eléctricas. Este proyecto sobre rapaces ayudará a conocer el porcentaje de rapaces que mueren electrocutadas, como utilizan las líneas de energía y donde es necesario realizar modificaciones a las estructuras.

- 7) Educación ambiental sobre aves de pastizal. Agrupación Dodo y The Nature Conservancy están trabajando una guía para maestros de primaria y secundaria, así como en material educativo para estos dos niveles. La guía y el material se darán a conocer a los maestros durante talleres que tendrán lugar en el Museo de las Culturas del Norte.

- 8) Creación de un jardín botánico en el Museo de las Culturas del Norte, Casas Grandes, Chihuahua. El jardín mostrará especies de plantas locales, en caso de ser de utilidad se especificará el uso que tiene. La exhibición incluirá mamparas informativas sobre el ecosistema de pastizales, su flora y fauna.

La conservación de los pastizales enfrenta numerosos retos, uno de los más urgentes es el incrementar la conciencia y sensibilidad de las comunidades que en ellos habitan. En una ocasión un vecino le preguntó a uno de los miembros de nuestro equipo sobre su trabajo, el le comento que atrapaba ratones, el hombre muy sorprendido le contestó - ¿y le pagan por eso? -. Nuestro trabajo ha contribuido a que los habitantes locales comprendan que el área donde viven es importante y única, lo cual es el primer paso hacia su conservación.

En el proceso para la conservación de los pastizales se encuentran investigadores, conservacionistas, propietarios de la tierra, gobiernos locales, estatales y federales, así como a la población local. En otros sitios de México se han obtenido grandes logros como resultado de alianzas entre diversos grupos de interés. Esperamos que esto ocurra a su vez en los pastizales. Se está trabajando para conseguir consensos y soluciones que permitan conservar y mantener sanos los pastizales del norte de México y salvaguardar la flora y fauna que en ellos habita.

A Multi-state Approach to Black-tailed Prairie Dog Conservation and Management in the United States

(invited paper)

Robert J. Luce *Prairie Dog Conservation Team*

Introduction

The black-tailed prairie dog (*Cynomys ludovicianus*) is unusual among species proposed for Endangered Species Act (ESA) listing in that several million individuals currently exist across a large area in the wild. The National Wildlife Federation's 1998 listing petition estimated the current area occupied by the species at 283,500-324,000 ha. Although widespread, the species occurs mostly in remnant, highly segregated subpopulations with little genetic interchange and limited potential for long-term persistence.

A multi-state conservation effort begun in 1998 included the following elements:

- 1) formation of the Interstate Black-tailed Prairie Dog Conservation Team (Conservation Team) by eleven state wildlife agencies, with each designating a representative to attend planning meetings
- 2) signing of a Memorandum of Understanding (MOU) for a range-wide management approach by nine state wildlife agencies (two states declined to sign)
- 3) agreement to cooperate with the nine Native American tribes that form the Inter-Tribal Prairie Ecosystem Restoration Consortium
- 4) development of a Conservation Assessment and Strategy (Van Pelt 1999)
- 5) agreement on an implementation schedule that set dates for completing various stages of the process
- 6) formation within each state of a Working Group that includes all major stakeholders

The Assessment portion of the Conservation Assessment and Strategy (CA&S) used published data and range maps, and gray literature to delineate historic and current distribution. It also summarized the management status in each state and presented a risk assessment based on the five listing criteria the U.S. Fish and Wildlife Service (Service) must consider when evaluating a species proposed for threatened or endangered listing.

The Black-tailed Prairie Dog Working Group in each state includes all entities involved with prairie dog

management. Private landowners are well represented, either by individuals who own land with prairie dog populations or by umbrella organizations such as Stockgrowers and Cattlemen's Associations, Farm Bureau, and Woolgrowers. Energy development organizations, conservation organizations, hunting outfitters, sportsmen, Bureau of Land Management, U.S. Forest Service, and state chapters of The Wildlife Society are some of the other entities represented. Each working group will write a management plan tiered off of the CA&S. The nine Native American tribes expect to develop a management plan for each reservation.

Management plans will identify factors limiting the species and the approach each state will take in dealing with those factors. Target goals for occupied habitat will be set based on the Adaptive Management Process (Federal Register, Vol. 65, No. 247, Friday, December 22, 2000), which recognizes that agencies or tribes may need to modify management plans and goals to develop more effective management as new conditions evolve and new data become available. The objective of the management plan process will be to remove threats to the species and provide long-term management.

Historical Background

Historically the black-tailed prairie dog range extended from Canada to Mexico through the Great Plains states and west to southeastern Arizona (Foster and Hygnstrom 1990). The current range is similar to historic, but the number of occupied acres has been dramatically reduced over much of the former range (Hoogland 1996).

Black-tailed prairie dogs historically occupied the shortgrass, midgrass, Chihuahuan desert grasslands, Nebraska sandhills, and tallgrass prairie terrestrial ecoregions (Ricketts, et al. 1999). The historical range encompassed approximately 162,000 ha (Black-tailed Prairie Dog Conservation Team Internal Planning Document 2000), of which an estimated 40-100 million ha were occupied by prairie dogs at any one time

(Mulhern and Knowles 1995). Black-tailed prairie dog populations have been restricted to about 405,000 ha in the United States (Black-tailed Prairie Dog Conservation Team Internal Planning Document, 2000) and 20,250 ha in Mexico (Ceballos et al. 1993).

At least six federal agencies; and state wildlife departments, agriculture departments, departments of state lands, weed and pest districts, counties and private land-owners in 11 states manage prairie dogs either directly or indirectly. Prairie dog management goals and objectives vary among these entities, and management between states varies significantly. This variation can range from total protection of prairie dogs to a legal mandate to exterminate. Most states classified the prairie dog as a pest in 1998; a few classified it as wildlife, often with opposing management goals between state agencies. Federal policy regarding prairie dogs has been inconsistent over time and across geographic regions.

Knowles (1995) and Mulhern and Knowles (1995) summarized ownership of occupied black-tailed prairie dog habitat in the seven states that comprise the majority of occupied habitat. They found that 55 percent of the habitat was private and state-owned, 29 percent was on Native American reservations, and 16 percent was under federal management. Of the area under federal management, 6 percent was under BLM management, 6 percent was under Forest Service management, and 3 percent was under National Park Service, Fish and Wildlife Service or other federal agency management (Knowles 1995).

The best black-tailed prairie dog habitat is found on non-sandy, flat ground with less than 10 percent slope (Koford 1958, Krueger 1986). The bulk of prairie dog habitat in areas suitable for cultivated agriculture has already been converted and lost as prairie dog habitat (Mulhern and Knowles 1995).

Livestock owners have long perceived a conflict between prairie dogs and cattle and have traditionally poisoned prairie dog colonies on both private and public land (Merriam 1902). However, research by Koford (1958), Bonham and Lerwick (1976), Gold (1976), Hansen and Gold (1977), O'Melia et al. (1982), and Archer et al. (1987) suggests that prairie dogs, both historically and currently, have had beneficial or neutral effects on livestock forage. Hansen and Gold (1977) documented an overlap in diets of cattle and prairie dogs of only 4-7 percent. At this level of competition 300 prairie dogs consume as much forage as one cow and calf (Uresk and Paulson 1989). Several studies have shown that both domestic cattle and wild ungulates preferentially graze on prairie dog colonies (Knowles and Knowles 1994). Prairie dog colonies historically occupied only a small portion of the rangeland, however they may have increased productivity of the entire rangeland ecosystem.

Black-tailed prairie dogs are herbivores and feed on a variety of vegetation including grasses and forbs (Koford 1958), and to some extent seeds and insects (Foster and Hygnstrom 1990). They clip grasses and other vegetation close to the ground to allow for a greater range of vision. The burrowing action of prairie dogs enhances soil structure (White and Carlson 1984) and forb growth (Coppock et al. 1983) within the colony. The black-tailed prairie dog's significant influences on ecosystem function cause it to be considered keystone species of the prairie grasslands (Miller et al. 1996).

Prairie dog predators include coyote (*Canis latrans*), golden eagle (*Aquila chrysaetos*), ferruginous hawk (*Buteo regalis*), and black-footed ferret (*Mustela nigripes*). Black-tailed prairie dogs are very susceptible to the introduced disease sylvatic plague, and it is one of the factors that limits colonies. Although probably not so historically, prairie dog populations now appear to be cyclic due to the presence of sylvatic plague. Dramatic die-offs severely reduce local populations and the recovery period can take up to 10 years (Knowles 1995).

Threats

The threats identified in the Service's 12-month finding for the black-tailed prairie dog were:

- 1) habitat loss over the range
- 2) over-utilization for recreational purposes (unregulated shooting)
- 3) the disease sylvatic plague
- 4) inadequate regulatory mechanisms (unregulated poisoning and pest status, unregulated shooting).

The Service, in its 12-month finding of February 3, 2000, determined that listing of the species was warranted but precluded by other priorities. The "warranted but precluded" finding will be reviewed annually. During the Candidate Assessment, the Service will evaluate whether biological conditions or other threats listed in the 12-month finding warrant issuing a new one.

Primary range-wide habitat concerns are conversion of prairie grassland to farmland, urbanization, and conversion of grassland and savanna to shrubs. Native grasslands have been reduced by 33-37 percent across the species' distribution, mostly as a result of conversion to croplands, but also in some areas through urban development. In the remaining rangelands, increased presence of shrubs has discourage prairie dog occupancy and reoccupation.

Even before human intervention, prairie dogs only occupied approximately 20 percent of available habitat in a constantly shifting mosaic (Miller et al. 1996). Prairie dog control programs and conversion of prairie habitats

to croplands, pasture and areas of human occupation have dramatically reduced and fragmented prairie dog habitat. As a result of past actions the species currently exists in isolated, disjunct, and relatively small islands of colonies of varying size that are vulnerable to extirpation from genetic inbreeding, plague, human development of the landscape, and stochastic events.

Dispersal and interchange, which would normally offset catastrophic losses, are now limited because distances between colonies are generally greater than maximum prairie dog dispersal distances. Prairie dogs are reasonably good dispersers over moderate distances of up to 8 km following roadways, trails, or drainages (Garrett and Franklin 1988 cited in Knowles and Knowles 1994). Habitat alterations between islands of remaining habitat often present impossible barriers to immigration that would repopulate extirpated colonies. These and other factors may interact to increase the probability of extinction more than would be the case if each factor operated independently (Wilcox and Murphy 1985).

Shooting may depress colony productivity and health, fragment populations, cause some loss of non-target species, and preclude or delay recovery of colonies reduced by other factors such as sylvatic plague. Recreational shooting can significantly impact colonies in areas where shooting is intense or persistent over an entire year.

Black-tailed-prairie dogs suffer almost 100 percent mortality when exposed to plague, and there is little evidence that they develop antibodies against or immunity to the disease (Tonie Rocke, personal communication 2000). Plague was first identified in the United States in a population of California ground squirrels in 1908. Since then, the disease has spread throughout the western states infecting at least 76 species of rodents, rabbits, hares, shrews, ungulates, and primates (Poland and Barnes 1979). Plague is primarily a disease of rodents, and its effect on the different rodent species varies. Sylvatic plague was first documented in black-tailed prairie dogs near Lubbock, Texas, in 1946-47 (Miles et al. 1952 cited in Cully 1989). The disease has subsequently infected populations throughout the species' range west of about the 103rd Meridian.

The black-tailed prairie dog was classified as a pest by all states within its historic range at the time the listing petition was filed in 1998. Some state statutes required eradication and all states permitted uncontrolled take (Van Pelt 1999). The major federal land management agencies, Bureau of Land Management and Forest Service, managed prairie dogs to meet multiple-use policy objectives, and generally allowed poisoning and shooting before listing was proposed.

Extensive poisoning throughout most of the black-tailed prairie dog's range from 1912 to 1972 sought to reduce competition between prairie dogs and domestic

livestock. This effort likely reduced the prairie dog occupied acreage from 20,250,000 ha to about 140,130 ha (Bureau of Sport Fisheries and Wildlife 1961 cited in U.S. Fish and Wildlife Service 1999). From the early 1900s through the late 1960s extensive eradication by landowners and state and federal agencies was funded largely with federal money.

Animal Plant Health Inspection Service (APHIS) and Environmental Protection Agency records indicate an annual average of 81,000 ha of prairie dog acreage are poisoned annually in the United States under the permitting authority of these agencies (Captive Breeding Specialist Group 1992, cited in Miller et al. 1996).

The Bureau of Land Management no longer allows control except in specific circumstances. The U.S. Forest Service currently restricts poisoning on National Grasslands.

Management Approach

The states of Arizona, Colorado, Kansas, Montana, Nebraska, North Dakota, New Mexico, Oklahoma, South Dakota, Texas, and Wyoming are concerned with addressing the threats identified in the Service's 12-month finding to prevent advancement of the species from "warranted but precluded" to "threatened." To that end they are:

- 1) Cooperating to determine each state's contribution to a range-wide occupied acreage and distribution objective; and maintaining, at a minimum, the current black-tailed prairie dog population and distribution over 11 states. This approach is both fair and biologically defensible in that the mega-population will be less vulnerable to plague and stochastic factors if widely distributed.
- 2) Cooperating with the Inter-Tribal Consortium Coordinator and tribal land managers to develop occupied acreage goals.
- 3) Working on 11 individual statewide black-tailed prairie dog management plans.
- 4) Monitoring the poisoning program within each state. Ideally, this process will include annual reporting of acreage controlled and location so the impact on prairie dog acreage and distribution objectives can be measured, and if necessary, adjustment made to assure meeting the acreage objectives set forth in the Management Plan.
- 5) Working to allow the wildlife agencies to promulgate prairie dog shooting regulations and close the season if monitoring indicates the occupied acreage falls below objective. Hunter questionnaires could be used to collect harvest information.

- 6) Addressing fragmentation by: a) maintaining per state one or more complexes of at least 2,025 ha in size, b) maintaining at least 10% of the total occupied acreage in complexes more than 405 ha in size, c) maintaining or improving distribution (i.e. acreage by county), d) maintaining distribution of colonies and complexes such that corridors allow genetic interchange and re-colonization.
- 7) Providing incentives to private landowners critical to management success. The majority of the land that is currently occupied, and most of the land that is suitable habitat for black-tailed prairie dog expansion is in private ownership and used primarily for crop production and livestock forage. Incentives may include financial benefits, authority to control nuisance prairie dogs, and continued use of lands to generate income. Financial incentives are not included in state management plans and therefore require outside funding sources. Without this key element, it may be impossible to engage private landowners in conserving black-tailed prairie dogs.

Summary

The black-tailed prairie dog currently occurs over most of its historical range although at well below the historical occupied acreage and population level. The threats to the black-tailed prairie dog are real and significant, therefore adequate management is needed to ensure long-term survival of the species. Fortunately the black-tailed prairie dog is a very resilient species, has moderately high reproductive capability, and is able to reoccupy suitable habitat even after severe population declines, whether natural or man-caused. Therefore a pre-listing management effort has a high probability of success.

State wildlife agencies are well suited to manage this species to maintain viable populations and adequate distribution and effectively address the threats listed in the Service's 12-month finding. Because habitat, management approach, private landowner participation, and other factors differ among states, each of 11 state wildlife agencies will have its own black-tailed prairie dog management plan. However, the multi-state cooperative effort will ensure that management of the species and its habitat is consistent across the range in the U.S.. Effective implementation of a management plan in each state will prevent the need to manage a listed species at some point in the future.

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Enfoque Multi-estatal Para la Conservación y Manejo del Perro Llanero de Cola Negra en los Estados Unidos

(resumen)

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El perro llanero de cola negra (*Cynomys ludovicianus*) es singular entre las especies propuestas para el listado de la Ley de Especies en Peligro (Endangered Species Act - ESA) porque actualmente existen varios millones de individuos viviendo en zonas silvestres extensas. La petición de listado de *The National Wildlife Federation* de 1998 calculó el área actual ocupada por la especie en 283,500 a 324,000 hectáreas. Sin embargo, aunque está distribuida ampliamente, la especie habita en su mayor parte en subpoblaciones remanentes altamente segregadas, con poco intercambio genético y un potencial limitado de persistencia a largo plazo.

En 1998 se inició un esfuerzo de conservación multi-estatal que incluye los siguientes elementos:

1. Formación del Equip de conservación interestatal del perrito llanero de cola negra (*Interstate Black-tailed Prairie Dog Conservation Team*) por once instituciones estatales de vida silvestre, con un representante designado para asistir a las reuniones.
2. Firma de un acuerdo de entendimiento (MOU por sus siglas en inglés) para un manejo de amplio rango por nueve estados.
3. Acuerdo para cooperar con las nueve tribus Americanas Nativas que forman el Consorcio Intertribal para la Restauración de Ecosistemas de Pradera (*Inter-Tribal Prairie Ecosystem Restoration Consortium*).
4. Desarrollo de una Evaluación y Estrategia de Conservación (Conservation Assessment and Strategy) (Van Pelt 1999).
5. Acuerdo sobre la implementación de un programa que establece fechas para completar varias etapas del proceso.
6. Formación dentro de cada estado de un grupo de trabajo que incluya a la mayor parte de los propietarios de tierras.

El grupo de trabajo en cada estado reúne al sector privado, a organizaciones de energía, conservación, caza, a dependencias federales y a organizaciones no gubernamentales, entre otros. Cada grupo de trabajo redactará un plan de manejo en base al proceso de evaluación y estrategia de conservación.

Los planes de manejo identificarán los factores que limitan la especie y el enfoque que cada estado tomará para tratar con esos factores. Las metas a alcanzar en los hábitat ocupados se realizarán en base al Proceso de Manejo Adaptativo (Federal Register, Vol. 65, No. 247, Friday, December 22, 2000), el cual reconoce que las agencias o tribus pueden tener la posible necesidad de modificar planes y objetivos a medida que las condiciones evolucionen y se obtenga nueva información.

Antecedentes Historicos

Históricamente, el perrito llanero de cola negra habitaba desde Canadá hasta México, a través de las praderas Gryes y al oeste hasta el sudeste de Arizona (Foster y Hygnstrom 1990). El área actual es similar a la histórica, pero el número de acres ocupados se ha reducido dramáticamente (Hoogly 1996).

Los perritos llaneros de cola negra en años pasados ocuparon los pastizales altos y medianos de Chihuahua, los cerriles arenosos de Nebraska y las ecoregiones terrestres con praderas de altos pastos (Ricketts et al. 1999). Los datos históricos mencionan una superficie de 162,000 ha (Black-tailed Prairie Dog Conservation Team Internal Planning Document 2000), de las cuales 40 – 100 millones de ha fueron ocupadas por perritos llaneros en algún tiempo (Mulhern y Knowles 1995). Las poblaciones de perritos llaneros de cola negra han sido restringidas a cerca de 405,000 ha en los Estados Unidos (Black-tailed Prairie Dog Conservation Team Internal Planning Document 2000) y a 20,250 ha en México (Ceballos et al. 1993).

Muchas entidades federales, estatales, municipales y privadas manejan perritos llaneros directa o indirectamente. Los objetivos de manejo varían entre estas entidades, y el manejo entre los estados varía significativamente. Esta variación abarca desde una protección total del perro llanero, hasta un mandato legal de exterminio.

Knowles (1995) y Mulhern y Knowles (1995) resumieron el tipo de propiedad ocupado por el perro llanero

en siete estados y encontraron que el 55% del hábitat es ocupado por propiedades privadas y estatales, 29% se ubica en reservaciones de Nativos Americanos y 16% está bajo manejo federal. De las áreas bajo manejo federal, 6% pertenecen al BLM, 6% al Servicio Forestal (Forest Service) y el porcentaje restante está bajo el manejo del National Park Service, el Fish y Wildlife Service y otras agencias federales (Knowles 1995).

El mejor hábitat para el perro llanero de cola negra se encuentra en suelos no arenosos, planos con pendientes menores al 10% (Koford 1958, Krueger 1986). La mayor parte del hábitat del perro llanero ha sido convertido en áreas agrícolas (Mulhern y Knowles 1995).

Desde hace mucho tiempo, los ganaderos han percibido un conflicto entre el perro llanero y el ganado, y tradicionalmente han envenenado las colonias en tierras públicas y privadas (Merriam 1902). Sin embargo, las investigaciones de Koford (1958), Bonham y Lerwick (1976), Gold (1976), Hansen y Gold (1977), O'Melia et al. (1982), y Archer et al. (1987) sugieren que los perritos llaneros, tanto histórica como actualmente, tienen efectos benéficos o neutrales en el forraje del ganado. Hansen y Gold (1977), sostienen que existe un traslape de solo 4 – 7% en las dietas del ganado y los perritos llaneros. A este nivel de competencia, 300 perritos llaneros consumen una cantidad de forraje igual a una vaca con su cría (Uresk y Paulson 1989). Otros estudios muestran que tanto el ganado doméstico como los rumiantes salvajes prefieren pastar en las colonias (Knowles y Knowles 1994), lo cual podría aumentar la productividad del ecosistema al sumarse a la diversidad.

Los perritos llaneros de cola negra son herbívoros que se alimentan de zacates y hierbas (Koford 1958), y en ocasiones de insectos y semillas (Foster y Hygnstrom 1990). Ellos cortan el forraje hasta el suelo para permitir un mayor rango de visibilidad. La acción excavadora de los perritos llaneros mejora la estructura del suelo (White y Carlson 1984) y el crecimiento de hierbas (Coppock et al. 1983) dentro de la colonia. Las influencias significativas de los perritos llaneros de cola negra sobre el funcionamiento del ecosistema hacen que sean la especie clave en los pastizales de pradera (Miller et al. 1996).

Además de sus depredadores naturales, los perritos llaneros son muy susceptibles a la plaga silvática, que constituye uno de los factores que limita la persistencia y expansión de las colonias (Knowles 1995).

Amenazas

Las amenazas identificadas son:

1. Pérdida de hábitat.
2. Uso excesivo para propósitos recreativos (caza no regulada).

3. Plaga silvática.

4. Mecanismos reguladores inadecuados (envenenamiento y caza no regulada, denominación de plaga).

Las tres cuestiones principales en relación al hábitat son la conversión de pradera de pastizal a tierras de cultivo, urbanización, y conversión de pastizal y sabana a matorral. Estas cuestiones, aunadas a los programas de control de perritos llaneros han reducido y fragmentado dramáticamente el hábitat de los perros de las praderas. La dispersión y el intercambio son limitados porque las distancias entre colonias y complejos de colonias son mayores que las distancias de dispersión de la especie. Los perros de las praderas son buenos para dispersarse en distancias de hasta 8 km a lo largo de caminos, veredas y drenajes (Garrett y Franklin 1988, citado en Knowles y Knowles 1994). Las alteraciones del hábitat entre islas presentan barreras que imposibilitan la inmigración para repoblar colonias extirpadas. Estos y otros factores pueden interactuar para incrementar la probabilidad de extinción que no sucedería si cada factor operara en forma independiente (Wilcox y Murphy 1985).

La plaga silvática, otro factor de reducción importante, afecta principalmente a los roedores, y su efecto en diferentes especies varía. Los perritos llaneros sufren casi 100% de mortalidad al exponerse a la enfermedad y existe poca evidencia de que ellos desarrollan anticuerpos o algún tipo de inmunidad contra esa enfermedad (Tonie Roche, comunicación personal 2000). La plaga fue identificada por vez primera en ardillas en el estado de California en 1908. Desde entonces, se ha dispersado por todos los estados del occidente donde infectó al menos 76 especies de roedores, rumiantes y primates (Poly y Barnes 1979). En perritos llaneros de cola negra fue primeramente documentada en Texas en los años de 1946 – 47 (Miles et al. 1952 citado en Cully 1989).

En 1998, el perro llanero de cola negra fue clasificado como una plaga en todos los estados dentro del hábitat histórico. Algunos estados en sus estatutos requirieron su erradicación y todos los estados en conjunto permitieron su caza incontrolada (Van Pelt 1999). De 1912 al 72 se llevó a cabo un envenenamiento extensivo para reducir la competencia entre el perro llanero y el ganado. Este esfuerzo redujo la superficie ocupada por el perro llanero de 20, 250, 000 ha a 140,130 ha (Bureau of Sport Fisheries y Wildlife 1961 cited in U.S. Fish y Wildlife Service 1999).

Los datos del Servicio de Inspección de Salud de Animales y Plantas (*Animal Plant Health Inspection Service*) y la Agencia de Protección Ambiental (*Environmental Protection Agency*) indican que un promedio de 81,000 ha de perritos llaneros son envenenados anualmente en los Estados Unidos bajo consentimiento oficial de esas instituciones (Captive Breeding Specialist Group 1992, citado en Miller et al. 1996).

Propuesta de Manejo

Los estados de Arizona, Colorado, Kansas, Montana, Nebraska, Dakota del Norte, Nuevo México, Oklahoma, Dakota del Sur, Texas y Wyoming están conscientes de la situación y están haciendo lo posible por situar a la especie en categoría de “amenazada”, para lo cual ellos están:

1. Cooperando para determinar la contribución de cada estado y manteniendo, al mínimo, la población y distribución de perritos llaneros de cola negra en 11 estados.
2. Cooperando con el Consorcio Intertribal para la Restauración de Ecosistemas de Pradera y los manejadores de tierras tribales para desarrollar metas en superficies ocupadas.
3. Trabajando con 11 planes de manejo estatales de perritos llaneros de cola negra.
4. Monitoreando el programa de envenenamiento dentro de cada estado.
5. Trabajando para permitir a las agencias de vida silvestre la promulgación de regulaciones para la caza de perritos llaneros de cola negra y cerrar la temporada de caza si el monitoreo indica que la superficie ocupada cae por debajo del objetivo.
6. Tratando la fragmentación mediante: a) el mantenimiento por estado de uno o más complejos de al menos 2,025 ha, b) el mantenimiento de al menos 10% de la superficie total ocupada en complejos mayores a 405 ha, c) el mantenimiento de la distribución (i.e. hectareaje por condado) y d) el mantenimiento de la distribución de las colonias y complejos de tal forma que los corredores permitan el intercambio genético y la recolonización.
7. Proporcionando incentivos a los propietarios de terrenos en situación crítica para obtener éxito en el manejo.

Resumen

Las amenazas al perro llanero de cola negra son reales y significativas. Se debe desarrollar un manejo adecuado para asegurar la supervivencia de la especie a largo plazo. Afortunadamente es una especie muy resistente, tiene una capacidad reproductiva moderadamente alta, y es capaz de recuperar su hábitat aún después de una disminución severa de la población. Por esta razón, un esfuerzo de manejo antes de incluir a la especie en el listado tiene altas probabilidades de éxito.

Puesto que el hábitat, el enfoque de manejo, la participación de terratenientes privados y otros factores difieren

entre los estados, cada una de las agencias de protección a la fauna tendrán un plan específico para cada estado. Sin embargo, el esfuerzo cooperativo multi-estatal asegurará que el manejo de la especie y de su hábitat sea consistente a lo largo de los Estados Unidos.

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Initial Results of Experimental Studies of Prairie Dogs in Arid Grasslands: Implications for Landscape Conservation and the Importance of Scale

(invited paper)

Charles Curtin *Arid Lands Project*

Introduction

Numerous ecologists and conservationists believe that prairie dogs increase ecosystem diversity and preserve the function of grasslands (Whicker and Detling 1988, Miller et al. 1994, Jones et al. 1994, Power et al. 1996, Weltzin et al. 1997, Miller et al. 2000), yet this perspective is controversial (Stapp 1998). In contrast, many ranchers and land owners view prairie dog conservation and restoration as a threat to their livelihoods because they believe that prairie dog holes pose a threat to livestock and the prairie dogs consume forage. While numerous studies of prairie dogs have been completed, few comprehensive experimental studies of the ecological effects of prairie dogs have been conducted and none of these studies have been completed in arid grasslands. Since 1999 we have been conducting experimental studies of the interaction of Black-tailed prairie dogs (*Cynomys ludovicianus*) with conservation and lands management. In this paper two fundamental questions are addressed. First, are ranching and other pastoral land uses compatible with the reintroduction of prairie dogs? Second, are the patterns of diversity and ecosystem composition noted from studies of the central and northern Great Plains relevant for desert grasslands?

In addition to an examination of the inherent conflict between conservationist and land manager perceptions of prairie dogs, we also undertake this study because experimental studies of herbivory by small mammals and cattle have convinced us that under current climatic conditions in the Mexico/U.S. borderlands (wet winter and dry summers over much of the past 25 years), herbivory can play a critical role in reducing climatically driven vegetation change and sustaining the biodiversity of arid grasslands (Brown et al. 1997, Curtin et al. 2000, Curtin and Brown 2001).

Experimental Design

In June 1999 we introduced 102 Black-tailed prairie dogs from the Turner Vermijo Park Ranch into four re-search pastures (25 animals per town) on the Gray Ranch in southwestern New Mexico. We have superimposed our reintroduction efforts on the experimental design of grazing and fire studies being conducted in the 8,870 acre (3,696 ha) McKinney Flats research area allowing us to contrast the major driving variables in southwestern grasslands (climate, fire, prairie dogs, and cattle grazing). Within each 2,200-acre (917-ha) sub-pasture is a 1-km² study area that contains four 500 x 500-m treatment areas composed of fire/grazing, fire/no-grazing, no-fire/no-grazing, and no-fire/grazing plots. Within each treatment area and on the prairie dog towns is a 200 x 200-m study area. Plant and animal density and diversity is sampled along five 150-m lines in the center of these study areas. Vegetation is sampled at two meter intervals within 40-cm quadrats for frequency and cover once a year in the fall. At every 30 m along the 150-m lines we have placed a stake resulting in a 5 x 6-m stake grid where lizard and mammal censuses occur. Lizards are sampled three times a summer using pit-fall traps located at the sampling stakes. Small mammal sampling is conducted at the sampling stakes using Sherman live traps. Prairie dogs were translocated into four colonies through the creation of artificial burrows using techniques developed by Dr. Joe Truett and the Turner Foundation. The prairie dogs have subsequently expanded into their own natural burrows. Current analysis involves contrasts of each prairie dog town, with the grazed-unburned plot within the same sub-pasture. We subjected data to paired analysis using a T-Test within the statistical program Statview TM.

Since initiating our study we have found that the prairie dog town in the northwest pasture, in addition to being isolated from the other colonies, is also considerably drier

(8 inches of precipitation annually versus 10 inches in the other towns) and thus is not a true replicate. Therefore for this analysis we will focus on the three towns with comparable conditions in the southwest, southeast, and northwest pastures.

Results

In 2000 and 2001 cover of shrubs, grasses, and bare ground were not significantly different on prairie dog colonies versus control plots ($p = 0.05$). Vegetation diversity was significantly lower ($p < 0.03$) on the prairie dog towns. Vegetation biomass in 2000 ($p < 0.002$) and 2001 ($p = 0.04$) were significantly higher on the prairie dog towns with a mean in 2000 of 56.6 (sd = 12.5) versus a control plot mean of 41 (sd = 3.6).

Measurement of small mammals from 1999 through 2001 ($n = 3$) did not differ significantly between prairie dog and control plots. The mean number on the prairie dog towns was 9.7 (sd = 9.7), while on the controls the number were 9.5 (sd = 9.6). The species numbers on the towns were 3.6 (sd = 2.1) compared to 3.4 (sd = 2.2) off the towns. Biomass on the prairie dog towns was 331.5 (sd = 402.2), while off the towns 351.7 (sd = 288.3).

In contrast to the mammals, the lizards showed a positive response to the prairie dogs. The number of lizards on the prairie dog towns was significantly higher on the towns than off ($p < 0.01$). The biomass was higher on the prairie dog towns, though this difference was marginally non-significant ($p < 0.06$). The lizard diversity was also higher on the prairie dog towns, but like the biomass was also marginally non-significant ($p < 0.07$).

Discussion

In response to the first question (Are ranching and other pastoral land uses compatible with the reintroduction of prairie dogs?), the increased vegetation biomass documented here, and higher nutrient content documented in numerous studies (Coppock et al. 1983, Krueger 1986, Whicker and Detling 1988, Delting 1998), suggests that prairie dog reintroductions can actually have positive benefits for ranchers, and that these patterns are in many ways more tangible than the benefits to conservation. This information, coupled with the disproportionate use of the prairie dog towns by cattle on the pasture, suggests there can be a positive feedback loop between cattle and prairie dogs. The prairie dogs increase forage quality and potentially increase biomass, while the cattle by grazing in the vicinity of the towns mow the grass short thereby reducing the prairie dogs

susceptibility to predators. Because the cows focus their foraging activities in an area about 40 percent larger than the actual prairie dog town, they in turn are expanding the area of potential prairie dog colonization, which in turn can lead to increased amounts of rich forage for the cattle. In addition, the hoof action and intense foraging of the cattle appears to have an effect of increased the micro-topography and habitat diversity on the landscape that is comparable to the effects of the prairie dogs. These observations suggest that much of the system diversity ascribed to many prairie dog towns is a reflection of not just the work of prairie dogs, but an interaction between prairie dogs and large ungulate species including not just native species such as antelope, bison, and deer, but also domestic species such as cattle.

In response to the second question (Are the patterns of diversity and ecosystem composition noted from studies of in the central and northern Great Plains relevant for desert grasslands?), the initial results of this long-term study indicate that prairie dog reintroductions have diverse impacts on ecological systems. At a local scale it is too simplistic to state that prairie dogs have a blanket positive impact on local biodiversity; rather, there are winners and losers. While the prairie dogs did not significantly alter vegetation composition, they did increase vegetation biomass, but decreased species richness. Small mammals show a negative or neutral response to prairie dog reintroduction, while lizards had a positive response. Yet crucial to any discussion of the biodiversity of prairie dogs is consideration of scale. At the scale of a single plot (Alpha diversity – Whittaker 1975) differences between prairie dog and non-prairie dog plots following two years were subtle. Yet the conservation value of prairie dogs lies not in their localized impacts, but in their overall contribution to landscape diversity (Beta and Gamma diversity – Whittaker 1975). This is because the ecological footprint of prairie dog towns extends well beyond their colony boundaries to regional contributions to overall species diversity and shifts in landscape function. For example, cattle and other grazers frequently travel long distances to prairie dog towns to forage, transporting nutrients into the vicinity of the towns (C.G. Curtin, Unpublished). Birds such as burrowing owls (*Athene cunicularia*) rapidly inhabit areas where they were previously scarce (C.G. Curtin, Unpublished). In summary, from both a conservation and management perspective, prairie dog contribution to biological diversity and landscape function lies not at the scale of discrete localized patches, but rather in the matrix of diverse habitats generated by prairie dogs through their activities, and their interaction with other biotic and abiotic patterns and processes.

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Resultados Iniciales de Estudios Experimentales en Perros Llaneros de Pastizales Áridos: Implicaciones Para la Conservación del Paisaje y la Importancia de Escala

(resumen)

Charles Curtin *Arid Lands Project*

Introducción

Hay numerosos ecologistas con la convicción de que los perros llaneros aumentan la diversidad del ecosistema y preservan la función de los pastizales (Whicker and Detling 1988, Miller et al. 1994, Jones et al. 1994, Power et al. 1996, Weltzin et al. 1997, Miller et al. 2000), aunque esta perspectiva es controvertida (Stapp 1998). En contraste, muchos terratenientes piensan que la restauración y la conservación del perro de las praderas es una amenaza porque creen que las madrigueras de esos animales presentan un riesgo para el ganado, además de que consumen forraje. Se han llevado a cabo muchos estudios sobre los perros llaneros, pero pocos trabajos experimentales existen en relación a los efectos ecológicos de los perros llaneros, y ninguno de estos estudios se ha realizado en pastizales áridos. Desde 1999 estamos llevando a cabo estudios sobre la interacción entre el perro de la pradera de cola negra (*Cynomys ludovicianus*) y la conservación y manejo de tierras. En el presente trabajo se abordan dos cuestionamientos fundamentales. Primero, ¿son compatibles los usos pastorales de la tierra con la reintroducción de perros llaneros? Segundo, ¿son relevantes los patrones de diversidad y de composición de ecosistemas tomados de los estudios de las zonas Centro y Norte de las Grandes Praderas para los pastizales desérticos? Nosotros quisimos realizar este estudio ya que varios estudios experimentales sobre herbivoría ocasionada por pequeños mamíferos y el ganado nos han convencido de que bajo las condiciones climáticas actuales en la región fronteriza México/USA, la herbivoría puede jugar un papel crítico al reducir los cambios en la vegetación producidos por el clima y, además, en sostener la biodiversidad de los pastizales áridos (Brown et al. 1997, Curtin et al. 2000, Curtin and Brown 2001).

Diseño Experimental

En Junio de 1999 introducimos 102 perros llaneros de cola negra provenientes del Turner Vermijo Park Ranch, en 4 pastizales de investigación del Gray Ranch en el suroeste de Nuevo México. Tomamos como modelo los estudios de pastoreo y de quema llevados a cabo en el área de investigación de McKinney Flats, para contrastar las variables más importantes en los pastizales del suroeste (clima, fuego, perros llaneros y ganado). Dentro de cada sub-pastizal hay un área de 1 km² dividida en 4 lotes experimentales de 500 x 500 m para separar los tratamientos fuego/pastoreo, fuego/no pastoreo, no fuego/no pastoreo y no fuego/pastoreo. Dentro de cada área de tratamiento y población de perros llaneros existe un área de estudio de 200 x 200 m. La densidad y diversidad de plantas y animales se muestrea a lo largo de 5 líneas de 150 metros en el centro de esas áreas de estudio. La vegetación se muestrea usando cuadrados de 40 cm de lado una vez al año en el otoño, para medir frecuencia y cobertura. Con el fin de censar lagartijas y mamíferos, a cada 30 metros a lo largo de las líneas, se colocó una estaca formando una red de estacas de 5 x 6. Las lagartijas se muestrearon tres veces en el verano usando trampas localizadas en las estacas de muestreo. El muestreo de pequeños mamíferos se realizan en las estacas de muestreo usando trampas vivas de Sherman. Los perros llaneros se colocaron en cuatro colonias, mediante la creación de madrigueras artificiales, usando las técnicas desarrolladas por el Dr. Joe Truett y The Turner Foundation. Esos animales se han expandido a sus propias madrigueras naturales.

Los análisis actuales involucran contrastes de cada colonia de perros llaneros con el tratamiento no fuego/pastoreo dentro del mismo sub-pastizal. Procesamos los datos en un análisis pareado usando una prueba de T dentro del programa de estadística StatviewTM.

Debido a que al encontrar que la colonia de perros llaneros del pastizal noroeste, además de estar aislada de las otras colonias es considerablemente más seca (2 pulgadas de precipitación menos que las otras), consideramos que no es una buena réplica para el experimento, por lo que decidimos enfocar nuestro análisis a las tres colonias con condiciones comparables.

Resultados

En el 2000 y 2001, la cobertura de vegetación y suelo desnudo no fue significativamente diferente entre las colonias de perros llaneros y los lotes de control ($p = 0.05$). La diversidad de la vegetación fue significativamente más baja ($p = 0.03$) en las colonias. La biomasa de la vegetación en el 2000 ($p < 0.002$) y 2001 ($p = 0.04$) fue significativamente más alta en las colonias con una media en el 2000 de 56.6 ($sd = 12.5$) contra la media del control de 41 ($sd = 3.6$).

El número de mamíferos pequeños de 1999 a 2001 ($n = 3$) no fue diferente entre las colonias y los lotes de control. La media en las colonias fue de 9.7 ($sd = 9.7$), mientras que en el control de 9.5 ($sd = 9.6$). El número de especies en las colonias fue de 3.6 ($sd = 2.1$) comparada con 3.4 ($sd = 2.2$) fuera de ellas. La biomasa en las colonias fue de 331.5 ($sd = 402.2$) mientras que fuera de las colonias 351.7 ($sd = 288.3$).

En contraste a los mamíferos, las lagartijas mostraron una respuesta positiva a los perros llaneros. El número de lagartijas en las colonias de perros llaneros fue significativamente más alto que afuera de ellas ($p < 0.01$). La biomasa fue más alta en las colonias, aunque la diferencia no fue significativa ($p < 0.06$). La diversidad de las lagartijas también fue más alta en las colonias pero sin diferencia significativa ($p < 0.07$).

Discusión

En respuesta al primer cuestionamiento, el aumento de la biomasa de la vegetación documentado aquí y el aumento en el contenido de nutrientes citado en numerosos estudios (Coppock et al. 1983, Krueger 1986, Whicker and Detling 1988, Delting 1998), sugieren que la reintroducción de perros llaneros puede tener beneficios positivos para los terratenientes y que esos patrones son, en muchas formas, más tangibles que los beneficios que ofrece la conservación. Esto sugiere que puede darse una retroalimentación positiva entre el ganado y los perros llaneros. Los perros llaneros aumentan la calidad del forraje e incrementan la biomasa, mientras que el ganado, al pastar en la cercanía de las colonias, reduce la altura del pasto y así también la susceptibilidad de los perros

llaneros a los depredadores. Puesto que las vacas se enfocan en comer en un área más grande que la colonia, expanden el área potencial de colonización de los perros llaneros, lo que a su vez lleva a un aumento en la calidad del forraje. Además, la actividad del ganado al pisar y pastar intensamente en el área, parece tener como efecto un aumento en la microtopografía y la diversidad del hábitat, comparable a los efectos de los perros llaneros.

En respuesta al segundo cuestionamiento, los resultados iniciales de este estudio indican que la reintroducción de perros llaneros tiene impactos diversos en los sistemas ecológicos. En una escala local es muy simplista afirmar que los perros llaneros tienen un impacto positivo en la biodiversidad local. Aunque los perros llaneros no alteraron significativamente la composición de la vegetación, sí incrementaron su biomasa, pero también redujeron la diversidad de especies. Sin embargo, el valor de conservación del perro de la pradera no se ubica en su impacto localizado sino en su contribución general a la diversidad (diversidad Beta y Gama – Whittaker, 1975). Esto es porque la influencia ecológica de las colonias se extiende mucho más allá de la frontera de la colonia y contribuye regionalmente a la diversidad de las especies.

En resumen, desde una perspectiva de conservación y manejo, la contribución del perro de las praderas a la diversidad biológica y al funcionamiento del paisaje se da no solo a escala de manchones localizados y discretos, sino en una matriz de hábitats diversos generados por los perros de las praderas mediante sus actividades y su interacción con otros patrones y procesos bióticos y abióticos.

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Grassland Rehabilitation

(summary)

Mario Royo *Campo Experimental La Campana, INIFAP-SAGARPA*

The main goal of grassland rehabilitation is to re-establish vegetation, with the objectives of reducing soil erosion, incorporating more rainwater into the soil and aquifer, maintaining biodiversity, restoring scenic beauty, and attaining a site's forage potential, as well as maintaining and reproducing the native fauna. Pastures can be rehabilitated naturally by balancing animal numbers with appropriate grassland area and distributing animals appropriately, by resting and rotating pastures, and by controlling invasive shrubs and toxic plants. Areas can be rehabilitated artificially by seed dispersal or by the transplanting of forage species, together with efforts to conserve soil and water.

Before rehabilitation operations, an evaluation of a site's state of health should be made to determine stability (to know if soil is being lost), hydrologic functionality (capability to capture, store, and distribute water), and biological integrity (proportion and distribution of plant and animal functional groups). If the results are poor, rehabilitation strategies should be planned.

Grassland deterioration can be seen first at heavily utilized sites, such as areas near watering holes, feeding troughs, salt licks, and corrals. Cost-effective strategies that offer maximum ecological benefit should be used first, principally:

- 1. Stocking capacity.** Modify the pasture's animal load in relationship to its annual forage production.
- 2. Grazing Management.** Use any grazing system that allows for uniform use of vegetation, maintenance of vigorous plant life, and production of abundant, high-quality seeds.

3. Toxic and Invasive Plant Control. Understanding species' biology is important in determining whether control is necessary, and if needed, the type of control to use. Biological-control practices should be used first, followed by mechanical, and finally, chemical. Adequately protected workers should apply chemical controls that do not leave residual effects—(or bio-accumulate)—only to the individual organisms to be controlled.

4. Water and Soil Harvesting. Where lack of vegetation does not permit sufficient water harvest or new plant establishment, mechanisms need to be put into place to retain soil, water, organic material, and seeds.

5. Planting and/or Transplanting of Forage Species. In sites that are barren and/or need an extensive time to recuperate, native species can be planted or transplanted. Transplanting is less risky, more successful and more beneficial than planting from seed.

After deciding to rehabilitate a grassland area, it is important to monitor and evaluate the results. Most importantly is awareness that conservation and rational use of natural resources is the best strategy, so that we may continue to receive such vital products as water, forage, and air—essential for us today and for our children tomorrow.

For more information write to royomario@hotmail.com, phone (614) 481-0769 or (614) 481-0257, or visit the offices of the Campo Experimental La Campana, INIFAP-SAGARPA, located at Avenida Hormero N. 3744, Col. El Vergel, Chihuahua, Chih.

Rehabilitación de Pastizales

(artículo invitado)

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La rehabilitación es un conjunto de prácticas culturales cuya intención es tratar de volver a establecer vegetación. Los objetivos serían perder menos suelo (erosión) por abajo de lo normal, incorporar más agua de lluvia en el suelo y en el acuífero (cosecha de agua), producir el forraje potencial para el sitio, mantener y reproducir la fauna nativa (calidad de hábitat), calidad de productos y servicios (calidad de agua, aire, extracción de plantas útiles al hombre y recreación). La rehabilitación puede ser de manera natural y/o artificial. De manera natural se puede rehabilitar los potreros utilizando técnicas de manejo como: carga animal adecuada, nivel de utilización adecuado, descanso, rotación y diferimiento de potreros, distribución del pastoreo, combate de arvustivas invasoras y/o plantas tóxicas. De manera artificial se puede rehabilitar las áreas dispersando semilla o transplantando especies forrajeras, acompañado con obras de conservación de suelo y humedad.

La rehabilitación tiene como objetivo darle a los pastizales su potencial forrajero, cosechar agua, evitar pérdida excesiva de suelo, mantener la biodiversidad y restaurar la belleza escénica. De manera general, se pretende recomendar algunas de las herramientas más importantes en la rehabilitación de pastizales y subrayar las bondades que cualquiera de las herramientas expuestas puede tener al ponerlas en practicas.

Antes de tomar una decisión para rehabilitar un sitio, área, pastizal o agostadero se debe hacer un diagnóstico del “estado de salud” del sitio. ¿Por qué hacer el diagnóstico del estado de salud del sitio? Este diagnóstico es importante ya que contempla tres aspectos relacionados con la funcionalidad del sistema: 1) estabilidad del sitio (nos indica si estamos perdiendo mas suelo del normal), 2) funcionalidad hidrológica (indica la capacidad de capturar, almacenar y distribuir agua del sistema) e 3) integridad biótica (proporción y distribución de grupos funcionales de plantas y animales). Estos tres aspectos nos dicen cuál es el estado actual del sitio y por el otro nos indica cuál es el potencial del sitio. Si el diagnóstico es favorable se sigue bajo el mismo esquema de manejo, pero si éste es negativo se determinará las estrategias de rehabilitación para lograr mejores condiciones en un tiempo dado bajo condiciones promedio de clima.

Cuando los pastizales empiezan a degradarse, los potreros empiezan a mostrar síntomas de deterioro. Primero en los sitios más frágiles como serían aquellos de

menor cubierta vegetal, mayor pendiente, áreas cercanas a aguajes, comederos, saladeros y corrales de manejo. Una vez que ya se tienen identificados los sitios con problemas se selecciona la o las estrategias a seguir. Se debe empezar por aquellas de menor costo económico y de mayor beneficio ecológico. Las principales prácticas de manejo que se recomiendan son:

- 1) **Capacidad de carga.** Ajuste de carga animal en los potreros según la producción de forraje anual del potrero (la utilización por el ganado debe ser del 60 %). Esto es que de 100 Kg de materia seca de forraje, 60 Kg son para el ganado y 40 Kg son para mantener suelos fértiles, protección del suelo de la erosión, protección de las primeras capas del suelo de altas temperaturas, protección y facilitación de la germinación de las semillas de zacates.
- 2) **Manejo del pastoreo.** Utilizar cualquier método o sistema de pastoreo que permita: a) tener una utilización uniforme de la vegetación b) mantener plantas con buen vigor y c) producir semilla abundante y de buena calidad.
- 3) **Control de plantas tóxicas e invasoras.** Es importante conocer la biología de las especies para decidir si se realiza algún tipo de control o no. El tipo de control será diferente si la especie es una hierba, un arbusto o una suculenta (cactáceas y agaves). Ciertas plantas tóxicas anuales se presentan bajo ciertas condiciones climáticas, de tal manera que se puede predecir la aparición de plantas tóxicas cuando se presenten estas condiciones de clima y así tomar las medidas preventivas que nos ahorren la necesidad de practicar algún tipo de control. Si se decide por una práctica de control, se recomienda utilizar primero mecanismos de control biológicos, después mecánicos y por último químicos. Para el control químico se recomienda utilizar protección adecuada para las personas que apliquen productos químicos. También seleccionar químicos que no tengan efectos residuales o acumulativos en los tejidos de las plantas y animales. La aplicación del químico se debe aplicar sólo a los individuos que se quieran controlar.
- 4) **Cosecha de agua y suelo.** Cuando nuestros agostaderos tienen tan poca cobertura vegetal que ya no es capaz de cosechar agua suficiente y permitir el establecimiento de nuevos individuos se recomienda hacer

obras mecánicas para cosechar agua. La obra tiene como objetivo retener suelo, agua, materia orgánica y semillas. En arroyos y ríos las obras de conservación de suelo detienen la velocidad del escurrimiento, crean bancos de suelo donde se establece nueva vegetación, se mantienen bancos de agua por más tiempo o permanentes, en las rocas y peñascos se establecen líquenes y musgos que influyen en la formación de suelo *in situ*. Además se crea un microclima en arroyos y ríos con mayor humedad relativa importante para la flora y fauna.

5) Resiembra y/o transplante de especies forrajeras.

Esta práctica sólo se debe de realizar en sitios con verdaderos problemas de cubierta vegetal y/o cuando el potencial de especies forrajeras del sitio está tan disminuido que se necesitaría mucho tiempo de buen manejo (20 años) para recuperar el sitio. Se recomienda utilizar especies nativas para los sitios de agostaderos a resembrar. Hacer inter-siembras, esto es, sembrar en bandas (no hacer resiembra total) son costosas y de alto riesgo económico y ecológico).

La resiembra de pastizales es de alto riesgo y costo debido a las fluctuaciones de la lluvia, donde para tener éxito es necesario tener el suelo saturado (húmedo) por varios días para que las semillas germinen y se establezcan las

plántulas. Por tal motivo se ha visto que el transplante de especies forrajeras es una buena opción, ya que con dos o tres eventos de lluvia se logra establecer algunas de las especies forrajeras, sobre todo los zacates. Además que con el transplante se incorpora al sitio microorganismos benéficos para las plantas. Estos microorganismos fijan nutrientes del aire y del suelo, poniéndolo a disposición para ser utilizados por las plantas.

Una vez que hayamos decidido recuperar los agostaderos será necesario seguir con un mecanismo de evaluación y/o seguimiento (monitoreo) para poder ver resultados y tendencia que sigue el pastizal. Esto nos servirá para seguir con el plan de manejo o hacer correcciones de emergencia. Pero lo más importante es hacer conciencia y entender que la estrategia más efectiva es la conservación y el uso racional de los recursos naturales, para que éstos nos puedan seguir dando los servicios (agua, forraje, aire, esparcimiento, etc.) tan necesarios para el hombre, hoy para nosotros y mañana para nuestros hijos. Para mayor información escribir a la dirección electrónica royomario@hotmail.com o llamar a los teléfonos (614) 481-0769 y 481-0257 o acudir a las oficinas del Campo Experimental La Campana, INIFAP-SAGARPA ubicadas en la avenida Hormero No. 3744, Col. El Vergel. Chihuahua, Chih.

Management Challenges for the Pronghorn in Chihuahua

(summary)

Manuel Valdés Unidos para la Conservación

After working with pronghorn for the last seven years, we know that two of the most important threats to the pronghorn population in Mexico are low offspring survival and habitat fragmentation.

Since the census of 1977, the pronghorn population has decreased and today our estimates show it to be between a minimum of 300 individuals and a maximum of 500. Also, throughout this time, two local populations might become extinct (i.e., Benavides and Julimes), due to isolation effects and grassland vegetation changes. Nevertheless, in terms of the distribution of the remaining population, it seems to have remained the same.

Historic range for the pronghorn included central Mexico and the desert prairies of North of Sonora and the Baja California Peninsula. Today, their habitat has been reduced to certain grasslands in the Chihuahuan desert and some arid lands in the Sonoran desert and the Viscaíno Peninsula in Baja California. Currently, the most important distribution areas for the pronghorn in the state of Chihuahua are: 1) to the Northwest between el Cuervo and El Berrendo, 2) a central area that includes a big polygon formed by Villa Ahumada, Gregoria, Rancho el 24, Coyame and Tosesihua. 3) La Perla Camargo.

Within these areas there are important places where pronghorn females are able to produce the highest number of offspring (e.g., 0.56 offspring per female at Sueco-Moctezuma). These areas are called continuance zones, and offer good topographic, grassland and plant

diversity to the population. Nevertheless, the construction of roads, highways and agricultural fields is increasingly isolating them.

Highways in Chihuahua divide grasslands areas and become impassable barriers. Although there are suitable grasslands in both sides of the Chihuahua-Ciudad Juárez highway, all of the pronghorn population is situated on the east side. Agricultural activities are also thought to be responsible for separating the southern pronghorn population of La Perla Camargo. Under such circumstances, habitat may not be lost, but isolated groups of animals are reduced in a way that they become more vulnerable to predation, poaching, and other factors. In the last phase of pregnancy, females are not as skillful in crossing fences. If coyotes chase them, they usually run alongside the fence until reaching the corner and cannot escape. At these corners we have found evidence of coyote predation on dead pregnant females. In order for pregnant females to be able to jump fences without any difficulty the barbed wire needs to be of a maximum of 45-50 cm high preferentially having the highest wire barb-less.

Finally, a direct anthropogenic factor that has been observed to reduce the recruitment of juveniles to the population is the locals' custom to take pronghorn calves home as pets. Thus, an education program for the local population about the ecological importance of the pronghorn is also necessary to improve their conservation.

Retos Al Manejo del Berrendo en Chihuahua

(transcripción)

Manuel Valdés *Unidos para la Conservación*

En los últimos siete años que hemos trabajado con el berrendo, particularmente en los estados de Chihuahua y Coahuila, se han observado diferentes problemáticas tanto sociales como biológicas. Dentro de las más importantes destacan la baja supervivencia de crías y los procesos de fragmentación del hábitat.

Los registros históricos del berrendo muestran que tenía una distribución amplia, ésta abarcaba todo el Altiplano central de México y las planicies desérticas del norte de Sonora y la península de Baja California. En la actualidad, su hábitat incluye sólo algunas áreas de pastizales del desierto Chihuahuense y zonas áridas de los desiertos de Sonora y el Vizcaíno en Baja California Sur.

Quizás la problemática de las barreras como los cercos y procesos de fragmentación son diferentes para los berrendos de los pastizales del desierto Chihuahuense, no así para el berrendo peninsular y el sonorense, ya que el desarrollo rural y las actividades agrícolas y ganaderas en estos lugares son de menor impacto que en los pastizales de Chihuahua. Sin embargo, la baja supervivencia de las crías podría ser un factor común en todas las áreas de distribución en México y está relacionado con la depredación y las prolongadas sequías de los últimos tiempos.

Ahora bien, si nos ubicamos en el escenario de los pastizales del desierto chihuahuense y analizamos la problemática de los cercos y la fragmentación de las poblaciones del berrendo, encontramos que éstas se han reducido y otras están quedando más aisladas. Si comparamos la distribución y el tamaño poblacional del berrendo (500 individuos) en Chihuahua, estimada por José Treviño en 1977, con lo que hemos encontrado en los monitoreos de los últimos seis años en las mismas áreas, vemos que el patrón de distribución es muy similar, sin embargo la población mínima encontrada por nosotros es menor (300) y por lo menos dos poblaciones (i.e., Benavides y Julimes) no fueron localizadas durante los monitoreos. De confirmarse su desaparición, estos serían ejemplos de extinciones locales por efectos de aislamiento y cambios de vegetación en las áreas de pastizales.

En la actualidad se pueden distinguir tres grandes áreas de distribución del berrendo en el estado de Chihuahua: 1) al noroeste, entre el Cuervo y el Berrendo, 2) el área central que incluye un gran polígono que va desde Villa

Ahumada a la Gregoria y al norte, del Rancho el 24 a Coyame y Tosesihua. 3) Por último la población más sureña y también la más aislada del resto es la que se encuentra en La Perla Camargo.

Dentro de estas áreas de distribución se encuentran zonas importantes como lo son las áreas de permanencia. Éstas presentan características topográficas y de vegetación (p. ej. pastizales y una diversidad de plantas anuales) particulares en las que se encuentra un buen promedio de crías por hembra (p. ej. 0.56 crías/hembra en el Sueco-Moctezuma).

La Perla es un buen ejemplo de estos procesos de aislamiento o fragmentación. La distancia que hay entre la población de la zona central y la Perla Camargo en el sur, es de aproximadamente 200 kilómetros. En este trayecto se pueden observar varios procesos de fragmentación por cambios de uso del suelo como lo son la construcción de carreteras, cercos, cambios de vegetación, etc.. Este tipo de barreras de aislamiento, propicia que el tamaño de los grupos disminuya más rápidamente que su hábitat.

Los grupos pequeños y aislados son más vulnerables a factores de depredación, caza furtiva y en algunos casos la captura de crías por los lugareños. Los sistemas de cercado que impiden los movimientos naturales y las rutas de escape a depredadores (coyotes) agravan el problema, aumentando el riesgo de mortalidad de las crías y hembras adultas durante el periodo de preñez.

Si colocamos un mapa de las principales carreteras de Chihuahua sobrepuesto a la distribución actual del berrendo, veremos el efecto de éstas como un factor de aislamiento. Ustedes podrían notar que en la zona central de Chihuahua, toda la población de berrendos queda del lado derecho, y del lado izquierdo de la autopista Chihuahua-Ciudad Juárez, aunque existen zonas de buenos pastizales no hay berrendos. La autopista es una barrera prácticamente infranqueable para los berrendos. Lo mismo sucede hacia la zona del Cuervo donde existe otra carretera, y si bien, no es autopista, el alto número de automóviles que la transita es mucho más importante que la carretera misma.

Un ejemplo más de la forma en que podría disminuir el tamaño de las poblaciones por el efecto de fragmentación que producen las carreteras y el incremento de las actividades humanas en el área, lo podemos ver en Sonora. En Sonora, la distribución mayor de berrendo en el estado se encuentra dividida por la carretera que va de

Caborca a Puerto Lobos. En esta parte se desarrolla una gran actividad agrícola que ha generado la construcción de una serie de carreteras pequeñas con flujo constante de vehículos. Por lo que un pequeño grupo de berrendos se ha quedado aislado al suroeste de Caborca lo que reduce sus posibilidades de supervivencia por los factores antes mencionados. En este tipo de aislamiento se puede perder más rápido el número de individuos que el hábitat. El número de animales que quedan aislados ahí es tan reducido que se vuelven mucho más vulnerables a la depredación, a la caza furtiva y a otra serie de factores y presiones que van haciendo que se reduzca el número de animales.

En un estudio realizado por Fernando Colchero utilizando datos de monitoreo aéreo para realizar predicciones sobre sitios potenciales para el manejo de berrendo, se encontró que existe una buena disponibilidad de hábitat para el berrendo. Sin embargo, el principal problema que tenemos en México es el número tan reducido de animales que nos queda. En Chihuahua tenemos una población mínima de 300 animales y una estimada de cerca de alrededor de 500 animales. Entonces, ¿cómo podemos elevar el tamaño de las poblaciones? Si concentramos los esfuerzos en las áreas de permanencia con mejor promedio de crías/hembra y aseguramos el mayor reclutamiento de juveniles, podríamos tener mejores expectativas de recuperación. La Perla, es un ejemplo de estas áreas con buena producción de crías, su población fluctúa entre 20 y 30 animales y en buenos años (precipitación pluvial) puede alcanzar hasta un promedio de 0.64 crías/hembra. Sin embargo, como les mencioné, esta zona se encuentra separada de otras poblaciones por unos 200 kilómetros y en el trayecto existen carreteras y una serie de actividades humanas. Esta población, bien manejada y vigilada

podría permitir la recuperación de un buen número de ejemplares. Lo que nosotros encontramos en el último año de monitoreo (2000), fue que a pesar de las presiones y la poca atención se mantiene una población de entre los 20 y 30 individuos. Hará unos 6 años aproximadamente que tuve la experiencia de estar trabajando 5 meses en esa zona y la gente a veces tiene la costumbre de tomar las crías y llevárselas a su casa como mascotas, eso trae como consecuencia menores posibilidades de reclutamiento de juveniles. Cuando estuvimos ahí hace 5 años con apoyo también de la Universidad de Chihuahua, se observó la supervivencia de 21 crías.

El otro problema que se presenta son las cercas o alambres de púas. Estas cercas dificultan el tránsito y movimientos naturales de los berrendos. Para que los berrendos puedan pasar estas cercas sin problemas hay que colocar el último alambre sin púas a una altura de 45-50 cm.

Conforme se crean más cercos para el manejo de ganado y rotación de pastizales las áreas para el berrendo se hacen más pequeñas. Esto se vuelve un problema particular en la última fase de preñez de las hembras y el periodo de crianza. En este periodo las hembras y las crías no son tan hábiles para pasar los cercos, y si son perseguidos por un grupo de coyotes o algún otro depredador, corren a lo largo del alambre hacia las esquinas, y de allí ya no pueden salir. Ahí hemos encontrado algunas hembras preñadas con evidencias de ataque de coyote. Esta problemática nos puede proporcionar una pérdida tanto de crías como de hembras y con el número tan pequeño de las poblaciones de berrendo que tenemos en México podemos perder estos grupos más rápidamente, si no se buscan alternativas para que los animales tengan alguna forma de escape.

Power-line Electrocution of Birds

(summary)

Patricia Manzano Fischer *Agrupación Dodo*

A result of rapid growth in human population and energy use, is proliferating power lines that electrocute birds, killing eagles and causing power outages. The United States was one of the first countries to recognize the significance of this problem. *Suggested Practices for the Protection of Raptors on Power Lines*, first published in the 1970s, has now been translated into Spanish; it discusses biological aspects of raptor electrocution, and explains which electric structures are dangerous and how they can be modified to prevent electrocutions. In the United States, however, the plethora of companies that supply energy has been an obstacle to implementing protective measures for raptors.

Raptor electrocution on power lines is a worldwide problem. Raptors are drawn to power lines because they are convenient high places to perch, nest, rest, defend territories, hunt, or find shade. In Spain, it is the principal cause of death of Imperial Eagles (*Aquila heliaca*). Nineteen different bird species have been found electrocuted under power lines in Germany. In South Africa and other African countries, vultures and Black Eagles are some of the species most commonly electrocuted. In the late 1990s in Baja California, Mexico, a problem with electrocution of ospreys was addressed by the construction of nesting platforms on the tops of power-line posts. In Chihuahua, Mexico, eagles, buzzards, owls, and a large number of crows fall victim to power lines.

On wooden posts, electrocution occurs on metallic crosspieces when a bird touches two energized cables, or one cable and an object that is touching the ground. On concrete posts, electrocution occurs when raptors perch on one of the metallic crosspieces while touching an energized cable or any other charged structure.

Specimens of 24 of the 40 North American raptor species have been reported as electrocution victims. Large birds are more commonly affected because they can more easily touch two cables or charged parts of a power-line structure at once. Young birds and wet birds are more susceptible to electrocution. The electrocution of birds on power lines not only affects bird populations, but also local economies. The number of power outages caused by bird electrocutions translates into costs to the communities left without power as well as to the companies that have to repair power lines.

Fortunately a clear solution exists, although identifying and then modifying existing problem power-line

structures can be costly. Incorporating bird-friendly technology when constructing new lines, however, is economically viable.

Chronological Summary of Bird Electrocutions in Janos-Casas Grandes, Chihuahua

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|---------------|--|
| 1996 | The power-line network was installed between the Mennonite communities of Buenos Aires and El Cuervo. The power-line network goes through the biggest colony of prairie dogs. Dead prey birds were found below the power lines of El Cuervo by volunteers doing Christmas bird counts. |
| February 1999 | The U.S. organization Hawks Aloft organized a field trip to search for electrocuted prey birds below the power lines that go through the Janos-Casas Grandes prairie-dog complex. The search included 1,612 poles. In 47 poles, 28 to 34 dead prey birds (including nine golden eagles and 15 ravens) were found. |
| March 1999 | Patricia Manzano met with Patricio Robles Gil and Carlos Manterola from the organizations Sierra Madre and Unidos para la Conservación to explain the bird electrocution problem in Janos, especially the high mortality of golden eagles. Because the golden eagle is a species of interest to these organizations, they decided to participate in the search for solutions to the problem. Thus, Patricio Robles Gil arranged a meeting with Alfredo Elías Ayub, the executive director of CFE (the Federal Power Commission). CFE agreed to collaborate in solving the problem. It was agreed to hire Rick Harness (U.S. expert) to conduct an assessment and suggest possible solutions. |
| May-June 2000 | Rick Harness and Patricia Manzano visited the power lines that lay above the Janos-Casas Grandes prairie-dog |

complex and inspected 852 three-phase power posts. The power structures consist of concrete posts, conductors and metal crossheads. Medium and large birds are electrocuted when they land on the crossheads and touch one of the cables.

Fifty-three birds were observed near the base of the power posts, including ten golden eagles, 30 ravens, two black vultures and 11 hawks (including red-tailed and ferruginous hawks). Rich Harness wrote a report to CFE outlining the problem and its possible solutions.

Mr. Nevares, CFE engineer, and his team came to the field to demonstrate the installation procedure of a PVC tube that insulates the crossheads from the insulators. This method has been used to prevent power cuts in the area. However, the use of PVC tube is not a long-term solution because this tubing rapidly deteriorates during the summer. A long-term solution is to replace the metal crossheads with wooden ones.

August 2001

Ted Anderson of the Western Area Power Administration donated 50 insulating covers to CFE, which installed the equipment in the agricultural areas where the electrocution problems were taking place.

November 2000-2001

Beginning in November 2000, Jean-Luc Carton and Robert Rogers monitored the power lines in Janos. Some power lines were monitored every month, and others were monitored on a rotational pattern. More than 1,000 posts were monitored. Starting December 2000, 163 dead birds were found. Most of them seemed to have been electrocuted (birds presented crinkled feathers on their wings). Most of the victims were prairie ravens ($n > 100$). Other species included red-tailed hawks, ferruginous hawks, ospreys, horned owls and great blue herons. For birds in general, summer to the beginning of the fall is the season with the highest electrocution rate. Red-tailed hawks especially are electrocuted in large numbers in this period. Golden eagles and ferruginous hawks, however, are electrocuted most often between fall and the beginning of the spring, and ravens are electrocuted

in terminal structures during the reproductive season. The raven chicks are electrocuted on posts adjacent to double structures with nests. During the fall, ravens are electrocuted in high numbers in areas where flocks meet (J.L. Cartron). Cartron and Roger searched power lines in other areas of Chihuahua. Most of the inspected power lines showed electrocuted red-tailed hawks or ravens. This leads to the believe that, at least for these two species, the total number of electrocuted birds every year must be in the range of thousands of individuals in the arid regions of northern Mexico (J.L. Cartron).

Summer 2001

The CFE in Casas Grandes has been modifying some of its power lines. In those responsible for the highest number of power cuts, they have replaced the metallic crossheads for wooden ones. Up to the winter of 2001, 850 crossheads had been replaced. The electrocution incidence seems to be much less on power lines where the crossheads have been replaced compared to those that have not been modified. The CFE is planning to modify more lines in the future.

March 2002

First workshop on bird electrocution due to power lines in Mexico: Towards a Diagnosis and Solution. This workshop took place March 6–7, 2002, at the National University of Mexico. Participants included experts on bird electrocution, and personnel from the CFE, governmental, academic, and non-governmental institutions. As a result of the workshop, a multidisciplinary committee to oversee this problem was created. The committee will give special attention to the identification of short-, mid-, and long-term actions, identification of research needs and opportunities, communication, training, and finance, the modification of power-line structures, legislation, and international cooperation, especially with the United States.

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Electrocución de Aves en Líneas Eléctricas en México

(artículo invitado)

Patricia Manzano Fischer *Agrupación Dodo*

La electrocución de aves en líneas eléctricas es resultado del rápido crecimiento de la población humana y de sus necesidades de energía. A principios de los años setentas, estudios realizados en los Estados Unidos comenzaron a dar evidencia de águilas electrocutadas en líneas eléctricas. Entre los más alarmantes se encontró una línea en Colorado de tan solo 88 postes, a lo largo de la cual se encontraron 37 águilas reales (*Aquila Chrysaetos*) electrocutadas; o el registro de 416 aves muertas a lo largo de 24 kilómetros de líneas en 6 estados del oeste (Avian Power Line Interaction Committee -APLIC-, 1996). Este problema no sólo afectaba poblaciones de especies en riesgo, como las del águila de cabeza blanca (*Haliaeetus leucocephalus*) o el águila real, también causaba cortes en el suministro de energía eléctrica.

Estados Unidos fue uno de los primeros países en reconocer que la electrocución de aves era un problema importante. A mediados de los años setenta un grupo compuesto por agencias del gobierno, compañías de electricidad y organizaciones no gubernamentales se reunieron para analizar la magnitud y buscar soluciones al problema de electrocución. Como resultado se obtuvo la primera impresión de "Prácticas Sugeridas para la Protección de Rapaces en Líneas Eléctricas", publicación que tiene ya tres ediciones y ha sido traducida al español para ser utilizada en Latinoamérica. Esta publicación reúne información sobre los aspectos biológicos de la electrocución de rapaces y brinda una clara explicación de los diseños de estructuras eléctricas que son peligrosos para las aves y de cómo pueden ser modificados para evitar futuras electrocuciones. Sin embargo, en los Estados Unidos existen cientos de compañías encargadas de proporcionar el suministro de energía eléctrica, lo cual ha sido un obstáculo en la implementación de las prácticas sugeridas para la protección de rapaces.

El problema de la electrocución de aves en líneas eléctricas ocurre a nivel mundial. En España la electrocución es la principal causa de mortalidad del águila imperial (*Aquila heliaca*). Estudios acerca de la sobrevivencia de pollos de águila imperial mostraron el impacto de la electrocución en esta especie. Un ejemplo que ilustra claramente este punto se dio al eliminarse una línea eléctrica que cruzaba por el centro del parque, la sobrevivencia de los pollos se incrementó de un 17.6% a un

80% en los primeros 6 meses de vida (Ferrer e Hidalgo 1991). En Alemania 19 especies (592 individuos) fueron encontradas electrocutadas debajo de líneas eléctricas (Haas in Suggested Practices 1996).

En Sudáfrica y otros países del continente Africano especies como el buitre del Cabo (*Gyps coprotheres*), el buitre egipcio (*Neophron pernopterus*), el águila marcial (*Polemactus bellicosus*) y el águila negra (*Aquila vereauxii*) son algunas de las especies que más se electrocutan en las líneas eléctricas. En una sola línea se encontraron más de 300 buitres del Cabo muertos a lo largo de un periodo de tres años (Ledger y Annegarn 1981). En América Latina se desconoce la magnitud del problema.

En México el único registro sobre conflictos entre aves y líneas eléctricas previo a 1997, es el caso del gavilán pescador (*Pandion haliaetus*) en Baja California, donde la población de esta especie se ha incrementado gracias al uso que hacen de estructuras artificiales (balizas de señalamiento, plataformas artificiales y postes del tendido eléctrico) como plataformas de anidación (Castellanos *et al* en Ferrer 1999). Sin embargo, el uso de los postes por los gavilanes causaba cortes en el suministro de energía y electrocución de aves adultas, problemas que han sido solucionados con la colocación de plataformas artificiales en dichos postes.

El único otro caso reportado es el de los tendidos eléctricos del área de Janos-Casas Grandes en Chihuahua. Esta zona está habitada por ejidatarios y Menonitas. Los primeros tendidos eléctricos para proveer de energía a los ejidatarios y ranchos privados fueron construidos en 1986. En 1996 las colonias Menonitas de Buenos Aires y El Cuervo fueron conectadas mediante una línea eléctrica que corre a través de la colonia de perros llaneros (*Cynomys ludovicianus*) más grande de Norte América. Fue entonces que se comenzaron a encontrar rapaces electrocutadas, y un par de años después inició un proyecto de monitoreo para buscar aves electrocutadas en otras líneas del área. Los resultados mostraron que el problema no es exclusivo a las líneas nuevas, sino común a otras líneas que cruzan las colonias de perros llaneros.

En general, las líneas de electricidad no están diseñadas tomando en cuenta a las rapaces, y México no es

una excepción. Entre las especies de aves electrocutadas encontradas debajo de los postes en Janos están: águila real, aguililla real (*Buteo regalis*), aguililla cola roja (*Buteo Jamaicensis*), zopilote aura (*Cathartes aura*), lechuza de campanario (*Tyto alba*) y una gran cantidad de cuervos (*Corvus cryptoleucus*).

¿Por qué se Electrocutan las Aves?

Las aves se electrocutan al posarse sobre las líneas eléctricas y cerrar el circuito. Esto puede ocurrir de varias maneras. En el caso de postes de madera con crucetas metálicas, la electrocución ocurre cuando el ave toca dos de las fases o cables energizados, o un cable y alguna parte conectada a tierra. En el caso de los postes de concreto con cruceta metálica un ave se puede electrocutar al posarse sobre la cruceta y tocar una de las fases energizadas o alguna otra estructura cargada eléctricamente.

Las aves, especialmente las rapaces, son atraídas a las líneas de energía eléctrica por diversas razones: por ser sitios elevados donde se puede perchar, anidar, descansar, defender territorios, cazar o encontrar sombra. Esto ocurre principalmente, aunque no exclusivamente, en áreas planas donde no hay árboles o en lugares con altas concentraciones de presas.

Veintiséis de las cuarenta especies de rapaces que habitan Norte América han sido reportadas como víctimas de electrocución (Suggested Practices 1996). Entre las aves más comúnmente electrocutadas en líneas eléctricas se encuentran las de gran tamaño, como las águilas real y de cabeza blanca, ya que su gran envergadura facilita que el ave toque dos cables energizados al extender sus alas para elevarse o aterrizar en un poste. Otros factores como la experiencia, edad y temporada del año afectan la susceptibilidad a electrocución. Entre las águilas reales es más frecuente que los juveniles, que carecen de experiencia tanto para volar como para cazar, se electrocuten. En temporada de lluvias es más frecuente la electrocución, ya que al estar mojadas las plumas se vuelven conductoras y no es necesario que el ave toque el cable con la parte carnosa del ala, porque el toque de la pluma mojada puede conducir la energía.

La electrocución de aves en líneas eléctricas es resultado del rápido crecimiento de la población humana y de sus necesidades de energía. La electrocución de aves no sólo afecta a las poblaciones de las especies involucradas, especialmente a las de rapaces y cuervos, sino que tiene a su vez un impacto considerable en la economía local. El número de cortes de energía causado por la electrocución de las aves se traduce en un alto costo tanto para las comunidades que se quedan sin energía, como para

las compañías de electricidad que deben mandar equipos de mantenimiento para arreglar el problema.

Afortunadamente este es un problema con una clara solución; se cuenta con una serie de medidas para modificar las estructuras causantes de electrocuciones y así mitigar el problema. Sin embargo la modificación de estructuras problema en líneas existentes puede resultar costosa y debe acompañarse de estudios de campo que identifiquen las estructuras causantes de electrocuciones y que sufren continuos cortes del suministro, para maximizar el costo-beneficio de estas operaciones. La construcción de nuevas líneas con lineamientos técnicos amigables para las aves, puede resultar inclusive económicamente viable.

Resumen Cronológico de Eventos Relacionados con la Electroculión de Aves en Janos-Casas Grandes, Chihuahua.

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| 1996 | Se construyó un tendido eléctrico entre las colonias Menonitas de Buenos Aires y El Cuervo. Esta línea cruza a través de la colonia más grande de perros llaneros. |
| 1997-1999 | Voluntarios realizando Conteos de Aves de Navidad encontraron rapaces muertas debajo de la línea eléctrica de El Cuervo. |
| Febrero 1999 | Hawks Aloft (organización de los E.U.) organizó una salida de campo para buscar rapaces electrocutadas debajo de las líneas eléctricas que cruzan el complejo de perros llaneros Janos-Casas Grandes. La búsqueda incluyó 1,612 postes y el resultado fue un total de 28-34 rapaces muertas (incluyendo 9 águilas reales) y 15 cuervos en la base de 47 postes. |
| Marzo 1999 | Patricia Manzano se reunió con Patricio Robles Gil y Carlos Manterola de Sierra Madre y Unidos para la Conservación respectivamente, para explicar el problema de electrocución de aves en Janos, especialmente la alta mortandad de águilas reales. Debido a que el águila real es una de las especies de interés para estas organizaciones, decidieron participar en la búsqueda de soluciones al problema, por lo que Patricio Robles Gil contactó a la CFE y concertó una cita con el Director General Ing. Alfredo Elías Ayub. La CFE accedió a colaborar en la solución del problema. Se convino |

en la contratación de Rick Harness (experto de los E. U. en este tema) para hacer un diagnostico y sugerir posibles soluciones.

Mayo-Junio 2000 Rick Harness y Patricia Manzano visitaron las líneas eléctricas que se encuentran en el complejo de perros llaneros de Janos y Casas Grandes, se inspeccionaron 852 postes trifásicos. Las líneas consisten en postes de concreto, conductores y crucetas de metal. Aves de tamaño mediano y grande se electrocutan cuando aterrizan en las crucetas y tocan uno de los cables.

Se detectaron cincuenta y tres aves cerca de la base de los postes de electricidad, incluyendo 10 águilas reales, 30 cuervos, 2 zopilotes aura y 11 aguilillas (incluyendo aguilillas cola roja y reales). Rick Harness escribió un reporte para la CFE explicando el problema y las posibles soluciones.

El Ing. Nevarez y su equipo de la CFE Casas Grandes nos acompañaron en el campo y demostraron la instalación de tubo de PVC para aislar las crucetas y aisladores. Este método ha sido utilizado para evitar los cortes de energía en el área. Sin embargo el PVC no es una solución a largo plazo ya que se deteriora con rapidez durante el verano. Una solución a largo plazo es cambiar las crucetas metálicas por crucetas de madera.

Agosto 2001 Ted Anderson, de Western Area Power Administration, hizo una donación a la CFE Casas Grandes de 50 cubiertas para boquilla. La CFE recibió la donación e instaló el equipo en áreas agrícolas donde se presentaban problemas con las aves.

Noviembre 2000-2001 Jean-Luc Cartron y Robert Rogers llevaron a cabo un monitoreo de las líneas de electricidad en Janos a partir de noviembre de 2000. Algunas líneas se revisaron cada mes, otras en una base rotacional. El número de postes revisados es de > 1000. A partir de diciembre de 2000, se encontró un total de 163 aves muertas. La mayoría mostraba signos de electrocución (por ejemplo plumas rizadas en el ala). La mayoría de las víctimas fueron cuervos llaneros (n > 100). Las otras especies

encontradas desde diciembre de 2000 son: aguililla cola roja, aguililla real, águila real, gavilán pescador, lechuza de campanario, búho cornudo y garzón cenizo. Aún y cuando las águilas reales y las aguilillas reales se electrocutan con mayor frecuencia del otoño a principios de la primavera, el verano y el principio del otoño son las temporadas con la tasa de electrocución más alta. Los cuervos se electrocutan en estructuras terminales durante la época reproductiva. Los pollos son electrocutados en postes adyacentes a estructuras dobles con nidos. En el otoño, los cuervos son electrocutados en números altos en las áreas donde se reúnen las parvadas. Las aguilillas cola roja son electrocutadas en grandes números a finales del verano y principios del otoño. (J. L. Cartron)

Cartron y Rogers realizaron búsquedas a lo largo de líneas de energía en otras áreas de Chihuahua. Casi todas las líneas revisadas presentaban aguilillas cola roja o cuervos electrocutados. Esto conduce a creer que, al menos para estas dos especies, el número total de aves electrocutadas cada año debe ser de miles a lo largo de las zonas áridas del norte de México (J. L. Cartron)

Verano 2001

La CFE en Casas Grandes ha estado realizando modificaciones en algunas líneas eléctricas, sobre todo en aquellas que presentaban el mayor número de cortes de energía. Se han cambiado las crucetas metálicas por crucetas de madera. Hasta el invierno del 2001 se habían cambiado 850 crucetas. En las líneas donde se cambiaron las crucetas la incidencia de electrocución parece ser mucho menor que en aquellas donde no se han hecho modificaciones. La CFE tiene planes de modificar más líneas en un futuro cercano.

Marzo 2002

Primer taller sobre electrocución de aves en líneas eléctricas en México: hacia un diagnostico y perspectivas de solución. Este taller tuvo lugar en la Universidad Nacional Autónoma de México el 6 y 7 de marzo de 2002. Participaron expertos en electrocución de aves, personal de la Comisión Federal de Electricidad, instituciones gubernamentales, académicas y no gubernamentales. El resultado

del taller fue la creación de un comité multidisciplinario que atenderá este problema, especialmente la identificación de acciones a corto, mediano y largo plazos, y la identificación de necesidades y oportunidades para investigación, comunicación, capacitación, financiamiento, modificación de estructuras en líneas de energía, legislación y cooperación internacional, especialmente con los Estados Unidos.

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Ecotourism

(invited paper)

William Forbes *Geography, Philosophy, Environmental Science. University of North Texas*

The objectives of this presentation are to: (1) describe how ecotourism differs from traditional tourism; (2) provide examples of ecotourism from the U.S.-Mexico region; and (3) suggest potential ecotourism development in the Casas Grandes area; and (4) describe potential problems related to such development. My background in ecotourism is related to two projects: (a) a \$200,000 countywide ecotourism development project I helped initiate and manage in Oregon (Forbes 1998); and (b) my dissertation on conservationist Aldo Leopold's 1930s visits to Municipio Casas Grandes and how ecotourism may now apply there (Forbes and Haas 2000).

Defining Ecotourism

Ecotourism is not just any tourism related to nature. More than 100 different codes of conduct define and guide appropriate ecotourism (The International Ecotourism Society 2001). The key concept to remember is *reciprocal* development—in appropriate ecotourism, *both* the economy and nature benefit. Other key aspects, many derived from the Oregon project, which involved several international leaders in the field, include:

- 1) *Develop lower-volume, higher-priced package tours.* Bring fewer people, who pay more, to a specific destination. This allows tour providers, who often work second jobs, to efficiently manage their time, market to specific customers, and plan ahead for both impacts and income.
- 2) *Keep profits local.* Avoid using franchise “chain” motels and foreign tour guides as much as possible. Develop local businesses to ensure that ecotourism income circulates through the local community.
- 3) *Minimize cultural impacts.* Consider local needs and cultural integrity through social surveys and placement of low-volume tourism. Highly commercial mass tourism has disrupted the ambience of previously quiet locales such as Cancún and Acapulco, eventually reducing their original appeal, transforming employment from largely independent agriculture or fishing to low-paying service jobs, taking favorite recreation sites away from locals, and disrupting indigenous peoples' traditional ways of life.

- 4) *Keep some revenues for cooperative marketing and habitat protection.* Ensure sustainability by depositing a percentage of trip fees in a nonprofit fund, to be used for regional cooperative marketing and protection and restoration of wildlife habitat and land health. Develop complementary businesses that can pool funds to cooperatively market the area and self-enforce standards; work together—there is enough competition from other locales.
- 5) *Remember that ecotourism is not a panacea; it has impacts, some unpredictable.* The temptation to bring more visitors and competition from other local businesses can lead to overdevelopment (Isaacs 2000); implementing controls can be difficult; working with private lands first may allow for initial control of numbers of visitors; unforeseen issues, such as water availability, may surface.

Examples of Ecotourism

- 1) *Curry County, Oregon* (north of coastal California). Nine diverse ecotourism businesses were started under a grant to help transition the economies of timber-dependent communities. Four of these enterprises still exist: kayaking, ocean birding, ranch visits, and photography. Cooperative marketing of quality tours was important at the start to gain word-of-mouth reputation—tour prices range near \$150/day/person. A \$19-million old-growth forest canopy walkway and visitor center was proposed but controversy over site selection put it on hold. A mechanism was discussed to return revenues for marketing and habitat maintenance through a nonprofit organization, but this has not been implemented. A new central reservation system for guides is successful—existing guides joined the system, and some existing businesses participated in the local ecotourism marketing theme. The county is satisfied with project results despite unpredictable outcomes, including the success of only selective businesses (Egret Communications 2001, Forbes 1998).
- 2) *Wyoming* (U.S. state north of Colorado). The state tourism office utilized its region's unique image by using glossy advertisements to market a

ranch-tourism program, including high-priced packages, such as \$1,500/week/person for a log cabin with private bath and fireplace. Though not all destinations fit the full definition of ecotourism, the program demonstrates the marketability of ranch stays (Egret Communications 2001, Wyoming Dude Ranchers Association 2001, Wyoming Tourist Association 2001).

- 3) *Belize* (small nation east of Mexico). Some communities found that remote sites are marketable—in fact, that is part of their appeal—and that good roads are not absolutely necessary to attract travelers. Good cooperation and conservation ethics developed among many local guides and lodges. Several large expanses of coastal mangrove forests were protected partly due to their tourism attraction (Egret Communications 2001).
- 4) *Monarch Reserve*, Michoacán, México. Ecotourism helped stop logging of critical monarch butterfly habitat. Locals dependent on the tourism supported forest protection. Some tourists, such as large weekend groups, have negative ecological impacts—many hike without guides, for example, resulting in trash, noise, and some loss of butterflies through vandalism (LaFranchi 2000).
- 5) *San Nicolas Totolapan* (near Mexico City). Balam Consultants won several awards for their work with *ejidos* (community land ownerships in Mexico) in ecotourism development (hiking, mountain biking). They spent a total of 600 hours working with *ejidatarios* (members of the community-held land) on marketing and public relations; for every hour of business-skills development, they spent four hours working with the *ejidatarios* on confidence-building. The project protected 5,693 acres (2,304 hectares) that would have otherwise been lost to illegal logging and urban sprawl. The project was mentioned in the September 2001 issue of *National Geographic* (Mader 2001).
- 6) *La Ruta Sonora* (Arizona-Sonora). This Tucson nonprofit organization developed three Arizona (U.S.) to Sonora (Mexico) tours, with desert–sea, river, and heritage themes. They manage a three-person office in Tucson and contract out for vans and local guides as needed. Part of the trip fees (3 percent) goes to habitat conservation. Tours emphasize ecological issues, including water conservation, bird watching, and environmental history at destinations such as the Colorado River Delta (La Ruta Sonora 2001).

Potential Ecotourism Development Near Casas Grandes

- 1) *Specialized nature-oriented travelers*. Bird watchers may be attracted by unique birds not found in most of the United States, such as the vermilion flycatcher, trogon, and thick-billed parrot. Rather than relying on a single bird species, however, tourist packages will likely need to encompass a variety of birds—grasslands, winter waterfowl, and forest birds—as well as nonbirding attractions such as the area's unique cultural and historical destinations, including archaeological ruins (Drewien 2000). Conservationists may be attracted to sites such as North America's largest prairie-dog colony near Janos, remote forests, or Aldo Leopold's 1930s campsite, where he saw "perfect" land health (Forbes and Haas 2000). Some enjoy participating in research or habitat-restoration projects during their trips. Both groups, bird watchers and conservations, can be targeted through specific nature periodicals and nonprofit organizations' membership lists. Ecotourism enterprises can save on the costs of placing advertisements and of covering travel writers' trip expenses by having members write their own articles for submission to appropriate media and by partnering with similar organizations.
- 2) *Paquimé visitors*. On the site of these 13th-century ruins, excavated in the 1970s, a million-dollar interpretive museum was opened in the early 1990s. European and Mexican visitation has increased since the ruins' 1998 designation as a World Heritage Site. European travelers are generally more adventurous than American travelers and will visit nearby remote sites if supplied with proper information. Opportunities to link heritage and nature tourism are frequently overlooked, such as using exhibits and brochures to market to existing visitors (Steele-Prohaska 1996). A visitor survey could be conducted in partnership with the museum to characterize and target visitors' hometowns and cities. The Mimbres-Paquimé Connection (2001) is a cross-border tourism partnership based on the similar cultural heritage of northwestern Chihuahua and southwestern New Mexico.
- 3) *Ranch and ejido visitors*. Home stays can offer an attractive alternative to hotels and traditional tourism. They may offer more intimate, reliable reservations; local hotels have been known to cancel small-group packages to accommodate overflow visitors from

other functions. Part of the trip fee could go to purchase local ejido school supplies, as a way to acknowledge and meet some of the community's social needs, as well as to marketing and conservation. Several local ranches are looking for alternative income due to recent drought and low cattle prices.

- 4) *General travelers.* Four U.S. cities having populations greater than 500,000 lie within one day's driving distance of the U.S.–Mexican border: Albuquerque, El Paso, Phoenix, and Tucson. Opportunities exist to attract additional general travelers by arranging package tours, and border parking and pickup (Hatch 1998).

Potential Problems With Ecotourism Development Near Casas Grandes

- 1) *Cultural impacts.* Local Old-Order Mennonites want to preserve cultural integrity and do not desire frequent contact with tourists (List 2001, Sawatzky 1971). Passing through a Mennonite colony is necessary to reach the largest concentration of prairie dogs near Janos. Local Mormons are not as sensitive to outside contact, having served as guides to sportsmen since the early 1900s, including Teddy Roosevelt, various U.S. senators, and Aldo Leopold (Hatch 1998). Indigenous population is low, although several mountain sites are sacred to Apaches now based in the United States (Goodwin 2000, Villa 1998).
- 2) *Spreading benefits.* Competition among hotels in Nuevo Casas Grandes could make cooperative marketing among them difficult. Some ejidatarios may benefit more than others. Mata Ortiz, an ejido town southwest of Casas Grandes, has spread tourism's benefits throughout the town by training locals in making replica Paquimé pottery; this may provide a model for ecotourism (Smith and MacMillan 1998).
- 3) *Linking with other economic development plans.* Major road and hotel development may allow too much access, tax the limits of water supplies, and ruin the appeal of some remote sites. Scale of development is critical (King and Czech 1995). Community leaders should recognize the economic appeal of remote natural sites to tourists, and the sites' potential for economic development—or overdevelopment.
- 4) *Wildlife impacts.* Some charismatic wildlife, including prairie dogs and thick-billed parrots, is thought to be at relatively low risk from visitors, but others, such as the golden eagle, may be at higher risk (List 2001, Snyder *et al.* 1999, Venegas 2001). These concerns should be incorporated into advance planning.

Conclusion

Ecotourism offers potential to benefit both the economy and nature, diversifying local incomes while generating reasons and funding to protect habitat, but it needs to be done carefully in areas such as Casas Grandes. Considering site specifics is important in order to take advantage of attractions unique to the area while being sensitive to cultural and biological integrity. Ecotourism initiatives on private land may offer more control over initial unpredictable results. The following references, including websites, offer further assistance and information.

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Ecoturismo

(resumen)

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Los objetivos de esta presentación son: (1) describir cómo difiere el ecoturismo del turismo tradicional, (2) proporcionar ejemplos de ecoturismo de la región México-Estados Unidos, (3) sugerir el desarrollo de ecoturismo potencial en el área de Casas Grandes y (4), describir los problemas potenciales en relación a dicho desarrollo. Mis antecedentes en ecoturismo se relacionan a dos proyectos: (a) un proyecto de desarrollo de ecoturismo a nivel municipal de \$200,000.00USD que ayudé a iniciar y administrar en Oregon (Forbes 1998); y (b) mi disertación sobre las visitas del conservacionista Aldo Leopold al municipio de Casas Grandes y cómo puede aplicarse el ecoturismo ahí ahora (Forbes and Haas 2000).

Definición de Ecoturismo

El ecoturismo no es sólo cualquier turismo relacionado con la naturaleza. El concepto clave es el desarrollo *recíproco*: en el ecoturismo apropiado tanto la economía como la naturaleza se benefician (The International Ecotourism Society 2001). Otros aspectos clave son:

1. *Desarrollar paquetes de recorridos de menor volumen y mayor precio.* Esto facilita a los proveedores del servicio a hacer un manejo más eficiente de su propio tiempo, servir a clientes específicos y prepararse para impactos e ingresos.
2. *Mantener las ganancias a nivel local.* Evita usar franquicias, cadenas de moteles y guías extranjeros.
3. *Minimizar los impactos culturales.* Toma en consideración las necesidades locales y la integridad cultural a través de encuestas sociales y la colocación de turismo de bajo volumen. De otra forma se reduce su atractivo original y se perturba el estilo de vida y de trabajo tradicional de la gente del lugar.
4. *Separar algunas ganancias para mercadotecnia cooperativa y protección del hábitat.* Asegura la sustentabilidad depositando un porcentaje de las ganancias en un fondo a utilizarse para mercadotecnia cooperativa y protección del hábitat natural y de la salud de la tierra.
5. *Recordar que el ecoturismo no es una panacea; tiene impactos, algunos impredecibles.* La competencia de otros negocios puede llevar a un desarrollo excesivo

(Isaacs 2000). Puede ser difícil implementar controles y pueden surgir asuntos no previstos, como disponibilidad de agua.

Algunos Ejemplos de Ecoturismo

1. *Curry County, Oregon.* Se crearon nueve empresas diferentes de ecoturismo para ayudar a la transición económica de las comunidades leñadoras. Se pospuso su desarrollo y aún no se implementa un mecanismo para reinvertir ganancias. El municipio está satisfecho con los resultados del proyecto, a pesar de los resultados impredecibles (Egret Communications 2001; Forbes 1998).
2. *Wyoming.* La oficina estatal de turismo promovió un programa de turismo en ranchos. No todos los destinos cumplen con la definición de ecoturismo, pero el programa demuestra la factibilidad de las visitas a ranchos (Egret Communications 2001; Wyoming Dude Ranchers Association 2001; Wyoming Tourist Association 2001).
3. *Belice.* Se desarrolló buena cooperación y ética de conservación entre las comunidades que explotan los sitios remotos para ecoturismo. A raíz de su atractivo turístico, se protegieron grandes extensiones de manglares costeros (Egret Communications 2001).
4. *Reserva Monarca* en Michoacán, México. El ecoturismo ayudó a detener la tala del hábitat esencial de la mariposa monarca. Sin embargo, los grupos grandes de turistas tienen un impacto negativo sobre todo cuando no traen a un guía local (LaFranchi 2000).
5. *San Nicolás Totolapan* (México). Balam Consultants trabajó con ejidatarios para desarrollar mercadotecnia y relaciones públicas. Se protegieron 2,304 hectáreas que de otra forma se hubieran perdido (Mader 2001).
6. *La Ruta Sonora.* Esta organización no lucrativa desarrolló tres recorridos de Arizona a Sonora. 3% de la tarifa se usa para conservación del hábitat y los recorridos enfatizan asuntos ecológicos (La Ruta Sonora 2001).

Desarrollo Potencial de Ecoturismo Cerca de Casas Grandes

1. *Viajeros especializados con orientación hacia la naturaleza.* Los observadores de aves podrían ser atraídos por pájaros no encontrados en muchos lugares de los Estados Unidos. La mercadotecnia podría combinar la observación de aves de pastizal, aves acuáticas de invierno y aves de bosque y podría mezclar con atractivos no relacionados con los recursos bióticos como la singular historia cultural y las ruinas arqueológicas del área (Drewien 2000). Los conservacionistas podrían ser llevados a sitios atractivos como los lugares de campamento de Aldo Leopold (Forbes and Haas 2000), y otros podrían disfrutar su participación en proyectos de investigación o restauración de hábitats durante sus recorridos.
2. *Visitantes a Paquimé.* Los visitantes europeos y mexicanos han aumentado desde que estas ruinas del siglo 13 fueron designadas patrimonio mundial en 1998. Existen oportunidades para ligar el turismo de herencia patrimonial con el turismo naturalista que pueden darse mediante trípticos o mercadeo hacia los visitantes potenciales (Steele-Prohaska 1996). La conexión Mimbres – Paquimé (Mimbres-Paquimé Connection 2001) es un turismo de herencia patrimonial a través de la frontera que une al noroeste de Chihuahua y el suroeste de Nuevo México.
3. *Visitantes a ranchos y ejidos.* Estas visitas pueden ser más atractivas que los hoteles, porque ofrecen reservaciones más íntimas y confiables. Parte de la tarifa del viaje podría usarse en útiles escolares para el ejido.
4. *Viajeros en general.* A un día de manejo hay cuatro ciudades de E.U. con poblaciones mayores a 500,000 habitantes para las cuales se pueden diseñar paquetes turísticos atractivos: Albuquerque, El Paso, Phoenix, and Tucson (Hatch 1998).

Problemas Potenciales Para el Desarrollo de Ecoturismo Cerca de Casas Grandes

1. *Impactos culturales.* Los Menonitas locales quieren preservar su integridad cultural y no desean contacto frecuente con los turistas. (Sawatzky 1971; List 2001). Los Mormones de la localidad no son muy comunicativos y solo han servido como guías de deportistas desde el inicio de los 1900s (Hatch 1998). La población

indígena es baja, aunque varios sitios montañosos son sagrados para los Apaches, ahora establecidos en los Estados Unidos (Villa 1998; Goodwin 2000).

2. *Distribución de los beneficios.* La competencia entre los hoteles de Nuevo Casas Grandes podría dificultar una mercadotecnia cooperativa. El ejido Mata Ortiz ha distribuido los beneficios del turismo capacitando al pueblo para hacer réplicas de cerámica Paquimé. (Smith and MacMillan 1998).
3. *Enlace con otros planes de desarrollo económico.* El desarrollo de la infraestructura podría permitir demasiado acceso, presionar el suministro de agua y arruinar el atractivo de algunos sitios remotos. La escala del desarrollo es crítica (King and Czech 1995).
4. *Impactos a la fauna silvestre.* El impacto a las especies en riesgo debe incorporarse en la planeación avanzada (Snyder *et al.* 1999; List 2001; Venegas 2001).

Conclusión

El ecoturismo ofrece beneficios potenciales tanto a la economía como a la naturaleza, diversificando el ingreso local, mientras se generan razones y fondos para proteger el hábitat.

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Section III

Toward Sustainable Borderland Ranching

Hacia una Ganadería Sostenible en la Región de la Frontera

Current Situation of Rangelands in Mexico

(summary)

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Rangelands are natural areas with certain characteristics that make them unsuitable for agriculture. They include several types of vegetation such as deserts, grasslands, shrubs, forests, and riparian areas. Cattle ranching, along with the products and services it engenders, is a prime activity that rangelands have traditionally supported.

For the year 2000, Mexico's Department of Agriculture, Ranching and Fishing, known by its acronym SAGARPA, estimated a national fodder production of 192.6 million tons. Of this amount, only 25 percent originates from rangelands; 42 percent comes from irrigated prairies, 24 percent from agricultural harvests, and 5 percent from fodder farming. SAGARPA reports that a herd of 35 million animal-units consumes 175 million tons of fodder annually, demonstrating an apparent balance in fodder supply and demand. When data is considered by region, however, the statistics change. In northern Mexico, for instance, more than 80 percent grows on rangelands, making rangelands the main fodder source in this region. Problems in this geographic area have been known since 1985, and include overgrazing, erosion, shrub invasion, toxic plants, rodents, and fire. On the other hand, since 1961 up to the present, the amount of fodder has been reduced from between 10 percent to 85 percent, depending on the type of rangeland.

In light of this situation, today more than ever, we need to diversify production systems in order to restore damaged rangelands. Other rangeland uses can acquire higher values, such as recreation, forestry, mining and hunting. Water represents another vital product that we currently undervalue. Rangelands work like hydrological basins in which water is captured, filtered, and stored for later use—either in rural areas or urban centers. Nationwide, Mexico has some 300 hydrological basins that could capture a total of 400 cubic kilometers of water. Nevertheless, the capacity of these basins has been reduced by damaged rangelands. The *Comisión Nacional de Agua* (National Water Commission) states that in 1950, 12,885 cubic meters of water per capita was

available. By 1995 this amount had decreased to 3,921 cubic meters, and for 2025 it is estimated at 2,774 cubic meters per capita.

Ecologically speaking, deterioration translates into a loss of function. From a productive stance this means reduced harvests. Because ranching is the most common activity in northern Mexico, this industry should be the target of intense campaigns toward the recovery of the rangelands' capabilities.

To this end, traditional management practices such as load adjustment, diet supplementation, grazing management, production registration, shrub control, reseeding, and projects for water collection and soil conservation might regain importance.

To determine priority areas and select more efficient practices, the U.S. Department of Agriculture and SAGARPA, in consultation with various agencies, have developed a quick method of rangeland "health" assessment. This method is based on the evaluation of three ecosystem attributes: hydrologic function, biotic integrity, and soil-site stability. Because these attributes are highly complex, they are assessed by 17 key factors: (1) rills, (2) water flow patterns, (3) pedestals and terracettes, (4) bare ground, (5) gullies, (6) wind scour, (7) litter movement, (8) soil resistance to erosion, (9) soil surface loss or degradation, (10) plant community composition relative to infiltration and drainage distribution, (11) soil compaction, plant functional/structural groups, (12) plant mortality, (13) litter amount, (14) annual production, (15) invasive plants, and (16) reproductive capability.

Once the "health" of the rangelands has been assessed, monitoring methods are applied to evaluate possible changes or adjustments to management systems. The significance of evaluating rangeland ecosystems using the same criteria and methodology represents, among other things, an efficient use of agency resources such as information exchange, fast implementation of successful management practices that can benefit the same region in one or both countries (U.S. and Mexico).

Situación Actual de los Agostaderos

(artículo invitado)

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Los agostaderos son áreas naturales que por tener ciertas características no son aptas para la agricultura. Estas áreas comprenden diversos tipos de vegetación: desiertos, pastizales, matorrales, bosques y áreas ribereñas. Dentro de los productos y servicios que los agostaderos ofrecen se encuentra, por tradición, la ganadería.

La SAGARPA en el 2000 estima una producción forrajera nacional de 192.6 millones de toneladas de forraje. Para todo el país sólo un 25% del forraje es producido en agostaderos, un 42% en praderas irrigadas, 24% son esquilmos agrícolas y un 5% son cultivos forrajeros. Esta Secretaría reporta un hato de 35 millones de unidades animal que consumen 175 millones de toneladas de forraje, por lo que aparentemente existe un balance en cuanto a demanda de forraje. Sin embargo, cuando vemos cada región las estadísticas cambian. Por ejemplo en el norte de México, mas del 80% corresponde a agostaderos, por lo que ésta es la principal fuente de forraje. En esta área desde 1985 se señaló la problemática que presentaban los agostaderos: sobrepastoreo, erosión, invasión de arbustivas, plantas tóxicas, roedores y fuego. Por otra parte, se han cuantificado reducciones de cantidad de forraje de 1961 a la fecha de un 10 a un 85%, dependiendo del tipo de agostadero.

Ante esta situación, hoy más que nunca debemos tener diversificación de sistemas de producción para recuperar agostaderos deteriorados. Existen otros productos que pueden adquirir aún un mayor valor como son la recreación, silvicultura, minería, cacería, etc. Actualmente un producto que puede ser el más importante y que no hemos valorado es el agua. Los agostaderos funcionan como cuencas hidrológicas donde se captura, infiltra y almacena el agua para su posterior uso tanto en áreas rurales como en los centros urbanos. A nivel nacional, México tiene alrededor de 300 cuencas hidrológicas que debieran captar 400 kilómetros cúbicos de agua. Sin embargo, la capacidad de estas cuencas se ha reducido debido al deterioro de los agostaderos. La Comisión Nacional del Agua indica que en 1950 la disponibilidad de agua era de 12,885 metros cúbicos *per cápita*, en 1995 disminuyó a 3,921 y para el 2025 se estiman 2,774.

Ecológicamente hablando, el deterioro es una pérdida de la funcionalidad de los agostaderos. Desde el punto

de vista productivo, es una reducción de la cosecha del producto que se está extrayendo. Dado que la industria ganadera es la actividad más generalizada en el norte de México, es a través de esta actividad en donde se deben de iniciar fuertes campañas para la recuperación de la funcionalidad de los agostaderos.

Así, vuelven a retomar importancia las prácticas tradicionales del manejo de pastizales como son: ajustes de cargas, suplementación, manejo del pastoreo, registro de producción, control de arbustivas, obras de captación de agua, resiembras, obras de conservación de suelo, etc.

Para determinar las áreas prioritarias y elegir así las prácticas más eficientes, el USDA (Departamento de Agricultura de los Estados Unidos) y la SAGARPA (Secretaría de Agricultura, Ganadería y Pesca) a través de diferentes agencias han desarrollado un rápido método de evaluación del estado de “salud” de los agostaderos. Esto se basa en la evaluación de tres atributos de los ecosistemas: funcionalidad hidrológica, integridad biótica y estabilidad del suelo/sitio. Por lo complejo de estos atributos, estos se evalúan a través de 17 indicadores que son: 1) canalillos, 2) patrones de escurrimiento, 3) pedestales y “terracetas”, 4) suelo desnudo, 5) canales, 6) erosión eólica, 7) movimiento de mantillo, 8) resistencia de la superficie del suelo a la erosión, 9) pérdida de la superficie del suelo o degradación, 10) composición de la comunidad vegetal y distribución relativa de la infiltración y escurrimiento, 11) compactación del suelo, 12) grupos funcionales /estructurales de plantas, 13) mortalidad de plantas, 14) cantidad de mantillo, 15) producción anual, 16) plantas invasoras y 17) vigor de plantas. Estos son indicadores cualitativos que son explicados en una guía para su fácil y rápida evaluación.

Una vez evaluada la “salud” de los agostaderos se aplican métodos de monitoreo para evaluar posibles cambios bajo sistemas de manejo y realizar ajustes a estos. La importancia de evaluar con los mismos criterios y metodologías es eficientizar los recursos entre agencias que trabajan en agostaderos en intercambio de información, aplicación rápida de prácticas o manejos ya probadas que benefician una misma área en un país o en ambos países, entre otros beneficios.

Ranching and Prairie Dogs

(invited paper)

Dustin Long *Turner Endangered Species Fund*

Joe Truett *Turner Endangered Species Fund*

Introduction

Black-tailed prairie dogs (*Cynomys ludovicianus*) historically occupied grasslands throughout much of the Great Plains and the American Southwest from Canada to Mexico (Hall 1981: 412-415). During the last 100 years this species has declined to a small fraction of its historic range and abundance because of eradication programs, loss of habitat and sylvatic plague (*Yersinia pestis*) (Miller et al. 1994). As more attention is focused on the plight of prairie dogs and the potential for their restoration, it becomes important to assess the compatibility of prairie dogs with ranching, the land-use practice most often associated with them.

Prairie dogs and large ungulates (hoofed mammals), primarily bison (*Bison bison*), evolved together. In much of their historically shared range, prairie dogs and wild ungulates developed a mutually beneficial relationship (Truett et al. 2001). The characteristic continual clipping of vegetation by prairie dogs improved the palatability of most grazing-resistant grasses by keeping them in an early growth stage. The availability of nutritious grasses in turn attracted ungulates, which grazed on and near prairie-dog colonies. The combination of large numbers of ungulates grazing and the mechanical impact of their hooves upon the earth improved horizontal visibility for prairie dogs, keeping them secure from predators and encouraging colony growth.

Suitable Vegetation Types for Prairie-dog Habitation

The three vegetation types most extensively occupied by prairie dogs are mixed-grass prairie, short-grass prairie and desert grasslands. The mutually beneficial relationship between prairie dogs and ungulates is most obvious in mixed-grass prairie (Krueger 1986). Here grazing by ungulates during the growing season may be required for prairie-dog colony survival, by improving prairie dogs' ability to see predators. Without grazing (or with deferred grazing schedules) colonies can quickly shrink and disappear (Knowles 1982). As a result and of ultimate benefit to ranchers, prairie-dog colony growth is most easily

controlled in this vegetation type (Snell and Hlavachick 1980, Uresk et al. 1982, Cincotta 1985).

The short-grass prairie is probably the ideal habitat for prairie-dog colonization and persistence (Winter et al. 2002). Dominant grass species of this vegetation type include blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloe dactyloides*). In most short-grass prairie settings, grazing by ungulates is not required for prairie-dog survival and expansion because the dominant grasses are naturally short (Truett et al. 2001). As a consequence, controlling prairie-dog colony growth in this vegetation type may be difficult by managing grazing regimes alone.

In general, the least productive and least studied of the three vegetation types are the desert grasslands. Historically fewer bison and prairie dogs were found in this vegetation type than in mixed-grass and short-grass prairies. Rainfall is more sporadic than in the Great Plains, and some of the dominant grasses in this vegetation type are less resilient to continuous grazing pressure. As a result, sustainable ungulate stocking rates and prairie-dog densities are commonly lower in the desert grasslands than in the other grassland types. Grazing by ungulates may be required during plant growth periods for prairie-dog survival, however this grassland type can be susceptible to rapid degradation under the combined grazing pressure of both prairie dogs and ungulates.

Vegetative Response to Grazing

Regardless of vegetation type, the combined grazing of ungulates and prairie dogs causes shifts in plant species composition. Most obvious are the increases in grazing-tolerant plant species and the decline or disappearance of grazing-intolerant species. Intensive grazing by prairie dogs tends to replace grasses with forbs (broad-leaved herbaceous cover). Heavy grazing by prairie dogs and ungulates also will cause a shift from tall and mid-height grasses to those of shorter stature (Detling 1998, Truett et al. 2001).

Some productive sites (see below) may show an increase in net annual primary production when exposed

to the combined grazing of prairie dogs (Williamson et al. 1989) and ungulates, which enhances soil fertility and stimulates plant growth (O'Meilia et al. 1982, Detling 1998). But in most cases moderate grazing is generally recommended because it keeps the vegetation in an early growth state and provides more nutritional value and less standing dead material for grazers (Detling 1998). One problem of course is that prairie dog grazing intensity is difficult to manage, and in dry years prairie dogs may consume most of the annual growth within colonies, leaving little for livestock.

Site Productivity

Another consideration when addressing the compatibility of large grazers and prairie dogs is site productivity, a good measure of which is precipitation, or more accurately, available soil moisture. The better-watered sites tend to support taller grasses and produce more forage for grazers. Productivity can vary dramatically from year to year depending on rainfall, especially in the desert grasslands. Regardless of vegetation type, productive sites usually will require more intense grazing by ungulates than less productive sites in order to keep the grass short and thereby optimum for prairie dogs.

Prairie Dogs and Ungulate Stocking Rates

Stocking levels of cattle or other ungulates play an important role in managing prairie dogs. In most cases, heavy overgrazing, especially in the growing season, will increase prairie dog colony acreage but reduce prairie dog densities. Summer-deferred grazing schedules in more productive grasslands may lead to a decrease in colony acreage but an increase in prairie dog densities.

Stocking rates can be used as a tool to help manage prairie-dog densities and colony growth on productive sites (Uresk et al. 1982, Cincotta 1985). On such sites grazing duration and intensity determine in large part the ability of prairie-dog colonies to persist and expand. The historical abundance of prairie dogs in higher-rainfall parts of the Great Plains regions apparently was tied to high stocking rates of bison or cattle (Truett et al. 2001).

Prairie-dog Colony Age

As prairie-dog colonies age, the center of the colony tends to shift from grasses to forbs and annuals (Detling 1998). Most ungulates, except for forb-feeders such as

pronghorn antelope (*Antilocapra Americana*), tend to reject these areas in preference for newly colonized areas (perimeter of prairie dog colony) where grasses are more abundant. Thus a young prairie dog colony often becomes less beneficial to cattle as it ages.

Conclusion

We have found that prairie-dog restoration and ranching can be compatible and in many cases mutually beneficial. The degree of compatibility between prairie dogs and ranching largely depends on vegetation type and production, ungulate stocking rates, acreage occupied by prairie dogs, and colony age. To manage both prairie dogs and ungulates effectively does require some measure of flexibility and knowledge. Based on our experience and that of others, ranching and prairie dogs can best coexist when smaller, younger prairie-dog colonies are scattered over the landscape and occupy approximately 20 percent or less of the available habitat. Ranching can continue with or without prairie dogs, but prairie dogs may need ranching throughout a significant portion of their range in order to persist.

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La Actividad Ganadera y los Perros Llaneros

(resumen)

Dustin Long *Turner Endangered Species Fund*

Joe Truett *Turner Endangered Species Fund*

Los perros llaneros de cola negra (*Cynomys ludovicianus*) han ocupado históricamente pastizales a través de gran parte de las Grandes Praderas y del suroeste americano, desde Canadá hasta México (Hall 1981: 412-415). Durante los últimos 100 años, la especie ha disminuido a una pequeña fracción de su rango y abundancia histórica a causa de programas de erradicación, pérdida de hábitat y a la plaga silvática, *Yersinia pestis* (Miller et al. 1994). A medida que nos enfocamos en la situación del perro de la pradera y del potencial para restauración, es evidente la importancia de evaluar la compatibilidad de los perros llaneros con la actividad ganadera.

Los perros llaneros y los mamíferos grandes, principalmente el bisonte (*Bison bison*), evolucionaron juntos. En gran parte de su historia compartida, los perros llaneros y los mamíferos salvajes desarrollaron una relación mutuamente benéfica, que mejoraba la calidad del forraje y que también mejoraba la visibilidad horizontal del terreno para los perros llaneros (Truett et al. 2001).

Tipos de Vegetación Aprovechados Para Sobrevivencia del Perro Llanero

Los tres tipos de vegetación más asociados con los perros llaneros son la pradera mezclada, la pradera de pequeñas gramíneas y los pastizales desérticos. La relación mutuamente benéfica entre el perro de la pradera y el ganado rumiante es más obvia en la pradera mezclada (Krueger 1986).

La pradera baja es quizá el hábitat ideal para la colonización y persistencia del perro de la pradera (Winter et al. 2002). En la mayoría de estos entornos, no se requiere que los rumiantes pasten en la zona para que sobrevivan los perros llaneros, porque el pasto dominante es naturalmente bajo (Truett et al. 2001). En consecuencia, el controlar el crecimiento de las colonias de perros llaneros

en este tipo de vegetación puede ser difícil si se manejan regímenes de pastoreo en forma aislada.

En general, los pastizales desérticos son el tipo menos productivo y menos estudiado de los tres tipos de vegetación. Históricamente, hay menos bisonte y perro de la pradera en estas áreas. La precipitación es más esporádica que en las Grandes Praderas, y algunos de los pastos dominantes en este tipo de vegetación son menos resistentes al pastoreo continuo. Como consecuencia, las capacidades de carga para sostener ungulados y poblaciones de perros llaneros son más bajas en los pastizales de desierto que en otros tipos de pastizal. El pastoreo por ungulados puede ser requerido durante los períodos de crecimiento vegetal para asegurar la sobrevivencia de los perros llaneros, sin embargo este tipo de pastizal puede ser susceptible de una rápida degradación bajo una presión de pastoreo combinada por ungulados y perros llaneros.

Respuesta de la Vegetación Al Pastoreo

Sin importar el tipo de vegetación, el pastoreo combinado de rumiantes y perros llaneros ocasiona cambios en la composición de las especies de plantas. Lo más obvio es el aumento de especies de plantas más tolerantes, y la disminución o desaparición de las menos tolerantes. Un pastoreo intensivo por perros llaneros tiende a reemplazar gramíneas por hierbas. Un pastoreo pesado por perros llaneros y rumiantes ocasiona también un cambio gramíneas altas y medianas a zacates de baja estatura (Detling 1998, Truett et al. 2001).

Algunos sitios productivos pueden mostrar un incremento en producción primaria neta cuando son expuestos a un pastoreo combinado con perros llaneros y ungulados (Williamson et al. 1989), lo cual mejora la fertilidad del suelo y estimula el crecimiento vegetal (O'Meilia et al. 1982, Detling 1998). Pero en la mayoría de los casos se recomienda un pastoreo moderado, porque mantiene la

vegetación en una etapa de crecimiento temprana, y se proporciona más valor nutritivo y menos material vegetal muerto para el ganado (Detling 1998).

Productividad del Sitio

Otra consideración, al tocar el tema de la compatibilidad entre ganado grande y perros llaneros, es la productividad del sitio. Una buena medida de la productividad es la precipitación. Los sitios con más agua tenderán a sustentar pasto más alto y producirán más forraje. La productividad puede variar dramáticamente año con año, dependiendo de la precipitación, especialmente en los pastizales desérticos.

Tasas de Carga Animal Para Perros Llaneros y Rumiantes

La densidad de ganado juega un papel importante en el manejo de las densidades de los perros llaneros y el crecimiento de sus colonias. En la mayoría de los casos el pastoreo pesado aumentará el área de la colonia de perros llaneros, pero reducirá su densidad. De la misma forma, el pastoreo en pastizales más productivos puede llevar a una disminución en el área de la colonia, pero a un aumento en sus densidades.

Las tasas de carga pueden ser usadas como una herramienta para manejar densidades de perros de las praderas y crecimiento de las colonias en sitios productivos (Uresk et al. 1982, Cincotta 1985). En tales sitios, la intensidad y duración del pastoreo determina en gran parte la habilidad de las colonias de perros llaneros para persistir y expandirse. La abundancia histórica de los perros llaneros en lugares de alta precipitación de las regiones de las Grandes Praderas, aparentemente fue sujeta a tasas elevadas de carga animal por bison o ganado doméstico (Truett et al. 2001).

Edad de las Colonias de Perros Llaneros

A medida que las colonias de perros llaneros envejecen, los patrones de vegetación tienden a cambiar. El ganado tiende a rechazar estas áreas, prefiriendo áreas recientemente colonizadas, donde el pasto es más abundante.

Conclusión

Hemos encontrado que la restauración de las colonias de perros llaneros y las actividades ganaderas pueden ser compatibles y en muchos casos, mutuamente benéficas. El grado de compatibilidad entre los perros llaneros y las actividades ganaderas depende en gran medida del tipo de vegetación y la producción, la densidad de ganado, el área ocupada por las colonias de perros llaneros y la edad de la colonia. Los perros llaneros y las actividades ganaderas pueden coexistir mejor cuando las colonias son jóvenes, más pequeñas, están distribuidas en la zona, y ocupan un 20% o menos del hábitat disponible.

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Coexistence With Predators

(transcription)

Bill MacDonald *Malpai Borderlands Group*

Mac Donaldson *Empire Ranch*

Caren Cowan *New México Cattle Growers Association*

Bill McDonald: We have asked Caren to join us, too, so we get at least three perspectives, because I don't think there is one particular philosophy with predators that anybody can say works in every case. If you were to ask me what my predator program is, I would say I don't really have one. That wasn't always the case. When I was young, I took great delight in sitting for hours with a game call and calling up coyotes and shooting them and I really felt like I was accomplishing something. We had somebody on the ranch who ran dogs and hunted lions with the idea that we were really helping out the calf crop. Quite frankly we were losing more calves at that time than we are now.

I lost a calf once to a golden eagle, but I'm going to address lions and coyotes, in particular, as predators. I can count on the fingers of one hand the number of calves that I know I have lost to coyotes. I know that coyotes have eaten on a number of dead calves, but in some cases you don't know if they were already dead. I suspect in many cases they were, and the coyotes were simply eating the carcass. Coyotes get to a dead animal very quickly and it's often difficult to tell whether the coyote was the cause or was just eating something that had already died. Where a coyote has actually killed the calf, I tend to hold it against the cow. I run my cows in one herd in the growing season, so they are all together. They are very aggressive. If any of you have cow dogs, you know that you don't take a pup out there by itself and start trying to move cows with it, because those cows will get after it. They are big and quick and they present a formidable obstacle to anything trying to get their calf. If they're not presenting that obstacle, I definitely hold it against the cow. I think it's much easier to get the right kind of cattle than it is to try to train a bunch of predators to do what you want them to do. I will concede, though, that that's just my experience on my ranch. I do know of areas, particularly ones close to towns, where whenever cows give birth, they are attacked by packs of coyotes and, in many cases, packs of dogs, not wild dogs, but domestic dogs that get together. So that's another issue. I'll get back to that when I talk about animal-damage control.

As far as mountain lions go, we aggressively hunted mountain lions for years and I still have a neighbor who

guides hunters to lions and sometimes does so on my place and sometimes at my request, if I have had a kill. But it's fairly rare, for two main reasons I think. One, we introduced some Angus blood into our livestock back in the late 60s and immediately saw a drop in the number of calves killed. Now, the Angus cows don't have horns, but they make up for it with attitude. They seem to be much more formidable to the lions and, I guess, more conscientious in protecting their calves than the straight-bred breed that we had before. We don't have straight Angus cows anymore but we still have a lot of Angus blood in the herd and I think that that helps protect them from mountain lion attack.

And the other thing is I tend to take cows off the Forest [National Forest allotment] soon after they calve. The calves start dropping in January. When I say "Forest," I'm talking about rugged mountain country that lions tend to like. I'm completely off the Forest by the end of March and it's a process where I am taking cows off as they calve, leaving cows that don't have calves on. I don't take all my cattle off the Forest at one time. It would be physically impossible to do, anyway, because this is rough country. So I think that has also contributed to the fact that I have very few losses to predators.

But I do know areas where lions have been and continue to be a problem. Ranchers have done some management and they have not been able to completely ameliorate their problem. I think there are places where you need professionals to come in. I'll give you one example. It has not to do with livestock. It has to do with pronghorn. Pronghorn were introduced 20 years ago into the San Bernadino valley. They are still there. They are doing fairly well. We just had a hunt. So they're doing well enough where they think they can be hunted, in spite of the droughts we have had the last few years. I'm convinced that they wouldn't have survived had there not been, for the first few years, some very aggressive coyote control from the state of Arizona, using U.S. Wildlife Services, because those pronghorns simply were not acclimated to that area and the coyotes were taking complete advantage of them. So I think there is a place for predator control.

These are observations made from my own experience as a rancher. I'm not a wildlife biologist or an animal behaviorist. I will say one brief thing having to do with the philosophy of Malpai Borderland Group, of which I am executive director. We don't have a group philosophy or group directive regarding predator control, but our actions have tended to be, especially in the case of the Mexican jaguar, of trying to discourage people from killing that animal. The Mexican jaguar rarely appears in the United States. When it does, we feel that's a pretty neat thing. The fact that we have a corridor that the jaguar can move in is important to a lot of people and should have some protection. On the other hand, if you have a situation where a rancher is losing a lot of livestock to this animal, I think there should be some compensation involved. As a result of Warner Glenn's experience in photographing the jaguar and the public interest it created ... it was on my ranch in my Forest allotment, we started a fund where we would reimburse ranchers in the United States and down into Mexico a little ways if they had losses from jaguars. So that's our attitude. We really believe you don't have to do intensive predator control in order to maintain a livestock operation, but you can't be naive either and pretend that you don't have the occasional problem.

M. Donaldson: We have a number of predators on the Empire cienega north of Sonoita, south of Tucson. Predominantly it is feral dogs. Of the natural predators we have—lion, bear, and coyote—we don't have much of a problem with them. Very rarely can a lion, even if it's hungry, or a bear, take a calf; the cows make taking a calf dangerous. During the 25 years we have been there, I think we've had probably three lion kills, and no bear kills that I know of. I think there have been about three to five coyote kills on calves in 25 years. It's usually a weak calf. There are two situations, two scenarios. One is that you'll have a brand newborn calf off of a first-calf heifer and she gets up and doesn't know what's happened. She doesn't know that she has calved, sort of a mysterious event, and she'll wander off, not being a very good mother, and leave that calf and then that calf will be gotten by a coyote. I'll sell that cow, just as much as Bill was saying, if she continues to behave in a nonmaternal manner. So I have eliminated that problem. I'm not going to try to find the coyote or the pack that did it.

Then there is another situation. During the first two weeks of nursing, when the calf is eating very little grass, from the point of view of a coyote the calf produces an extremely desirable excrement. A lot of times the excrement gets stuck on the calf. The mother goes off to water. We're in a fairly arid area and the cow might go as much as a mile, a mile and a half, to water. She'll leave her calf with a nursery sometimes, but maybe sometimes not, and the coyote will smell that fecal matter. They'll

be eating it on the ground and then they'll find the calf, which is defenseless, and they'll start to eat fecal matter off the calf and then, of course, they'll eat the calf if there is nothing to chase them away. But I don't think that's a targeted, an intentional kill. That's not a carnivorous kill. That's actually the habits of the coyote, that it eats everything from mesquite beans and feces to grass to whatever. So I don't really feel that coyotes present that much of a problem.

The real problem is feral dogs. We're close to the municipality of Tucson, which is getting close to a million people. A lot of people buy dogs, and then they decide they don't want dogs, so they say, "Let's take it out and turn it loose so that it can have a happy life out in nature." These animals pack. The most dramatic winter, we lost 14 head of yearlings. Some dogs castrated one young bull. And they were just doing it for sport. They weren't doing it for the meat. The pack was as big as 13 to 14. So that is the responsibility of humans. It's got nothing to do with the natural situation. But, to me, that is a predator situation and I can't get Wildlife Services to do anything about it, because dogs are not considered a trappable animal.

I know personally of a rancher near Santa Fe. Santa Fe has a tremendous problem with feral dogs. This fella, he carries a gun with him all the time. He kills in excess of 75 dogs a year on his place. People just turn them loose. That's the predator problem that I face. I don't face a natural predator problem. When the pronghorn were reintroduced on the ranch, there was some trapping done to remove coyote for that particular time period. They don't trap them anymore. The pronghorn have been there about 15 years now. You can see the dramatic change in the population of the fawns according to the coyote population. But, more than predators, the forces affecting winter growth key into whether the fawns make it or not. I think that Wildlife Services could help me if they could eradicate some of these feral dogs. So, I agree with Bill. I think there is a place for predator control.

Because I have a federal permit, I'm sure I'm going to get some black-tail prairie dogs and I'd like to see how they do. I'm curious what Wildlife Services will do with the coyote population before the prairie dogs arrive because they are going to reintroduce them on the plains and the prairies, where the coyote does his work, rather than in a wooded or a riparian habitat.

C. Cowan: While my family has a ranching operation in Southern Arizona, kind of between where Bill's and Mac's places are, I work for the New Mexico Cattle Growers Association, so I will speak in much more general terms. I don't have the day-to-day experience these fellows do. Livestock producers are in the business of raising animals, and that's what they want to do. When predator management becomes necessary, it is

a necessary evil, as you have heard from both of these gentlemen, something that you do to maintain some balance so that you can protect your private property and coexist with nature. We believe that the Wildlife Services program is necessary. As you have heard from both Bill and Mac, predators hurt not only domestic animals, but wild animals as well. In New Mexico, in many areas of the state, we're losing deer populations because we have more predators than those areas can stand. So our game and fish department is addressing that. The New Mexico Game Department is attempting to reestablish bighorn sheep populations and they are having a terrible problem with mountain lions. So I think probably the whole message of this is that we need to achieve some balance. Everybody has to find a way to coexist. Unfortunately once and a while that means using a lethal method, but most producers are going to try a nonlethal method first, as Bill and Mac have talked about. In New Mexico we have had huge sheep numbers in the past. A lot of those sheep producers are switching to cattle, because cattle can protect themselves from predators better than sheep can. So balance is what we're looking for, and the ability for all of us to coexist.

Coexistencia Con Depredadores

(resumen)

Bill MacDonald *Grupo de Tierras Fronterizas Malpai*

Mac Donaldson *Rancho Empire*

Caren Cowan *Asociación Ganadera de Nuevo México*

Bill MacDonald: Una forma de proteger a los becerros de depredadores es dejar que el ganado forme una sola manada durante la época de crianza. De esta forma las vacas siempre están juntas y son muy agresivas y es muy difícil que cualquier animal pueda acercarse a las crías.

Debido a que los coyotes pueden encontrar un animal muerto rápidamente, es difícil saber si el coyote fue la causa de esa muerte o si sólo se comía algo ya muerto. Pero sospechamos que en muchas ocasiones la muerte del animal no fue causada por el coyote. En los casos en que un coyote mata un becerro, con frecuencia es por negligencia de la vaca, porque en general, las vacas son obstáculos formidables para un depredador como el coyote. Por eso, en estos casos prefiero deshacerme de la vaca. Es mucho más fácil y barato seleccionar vacas que sepan proteger a sus crías que tratar de controlar la población de depredadores en la región.

La pérdida de crías por ataques de puma ha sido mínima en nuestros ranchos debido a que se introdujo sangre Angus en el ganado, lo que los hace más conscientes de la protección a sus becerros. Además, las vacas bajan del bosque poco tiempo después de dar a luz, por lo que la manada que permanece en territorio de pumas consiste sólo de adultos.

A diferencia de los ejemplos arriba mencionados existen algunos casos donde es necesario el apoyo del Estado para el manejo y control de depredadores. Por ejemplo, hace 20 años se introdujo berrendo en el valle de San Bernardino, y las poblaciones han sobrevivido bien. Esto no hubiera sucedido si el Estado de Arizona no hubiera implementado un agresivo programa de control de coyotes, porque el berrendo no estaba aclimatado al área y los coyotes tomaban ventaja de esto. Recuerde, el control de depredadores debe usarse para tratar la causa del problema en lugar de los síntomas.

Mac Donaldson: En nuestra área de trabajo, en el sur de Tucson, Arizona, nuestros principales problemas de depredación son causados por perros salvajes. Una gran cantidad de gentes compran perros y luego deciden que ya no los quieren y los liberan en los alrededores para liberarse de ellos. Estos animales, después, tienen que matar animales indefensos para sobrevivir, convirtiéndose en una plaga para los ganaderos. Un rancho de Santa Fe, NM, menciona que en un año ha logrado cazar hasta 75 perros salvajes en su rancho.

Caren Cowan: En Nuevo México se están perdiendo poblaciones de venado a causa de la alta densidad de depredadores en esas zonas. El Departamento de Caza de Nuevo México está tratando de reestablecer las poblaciones de borrego cimarrón y enfrenta grandes problemas con el puma. Frente a estas circunstancias, la intervención del gobierno en el manejo de depredadores es necesaria para mantener un equilibrio, proteger la propiedad privada y coexistir con la naturaleza.

El caso del jaguar mexicano es especial, porque este animal se mueve por un corredor a través de la frontera y debido a su importancia ecológica es importante protegerlo. En este caso no es necesario llevar a cabo un control intensivo de este depredador para mantener una operación ganadera productiva.

El problema real al que algunos rancheros se enfrentan son los perros salvajes. En el municipio de Tucson hay cerca de un millón de personas, y muchas de ellas abandonan a sus perros en el campo cuando deciden que ya no los quieren. Estos animales se mueven en manadas y son peligrosos porque atacan al ganado por diversión. Esto es responsabilidad de los humanos porque no tiene nada que ver con la situación natural. La solución a este problema requiere que el público, el gobierno y los rancheros actúen y colaboren de forma conjunta.

Value-added Beef Products

(transcription)

Mac Donaldson On Behalf of Will and Jan Holder

I'm speaking for Will and Jan Holder, who couldn't be here. I happen to be familiar with Will and Jan's company, Ervin's Natural Beef, and its program because I've sold them cattle. Will and Jan's value-added beef program is based on their family ranch in the area known as The Blue, in the mountains of eastern Arizona.

The beef industry has recently used the niche-marketing concept to enable packing houses to increase sales of specific breeds of cattle. Certified Black Angus beef, as we've probably all seen in the United States, has done a very successful job of that. A number of producers have been dissatisfied with normal retailing of beef in general. In order to change that, marketers have attempted to offer unique products targeted to specific clientele.

The Holders have established a group or a set of offerings within their beef program that they make available to a more environmentally conscious buying public. They market their operation as predator friendly, a ranch that doesn't shoot predators and allows for some wolf reintroduction on their home ranch up on The Blue. The beef comes from cross-bred cattle, but they attempt to maintain quality by eliminating dairy breeds and limiting Brahman influence to about 20 percent.

The main selling point has been that Ervin's Natural Beef is ranch-raised, produced without hormones or grain, and is grass-fattened. Will and Jan are also using their contacts and abilities to develop a plan on the Forest to manage five or six allotments cooperatively. Eight to ten ranchers and the agencies connected with the ranches are getting involved in the project. The group is attempting to look at a larger scale management for the Forest allotments, tying the management plan into wildlife corridors and larger resource concepts. This is another element of their value-added natural beef product that has a lot of appeal to certain portions of the public.

Conceptually it's a very valid project, but accomplishing it has been difficult. Will and Jan and Will's father made a lot of effort to find suppliers with a product that meets their requirements and is acceptable to the public. This is what they had to do. Since they are in an arid situation, they know that the quality of their beef is going to fluctuate with the season and the amount of

precipitation. They can possibly have fat cattle ready to market in August, September, or even October, but if they try to market a fat calf, a cow, or a yearling from grasslands like these here in Chihuahua in November, the beef is not going to be very tasty, nor is it going to be acceptable to the public. So there has been a supply problem. But the Holders have worked with different processors and storage facilities, so that if they kill at volume at specific times, they have some product available to market. I think the Holders would agree that to have a value-added beef program that offers an original product and targets a specific market, it is important to ensure a steady supply before you create demand.

I'll give you an example that Will shared with me. A chef in New York City heard about the Holders' program—Arizona range beef, free of hormones, not fed on grains, from a predator-friendly ranch. It met all the parameters he was looking for. The chef called Will and arranged to get some prime rib. The chef put it on his menu, and people began raving about it. The customers really liked the product, the chef really liked the product. So the chef told Will, "Okay, I need more. I need more." But Will was thinking, "I don't know where I'm going to get more and more and more." So Will had created a market where he couldn't meet the supply needs. I think one of the caveats here is that when you do start a specific program, make sure that you do advance planning. Try not to overstep your bounds, or make promises for more than you are capable of doing. Then, as you move into something slowly, try to keep the supply and product quality consistent with demand. Ervin's Natural Beef is an excellent example of creating a bridge between cattle producers and the ecologically minded consumer.

Will Holder can be reached at:

Ervin's Natural Beef

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Productos Cárnicos con Valor Agregado

(resumen)

Mac Donaldson En substitución de Will y Jan Holder

En la industria cárnica, existe un número de productores que no están satisfechos con la forma en que se vende el producto. Para cambiar eso han orientado la mercadotecnia del producto hacia un tipo específico de cliente, promoviendo un conjunto de características para atraer a un público ambientalmente consciente. Algunas de estas características son las prácticas amigables a los depredadores.

La mercadotecnia se basa en que es ganado de rancho en pastizal, sin hormonas ni grano, y proveniente de ranchos en donde no se caza a los depredadores. Para que el concepto funcione es necesario tener una oferta que sea aceptable para un mercado específico. Además, debe existir la oferta antes de crear la demanda.

Si se crea la demanda antes que la oferta pueden surgir problemas. Por ejemplo, en una ocasión, un chef en Nueva York supo de este programa, de ganado de Arizona libre de hormonas y de grano, proveniente de ranchos que no cazan a los depredadores. El chef empezó a ordenar costilla y a ofrecerla en su restaurante. El público recibió bien el producto y la demanda empezó a crecer. De esta forma, el ganadero creó un mercado que rápidamente supero lo que él le podía suministrar. La lección aquí es: antes de empezar un programa específico, asegurarse de planear a futuro, sin sobrepasar tus límites o tus capacidades de producción. Siempre tratar de mantener un nivel y calidad de producto a la altura de las exigencias de los clientes.

Si a usted le interesa aprender más sobre la producción de productos cárnicos con valor agregado, favor de contactar a Will Holder de Carne de Res Natural (Ervin's Natural Beef):

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Ranching and Conservation in the Santa Cruz River Region, Sonora: Milpillas Case Study

(summary)

Joaquin Murrieta-Saldivar *Sonoran Institute*

Introduction

The Sonoran Institute (SI) is a non-profit organization working with people toward common conservation goals. Two objectives guide the work of the Sonoran Institute in the Santa Cruz River Region in Sonora, Mexico: to establish projects with community participation that can result in tangible and long-lasting benefits to the environment, and to ensure success by developing projects that engage communities in activities beneficial to the community and the environment. The Institute understands that landowners participate more actively in conservation when projects address critical needs.

SI conservation projects in the Santa Cruz River region focus on three main areas: working with cattlemen to improve grassland management and implement restoration practices; undertaking socio-political and natural resources research; and promoting the understanding of the community in matters of conservation and adequate use of natural resources.



Figure 1. Trincheras (rock curtains), built during spring 2003 retain sediments and increase humidity in Milpillas, Sonora.

The cattlemen of the Santa Cruz region are working to improve the quality of their cattle operations through controlling erosion, increasing water retention and grassland availability. Higher water retention results in improved plant coverage and riparian biodiversity restoration, thereby maintaining the functionality of the ecosystem. Two specific activities improve water retention and grassland productivity in the Santa Cruz River: construction of rock curtains, commonly called *trincheras*, and implementation of pasture division and rotation.

Construction of Trincheras (Rock Curtains) Across Channels and Arroyos to Control Erosion Problems

Rock trincheras are small containment dams built across eroded channels and streams to promote water and soil retention. They prevent erosion, soil loss, and encourage increase plant coverage.

Rock trincheras are used in unstable streams and channeled beds. Negative changes due to mismanagement have affected the environment of several pastures in the Milpillas area, making the pastures prone to drought, destabilizing soil and decreasing ability to support forage. Trincheras can reverse this destructive erosion process, and eventually reestablish original channel, shape, improving water availability.

Eroded and unstable channels promote desertification. As channels erode they drain more effectively. The reduction in water retention affects forage availability, and thus the economic productivity of the pasture.



Figure 2. Same trincheras (rock curtains), after summer rains of 2003, showing positive results in soil retention and humidity increment; note new seedlings coming up. Photo by Murrieta and R. Emanuel, 2003.

With trincheras the actual physical conditions of landscape can be improved along with productivity and economic returns for the producers.

Trincheras reduce the energy of the water flow and its soil-dragging capabilities. With trincheras, stream flow deposits soil behind the structure eventually covering the channel with sediment and improving water availability. Water and soil retention also aid the natural re-growth of grasses in the area.

For eroded channels, trincheras can be built using locally available rock and stone. The tools commonly used are bars and shovels, but a small mechanical shovel and a cart are recommended. The trincheras should be built in groups, extending along a lengthy section of the channel. It is better to begin upstream to keep the current from dragging the trincheras. Location is critical to effectiveness, and coordinating efforts with people experienced in this strategy is highly recommended.



Figure 3. Demonstrative native grasses plot, established in Milpillas by Group #5 members of Ejido Miguel Hidalgo, Sonora. The Sonoran Institute and Group #5 have been collaborating in cattle and conservation projects since 1999. Photo by R. Emanuel 2003.

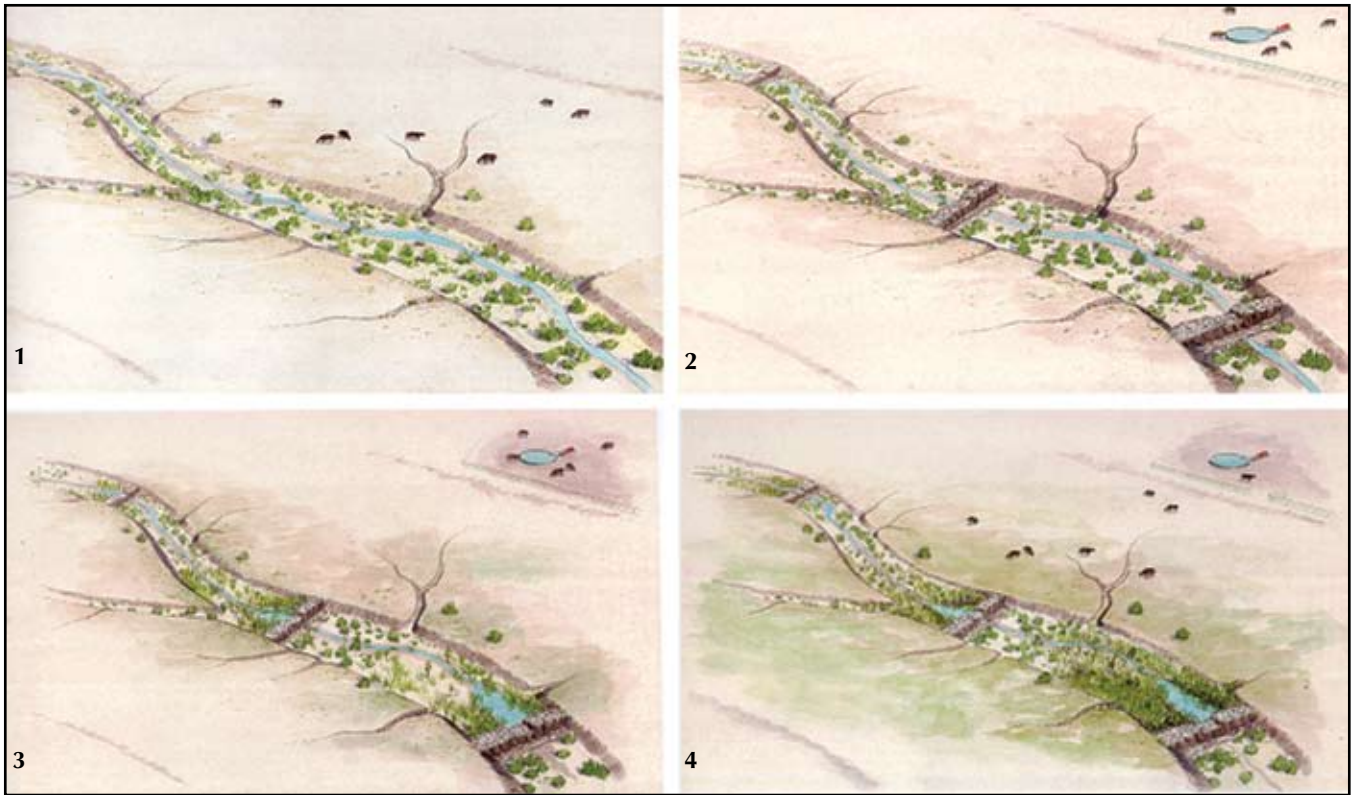


Figure 4. Simulated representation of positive effects in soil and forage plants restoration due to trincheras (rock curtains) construction and good cattle management practices:

1. Representation of arroyos and rangelands before trinchera (rock curtain) construction, presence of cattle without exclosures.
2. Arroyo with trincheras (rock curtains), alternative water source, and fences to exclude cattle (Year 1, construction).
3. Same arroyo after 2-3 years (with precipitation) after trincheras (rock curtains) were built. Grasses and vegetation regenerated due to soil and water retention. Cattle are excluded. Alternative water sources exist.
4. Arroyo after 2-5 years (with precipitation) after gabion construction. Notice grass and vegetation restoration vegetation abundance behind trincheras (rock curtains), and the grassland restoration beyond the arroyo. Under controlled access and grazing rotation, the pasture is used in an integrated way. Drawings by the Sonoran Institute

Pastures Division and Rotation

Pasture division and rotation begins with dividing grasslands into sections through fencing and developing a rotational grazing plan that allows each section to regenerate.

A division and rotation program provides better control over cattle grazing, allowing effective use of grasslands. The objective of rotational grazing is sustainable use of grasslands. In addition to rotation, reversal of poor grazing strategy can be accomplished by changing the number of cattle, grazing intensity, and water distribution.

Overgrazing can be caused by heavy grazing, grazing year-long, or grazing on sensitive lands (sloped terrain, shallow soils, low foliage density, etc). A division and rotation program should include strategically located water sources in each pasture. Cattle can then be rotated, balancing the grass regeneration cycle and the needs of the cattle.

With fencing, pastures can be divided to restrict access selectively protecting cattle and allowing grassland regeneration. Fences can be used to exclude riparian areas, riverside grasslands, or other areas of special interest. It is important to note the possible results of fencing riparian corridors, because wildlife like deer may be prevented from crossing fences. Possible solutions include gates, reduction of fence height, or lowering fences to ground level during certain periods in the year.

Before beginning division plans it is advisable to make a general assessment of the rangeland and the particular condition of each pasture. The assessment should identify vegetation types, wildlife activity, and individual management needs for each pasture. It is important to develop the necessary infrastructure for the rotational plan, but the most important element is the commitment to undertake the management and scheduling plan, which is the responsibility of the land-owners and users.

Ganadería y Conservación en la Región Del Río Santa Cruz, Sonora: El Caso Del Grupo Milpillas

(artículo invitado)

Joaquin Murrieta-Saldivar *Sonoran Institute*

Introducción

El Sonoran Institute es una institución no lucrativa que trabaja con la gente para alcanzar metas comunes de conservación. Dos convicciones guían el trabajo del Sonoran Institute en la región del Río Santa Cruz, Sonora, México. Primero, los proyectos con participación comunitaria pueden producir beneficios al medio ambiente, tangibles y duraderos. Segundo, para asegurar éxito, los proyectos deben involucrar a las comunidades en actividades que resulten benéficas y tangibles tanto a la comunidad como al medio ambiente. El Instituto entiende que los propietarios del terreno participan con más entusiasmo en la conservación cuando el proyecto confronta una necesidad identificada por ellos mismos.

Nuestros proyectos de conservación en la región del Río Santa Cruz, se enfocan en tres áreas generales: trabajando con los ganaderos para mejorar el manejo de pastizales e implementar practicas de restauración;

realizando investigación de recursos naturales y socio-políticas; e incrementando el entendimiento de la comunidad en cuestiones de conservación y el uso apropiado de los recursos naturales.

Como ejemplo, los ganaderos-ejidales del Santa Cruz están involucrados en trabajos que mejoran la calidad de su ganado a través del control de la erosión del suelo, aumentando la retención de humedad y disponibilidad del pastizal. Con el aumento en la retención de la humedad, se mantiene una mejor cobertura vegetal y restauración ribereña, manteniendo la funcionalidad del ecosistema. El ganadero se beneficia con una mejor calidad del pastizal, obteniendo mejor peso y salud de su ganado. Esto es un incentivo para que el ganadero se involucre en prácticas de conservación del hábitat. En este artículo mencionamos dos actividades específicas que ayudan a la retención de humedad y la productividad del pastizal que ya se están llevando acabo en el Río Santa Cruz: la construcción de cortinas y la división y rotación de potreros.



Figura 1. Cortinas hechas de piedra para retener sedimentos e incrementar humedad en Milpillas, Sonora, construidas en la primavera 2003.

Construcción de Cortinas de Piedra en Canales y Arroyos Para Controlar Problemas de Erosión

¿Qué son las cortinas de rocas? Las cortinas de rocas son pequeñas represas de contención que están construidas a lo ancho de los canales y/o arroyos erosionados. Estas cortinas promueven la retención del agua y del suelo. Usualmente, las cortinas son construidas con roca o piedra y son sencillas de construir produciendo beneficios tanto para el medio ambiente como para la economía del ganadero.

¿Cuáles son los problemas que las cortinas pueden abordar? Las cortinas son buenas herramientas donde existen problemas de erosión, pérdida de suelos y pobre cobertura vegetal. Estas cortinas se pueden implementar si existen características de arroyos inestables y cortados en sus fondos (lechos), formando canales estrechos y profundos donde no existían anteriormente. Este cambio en

el terreno – de no tener canales marcados a tener canales estrechos y profundos – ha afectado el medio ambiente de varios potreros, haciéndolos más propensos a la sequía y el terreno no puede soportar el forraje como antes (vea los párrafos abajo). Poniendo las cortinas en los canales erosionados se puede dar marcha atrás a este proceso destructivo que empezó con la erosión de los canales. Construyendo las cortinas de roca, eventualmente se conducirá al restablecimiento de la forma original de los canales y un mejoramiento de la cantidad del agua y la condición del forraje.

¿Cuáles son los beneficios en construir las cortinas? Primordialmente, donde la base económica es la ganadería, cuando el número de cabezas de ganado es alto y la salud del rebaño es generalmente buena, la economía es sólida. Cuando hay una sequía o una enfermedad que reduce el número de ganado, la economía también se ve reducida.

Los canales erosionados e inestables hacen una especie de coladera del agua que promueve condiciones de sequía. A medida que la erosión de los canales avanza el “drenaje” se hace más efectivo en acarrear o sacar el agua de los potreros y en promover condiciones de sequía. Esto da como resultado, la reducción de la cantidad del agua en los suelos afectando la disponibilidad del forraje. Con menos agua, hay menos forraje. Con menos forraje, la tierra no puede soportar la misma cantidad del ganado, lo que reduce la productividad económica del potrero.

Con la construcción de las cortinas se puede dar marcha atrás a esta serie de eventos destructivos que han afectado a los arroyos. Como se menciona mas adelante, construyendo cortinas en canales erosionados se puede mejorar la condición del área hasta que llega a un punto donde hay más agua y forraje para el ganado. En resumidas cuentas, el resultado final de construir las cortinas es el de mejorar las condiciones del suelo y apoyar el bienestar económico y productivo del ganadero. Para observar los efectos de estas cortinas se sugiere iniciar en terrenos con características de suelos erosionados, canales bien marcados, fácil acceso a bancos de piedra, y buen potencial de recuperación del terreno entre otros.

¿Cómo funcionan las cortinas? El objetivo principal de construir las cortinas en los canales erosionados es reducir la velocidad del flujo del agua en el canal. Esencialmente, las cortinas son como pequeñas represas que reducen la velocidad del flujo del agua. Al reducir la velocidad del agua, las cortinas reducen la energía del flujo y su habilidad de



Figura 2. Misma cortina, después de las lluvias de verano 2003 muestra resultados positivos en la retención de suelo e incremento de humedad. Note las primeras plántulas brotando. Foto Murrieta y Emanuel 2003.

arrastrar o lavar el suelo. Con las cortinas, la velocidad de la corriente en los canales se reduce y el flujo deposita este arrastre de suelos atrás de las cortinas. Así, las cortinas promoverán el depósito del suelo y eventualmente el canal se cubre con el sedimento. El suelo que es depositado atrás de las cortinas funciona como una esponja que retiene agua. Por lo tanto, como el canal está relleno de suelo, la cantidad del agua y retención de humedad también aumentan. Esta retención de suelo y humedad también empiezan a actuar en el restablecimiento natural de zacates germinando en los alrededores de las cortinas, así, con el aumento en la cantidad del agua y suelos el forraje que existía antes de la erosión de los canales empieza a restablecerse.

¿Cómo se construyen? Para los canales erosionados, las cortinas pueden ser construidas usando piedra y/o rocas que están disponibles localmente. Las herramientas que más comúnmente se utilizan son herramientas de mano, como barras y palas, las cuales son usadas para construir y fijar las cortinas en los canales. En ocasiones es recomendable el uso de una pala mecánica pequeña y una batanga para acarreo y acomodo de rocas.

Generalmente las cortinas de rocas no están construidas de forma aislada, pero están colocadas en los canales en una serie que consiste en un grupo de cortinas que se extiende a lo largo de una extensión significativa del canal. Se recomienda empezar al inicio (aguas arriba) del arroyo ya que de otra manera las mismas corrientes pueden arrastrar las cortinas. La ubicación de las cortinas es básica para que sean eficaces. En el inicio de la construcción de las cortinas es muy recomendable un

esfuerzo coordinado con personas que ya cuentan con el conocimiento y la experiencia de usar esta estrategia para controlar la erosión. Algunos productores del Santa Cruz ya cuentan con esta experiencia.

División y Rotación de Potreros

¿Qué es la división y rotación de potreros? La división y rotación de potreros como su nombre lo indica es básicamente la división del terreno de agostadero en varias secciones o potreros a través del uso de cercas. Una vez establecidas estas divisiones se diseña un plan de rotación del ganado. La idea es de proporcionar suficiente descanso a cada uno de los potreros para fomentar el vigor del pastizal, la acumulación de energía vegetativa y asegurar que el pastizal se regenere con suficiente fuerza para ser pastoreado.

¿Cuáles son los beneficios de establecer un programa de división y rotación de potreros? Con un programa de división y rotación de potreros se tiene un mejor control del ganado y un uso más eficiente de los pastizales. El principal objetivo del desarrollo de una estrategia de pastoreo rotativo o especializado es provocar una situación en la que el ganado utilice el terreno en una forma sustentable. Existen, sin embargo, muchas maneras en las que una estrategia de manejo de pastoreo inadecuado (una que conduce al deterioro ecológico) puede ser modificada. El tipo (ganado vacuno o bovino), la clase (becerros, novillos o vacas) y el número

de cabezas, así como la intensidad del uso, pueden ser cambiadas. Por ejemplo, se puede requerir la presencia de vaqueros, se pueden instalar cercos o se pueden implementar fuentes de agua en tierras arriba de los diferentes potreros. Todos, o una combinación de estos métodos pueden llegar a producir resultados positivos en una situación determinada.

¿Cómo funciona la división y rotación de potreros? Las estrategias de descanso rotativo eliminan el uso de una área determinada para el pastoreo a la vez que el resto de los potreros continúan siendo aprovechados. Esta estrategia requiere mover al ganado de una área a otra a un tiempo determinado.

Es bueno hacer notar que no es el pastoreo lo que afecta negativamente a los agostaderos ribereños,



Figura 3. Parcela demostrativa de pastos nativos establecida en Milpillars por el Grupo #5 del Ejido Miguel Hidalgo, Sonora. El Sonoran Institute y Grupo #5 han venido colaborando en trabajos de conservación y ganadería desde 1999. Foto Emanuel 2003.

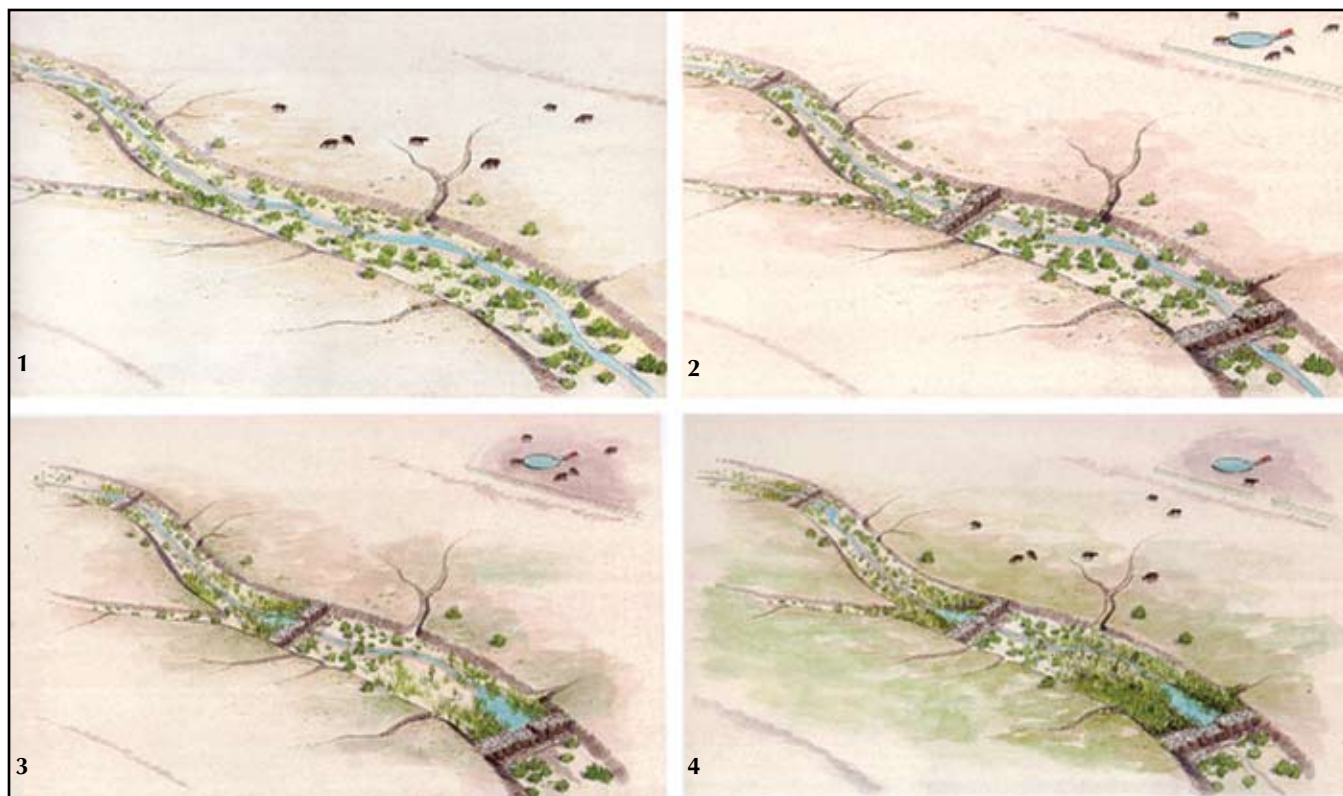


Figura 4. Representación simulada de los efectos positivos en la recuperación de suelos y forrajes gracias a la construcción de cortinas y buen manejo de ganado:

1. Representación de la situación actual de arroyos y agostadero antes de las cortinas y con ganado suelto.
2. Arroyo con serie de cortinas, fuente alternativa de agua y cercos para el control de acceso al ganado. (Año 1, construcción).
3. Mismo arroyo después de 2-3 años (con lluvias) de establecidas las cortinas. Se empieza a notar regeneración natural de zacates y vegetación debido a la humedad y suelos retenidos. Se continúa con el control de acceso al ganado y el funcionamiento de la fuente alternativa de agua.
4. Arroyo después de 2-5 años (con lluvias) de construidas las cortinas, nótese la recuperación y abundancia de zacates y vegetación detrás de las cortinas, además de la recuperación del pastizal fuera del arroyo. Con acceso controlado y rotación permanente de ganado, se empieza a aprovechar integralmente este potrero. Dibujos del Sonoran Institute.

sino el sobrepastoreo. Es más posible que ocurra un sobrepastoreo cuando el potrero es pastoreado repetidamente sin intervalos de descanso de suficiente duración para su recuperación. Las condiciones de sobrepastoreo pueden resultar también cuando se pastorean severamente tierras sensibles (como las que se caracterizan por la presencia de pendientes empinadas, suelos poco profundos, densidades vegetales bajas, etc.).

Básicamente el programa de rotación de potreros funciona llevando a cabo un plan de manejo donde se incluya la concentración del ganado en uno o dos potreros y el resto de los potreros esté sin ganado. Esto elimina que el ganado ande libremente por todo el agostadero gastando energía y esfuerzo. Es importante notar que aunado al plan de división y rotación de potreros, se debe considerar la construcción de abrevaderos apropiados y estratégicamente ubicados en cada potrero. Así sucesivamente se va rotando el ganado a los siguientes potreros, respetando la calendarización de rotación y el ciclo de regeneración del pastizal aunado a las necesidades del ganado.

Cercas. La división de potreros se realiza a través del establecimiento de cercas. Restringir el acceso selectivamente con el uso de cercas ofrece, un mayor grado de protección y mayores posibilidades de recuperación de algunos potreros en el menor tiempo. Las cercas también pueden ser usadas para dividir al pastizal ribereño u otros potreros de interés especial en unidades de manejo más pequeñas para que, por lo menos, una porción de ellas pueda dejarse en reposo cada año.

Existen algunos problemas con la instalación de cercas y, en general, no deben ser vistas como la panacea en la resolución de las dificultades asociadas con el manejo del ganado en las zonas ribereñas. El costo puede ser prohibitivo. También se deben ver los posibles efectos secundarios de cercar corredores ribereños. En especial, se pueden generar problemas serios con animales de gran talla, como lo son los venados, que muchas veces son incapaces de cruzar el cercado. Usar portalones, reducir la altura de las cercas o, incluso, bajarlas totalmente durante ciertas épocas del año, son algunas de las prácticas que

pueden reducir los impactos que tienen las cercas sobre la vida silvestre.

¿Cómo se establece un programa de división y rotación de potreros? Antes de iniciar cualquier plan de división de potreros es recomendable realizar un diagnóstico del agostadero en general. Este diagnóstico da lineamientos sobre la situación actual de cada potrero y su potencialidad de carga animal, así como de la regeneración natural del pastizal. También identifica el tipo de vegetación presente en cada potrero y la actividad de la fauna presente. Parte importante de este diagnóstico es el de dar recomendaciones de manejo para cada potrero en particular. Estas recomendaciones se basan en las condiciones actuales del terreno y la infraestructura ganadera existente. Una vez teniendo estas herramientas a la mano se procede a diseñar un plan de división de potreros si es que es necesario o a establecer el plan de manejo recomendado basándose en los expertos de manejo de pastizales y la experiencia del o los propietarios. De marcada importancia es el desarrollar la infraestructura necesaria para que el plan de rotación de parcelas funcione adecuadamente. Pero todo esto no funciona si no se tiene el compromiso de llevar a cabo el plan de manejo siguiendo la calendarización propuesta. Lo más importante de este plan es la responsabilidad de los propietarios y usuarios del terreno.

Installation of Devices in Water Tanks to Prevent Drowning of Wild Animals

(summary)

Alberto Lafón *Facultad de Zootecnia, Universidad Autónoma de Chihuahua*

Introduction

Domestic farm and ranch properties use a variety of water retention structures and water supply infrastructures that benefit wildlife. Some water supply systems, however, are harmful to wild birds, small mammals, and reptiles. Water supply systems include metal water tanks, cemented reservoirs, or excavated earthen retention ponds (or *tanques* as they are known in northern Mexico and the southwestern United States). Wildlife may drown in water tanks, when drinking, bathing or catching previously trapped animals. This problem is more common in arid and semiarid areas, where natural water sources are absent. In the last two years we have found many drowned birds-of-prey in certain well-monitored areas in Chihuahua. Drownings may be more widespread than previously believed, and as such should be addressed immediately.

La Tierra Environmental Consulting sought the support of the U.S. Fish and Wildlife Service to construct ramps in some problem areas, and it proposes the following:

- the placement of floating boards that would allow animals to access water while providing a mean to egress;
- the carrying out of informational campaigns among farm owners and workers, emphasizing the importance of saving these species, while avoiding collateral problems such as impaired water quality.

Methodology

To begin this program we spoke with farmers and requested their permission to install inclined ramps in water tanks. We started with tanks located near Aplomado falcon nesting sites, where drowned animals had been found previously. Twenty ramps were made of one-inch thick pieces of wood, one foot by six feet in dimension; these were attached to metallic steplike structures (Figures 1 to 3). Each board—treated with a sealant and having a 10-centimeter hole drilled in one end—is placed so that it is always floating near the edge of the tank. Floaters



Figure 1. Ramp structure

Figure 2. The rod, axis and counterbalance.

Figure 3. Putting in site the rod and counterbalance.

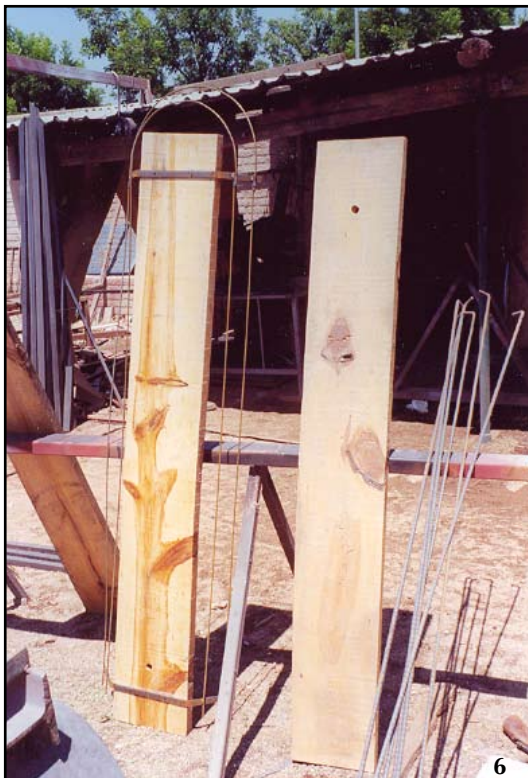
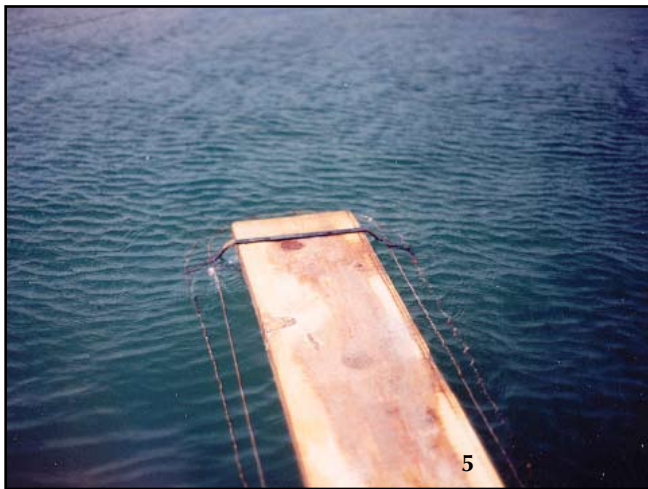


Figure 4. Attaching floaters to the ramp.

Figure 5. Floating ramp totally installed and ready to operate.

Figure 6. Ramps.

attached to the underside keep the board from sinking (Figures 4 to 6). In addition, we designed and provided a pamphlet to the *Union Ganadera Regional de Chihuahua* (Regional Ranching Union of Chihuahua) emphasizing the advantages of maintaining clean water and avoiding dead animals in the water supply.

Results

Ramps were installed primarily in tanks where drowned falcons had been found, in falcon territory, and areas frequented by falcons. Twenty ramps were installed at eight different ranches.

Conclusions and Recommendations

We conclude that these types of structures should be promoted to local agricultural associations with the intention to accomplish the following goals:

- Reduce the incidence of wildlife drowning.
- Provide birds with easy access to water supplies.
- Maintain good-quality water in water ponds due to decreased contamination by dead animals.

We recommend seeking support from people and conservation organizations that can advocate for such alternatives, needed especially where water to support wildlife is scarce.

Instalación de Estructuras Dentro de Tanques de Agua Para Evitar el Ahogamiento de Animales Silvestres

(artículo invitado)

Alberto Lafón *Facultad de Zootecnia, Universidad Autónoma de Chihuahua*

Antecedentes

Dentro de los predios ganaderos existen diferentes tipos de obras de infraestructura de retención y suministro de agua para el ganado doméstico como presones, pilas o tanques que no solo benefician al ganado sino también a una gran variedad de fauna silvestre, particularmente en zonas áridas y semiáridas. Debido a ello, muchos animales silvestres se ahogan en los tanques o pilas, lo que puede ocurrir cuando pretenden beber agua o tomar un baño en esos sitios, o tal vez en el caso de especies de aves rapaces suceda al intentar capturar a un animal que haya caído al agua y se muestre atrapado sin poder salir. Aunque estas razones aún no han sido del todo documentadas, se han obtenido muchos reportes de animales ahogados en tanques de agua, siendo los más comunes aves, pequeños mamíferos y reptiles.

Esta problemática es más evidente en zonas desérticas y semidesérticas ya que estas estructuras son probablemente los únicos lugares donde se pueda encontrar agua en muchos kilómetros a la redonda.

En los últimos dos años hemos encontrado un gran número de aves ahogadas, incluyendo seis halcones aplomados, un águila real, algunas aguilillas y lechuzas en las áreas de Sueco, Municipios de Chihuahua y Villa Ahumada, y en Tinaja Verde, Municipio de Coyame dentro del Estado de Chihuahua. Consideramos que este problema se ha hecho más notable porque esas áreas están siendo constantemente monitoreadas y debido a las condiciones de sequía que se han tenido desde hace ya más de siete años, sin embargo quizá sea un problema mucho más común y frecuente de lo que se piensa, por lo cual debe ser atendido inmediatamente.

En base a la detección de este problema La Tierra Environmental Consulting, buscó el apoyo del U. S. Fish and Wildlife Service para la construcción y colocación de las rampas en los sitios detectados como de mayor incidencia.

Y a través de una reunión de trabajo se propuso lo siguiente para mitigar este problema:

- Colocar tablas que floten para permitir a los animales tener acceso al agua para beber o bañarse y que en caso de caer al agua puedan tener un escape a través de estas estructuras.
- Hacer una campaña de información sobre este problema entre los propietarios y trabajadores de los predios, destacando la importancia de evitar pérdida de especies y los problemas colaterales que tiene como la disminución en la calidad del agua para el ganado.

Secuencia Metodológica

Para dar inicio a este programa se platicó con ganaderos y se solicitaron las autorizaciones para la colocación de rampas, iniciando en aquellos tanques de agua donde se tenían antecedentes de animales ahogados y con los que se encontraban cercanos a los sitios de anidación del proyecto halcón aplomado.

Se construyeron 20 rampas de madera de 1" x 1' x 6' a las que se colocó una estructura metálica hecha de solera de 1" y varilla pulida de 5/16, la cual tiene la función de escalera. A cada tabla se le bañó de una sustancia selladora para evitar que absorban humedad y se le hizo un agujero en uno de los extremos aproximadamente a 10 cm de la orilla, por donde la tabla se mueve libremente y en forma perpendicular sobre una varilla que funciona como guía, dicha varilla está anclada con un contrapeso en el fondo de la pila y sujeta con alambre en la parte superior. Esto permite que la rampa esté siempre flotando completamente y cerca de la orilla de la pila, evitando que se encuentre a la deriva. Además fueron colocados flotadores debajo de las rampas para asegurar que éstas no se hundan con el tiempo.

Otra medida adicional para evitar el problema de ahogamiento fue el diseño de un tríptico que fue entregado a la Unión Ganadera Regional de Chihuahua y en el cual se hacen ver las ventajas de mantener el agua de abrevaderos limpia y de evitar muertes en las fuentes de agua.



1



4



2



5



3



6

Figura 1. Estructura de escalerilla.
Figura 2. La varilla: guía y contrapeso.
Figura 3. Colocando la varilla, riel y el contrapeso.
Figura 4. Sujetando flotadores a la rampa.
Figura 5. Rampa flotando, totalmente instalada y lista para su funcionamiento.
Figura 6. Rampas.

Resultados

Para instalar las rampas primeramente se seleccionaron las pilas donde se habían encontrado halcones aplomados ahogados y posteriormente aquellas que se encuentran dentro de los territorios de los halcones y que son más frecuentadas por éstos. Se instalaron un total de 20 rampas en ocho ranchos diferentes.

La ubicación de las rampas instaladas se presenta en el siguiente cuadro:

ÁREA	RANCHO	PILA	UTM	
			ESTE	NORTE
Tinaja Verde	Santa Anita	Sur	471863	3275786
Tinaja Verde	Santa Anita	Centro	472764	3278347
Tinaja Verde	Santa Anita	Norte	472737	3281824
Tinaja Verde	Tinaja Verde	El Palomo	468686	3291519
Tinaja Verde	Tinaja Verde	La Paloma	467143	3296013
Tinaja Verde	Tinaja Verde	Pasta Toros	472302	32911722
Tinaja Verde	Tinaja Verde	TO Sur	479070	3289575
Tinaja Verde	Tinaja Verde	TO Centro	478378	3292778
Tinaja Verde	Tosesihua	En medio	461212	3295505
Sueco	Sueco	Rancho	363067	3310106
Sueco	Sueco	Cerco 1	361462	3310811
Sueco	Sueco	Cerco 2	362525	3312151
Sueco	Sueco	Escondido	363998	3306978
Sueco	La Gregoria	Primer Pila	374138	3278292
Sueco	La Gregoria	La Berrenda	372216	3277183
Sueco	Coyamito Sur	El Uno	391188	3290548
Sueco	Coyamito Sur	El 15	396957	3285645
Sueco	Coyamito Norte	Trojas	390945	3293642
Sueco	Coyamito Norte	La Lagunita	391325	3292669
Sueco	El Ágate	Matreros	388292	3301250

Conclusiones y Recomendaciones

Se puede concluir que este tipo de estructuras debería ser promovida en las diferentes asociaciones ganaderas locales con lo que pudiera esperarse los siguientes beneficios:

- Disminuir la mortalidad de fauna silvestre por ahogamiento.
- Proveer un acceso fácil al suministro de agua para aves en general.
- Mantener una buena calidad de agua en los abrevaderos debido a una menor fuente de contaminación por animales muertos.

Se recomienda la búsqueda de apoyos de personas y organizaciones de conservación que puedan impulsar este tipo de alternativas en pro de los recursos naturales.

Photo Essay: Trinchera Dams for Erosion Control and Streambed Restoration

Valer and Josiah Austin

Loose rock structures, called *trincheras* or rock curtains, can be constructed across streambeds to slow water flow, allowing water to seep into the ground. Soil and debris collect behind the rocks, forming a bed for vegetation.

Even during the dry season the soil behind these structures is wet and the grasses on the banks near them are green. Generally pools of water can be found where the water is still seeping underground.

Ruben Ruiz, author of *Harvest Rain*, a DVD about *trincheras*, or loose rock structures, stated that he hoped that “when our time comes to leave this world,... there will be thousands upon thousands of rock structures lined throughout the land we love.... [with] countless animals drinking from the pools of water contained in these structures. Our little rock monuments for the preservation of wildlife will be around long after we are gone.”

The following examples show restoration gradually evolving behind the dams.



Loose rock structures constructed across streambed.



Loose rock structure with flowing water.



Loose rock structures successfully collecting soil and generating vegetation growth.



Loose rock structures withstanding flood waters.

Foto Ensayo: Trincheras Para Controlar La Erosion y Restaurar El Cauce de Los Arroyos

Valer y Josiah Austin

Estructuras de roca, comunmente llamadas trincheras o cortinas de roca, se pueden construir perpendiculares al cauce del arroyo para retardar el flujo del agua, permitiendo que el agua se filtre en la tierra. Componentes del suelo y fragmentos de ramas se acumulan detrás de las rocas, formando sustrato para la vegetation.

Aun durante la estación seca, el suelo detrás de estas estructuras mantiene la humedad y la hierba cerca de ellas se conserva verdes. En estas tinajas o repesos generalmente se puede encontrar que todavía se está filtrando el agua subterráneamente

Ruben Ruiz, autor del video “la cosecha de la lluvia”, un DVD sobre estas trincheras, o estructuras de roca, indicó que él esperaba que: “cuando venga nuestro tiempo de dejar este mundo... habra miles y miles de trincheras alineadas en la tierra que amamos.... [con] incontables animales bebiendo de las tinajas de agua contenidas en estas estructuras. Nuestros pequeños monumentos para la preservación de la fauna estarán presentes por mucho tiempo después de que nos hayamos ido....”

Los siguientes ejemplos muestran la restauración gradual de las presas.



Trincheras perpendiculares al cauce del arroyo.



Trincheras con agua fluyendo.



Trincheras durante la corriente.



Trincheras después de la corriente.

Sustainable Ranching: A New Paradigm

(summary)

Iván Aguirre *Rancho La Inmaculada*

Today, rural communities need to take a new approach to decision-making and administration with regards to the causes and solutions to the processes of land deterioration. If the damages caused by drought, flood, and erosion were valued in monetary terms, opportunity costs, and value of human life, we would readily realize the benefits of investment in rural production methods.

In Chihuahua and Sonora, ranching is the productive activity that has the greatest impact on soil, plant, and animal communities. In Sonora, 88% of the state's surface is devoted to ranching. This land captures the majority of water ultimately available to the general population, industries, and agriculture. Thus, ranching plays a key role in the availability of water to the region. In Sonora, specifically in the municipality of Pitiquito, my family is initiating a national crusade for the conservation, restoration, and development of the rural environment.

Our efforts focus on ranching activities, based on our rural and family background, with a goal of managing ranches in common. We have a holistic vision of goals and operating procedures. We believe in civil participation and co-management as ways to achieve mutual agreements and cooperation. We also promote growth and diversity of rural economic alternatives.

Productive activities on our ranch include: raising cattle and horses, operation of grazing services, rational and selective use of forests for the production of lumber and finished wood products, utilization of mesquite pods to produce flour, and game-hunting tourism. These activities generate a variety of products and services, both domestic and environmental, that guarantee the health of our natural landscapes and are the base of our prosperity.

Our objective is to implement alternative administrative processes, and reverse the many deficiencies of traditional practices in the cattle industry. We believe that to improve our quality of life we need to be actively involved in environmental education. However, we have also learned that we do not need to compromise our ranch properties or our financial situations in order to attain sustainability on our grasslands. In order to succeed in the objectives mentioned above we need to change our habits, traditions, and culture. For instance, in ranching, the current beliefs that guide decision-making are: (1) nature is mechanical and linear; (2) allowing the land to rest helps to restore biological diversity; (3) severe grazing harms vegetation; (4) overgrazing is caused by too many animals feeding in a same area; (5) trampling is destructive to the soil and plants.

We have learned, through study and practice, that these concepts are not always true. Using a holistic point of view it is possible to see that: (1) resting land is not natural, and in many places rest causes reduction of biological diversity; (2) heavy grazing is required by some grasses and shrubs at certain points in their life cycles; (3) factors that lead to overgrazing are more related to duration of exposure between plant and herbivore, than to the quantity of herbivores in an area; and (4) trampling the ground can help restore soils, plants, and the rest of the biotic community.

Finally, we are convinced that the introduction of alternative models related to philosophy and decision-making, will reverse current environmental degradation that can be observed on many ranches.

Ganadería Sustentable: Un Nuevo Paradigma

(transcripción)

Iván Aguirre *Rancho La Inmaculada*

El deterioro del medio ambiente es un hecho real conocido por la mayor parte de la gente que tiene acceso a la información y a cierto nivel cultural. Aunque el medio rural se ve seriamente afectado por los efectos de la degradación, estos cambios son más fácilmente reconocidos por la población del medio urbano. Por lo que es clara y prioritaria la necesidad de hacer un replanteamiento a la gente del medio rural en cuanto a la toma de decisiones y administración del deterioro de las tierras, sus causas y sus soluciones.

Si los daños como las sequías, inundaciones, erosión (que en sí son solamente efectos de la pérdida de la diversidad biológica), se evalúan en términos de dinero, tomamos en cuenta el costo-beneficio de la prevención, costos de oportunidad, o el valor de la vida humana en términos salariales, observamos que tendremos mayores beneficios si cultivamos culturalmente al usuario directo del recurso del medio rural. En lugar de atacar los síntomas de la pérdida de la biodiversidad es más redituable atacar el factor que fundamenta la productividad de toda comunidad que busca sustentabilidad a largo plazo, tanto económica como familiar o social.

Reconocemos que de todas las actividades productivas que desarrollamos en los campos del noroeste de México, incluyendo Chihuahua y Sonora, la ganadería es la que ejerce la mayor influencia e impacto sobre las comunidades de suelos, plantas y animales. Estas comunidades juegan un papel preponderante en el ciclo de nutrientes, ciclo hidrológico o en el continuo flujo de energía y a su vez nos permiten llevar a cabo nuestra actividad primaria entre otras muchas más actividades.

En Sonora, estado de donde venimos, aproximadamente el 88% de la superficie del estado es de uso ganadero. La gran mayoría de estas tierras, captan y liberan, a través de escurrimientos y la recarga de acuíferos, el agua que sustenta el desarrollo de las poblaciones incluyendo la industria, la agricultura y el uso doméstico. La actividad ganadera en estas tierras juega un papel clave en la disponibilidad y estabilidad del agua. Por lo tanto el gobierno y la sociedad en su conjunto reclaman el ordenamiento de este sector rural. Pitiquito, Sonora, el municipio en donde vivimos, tiene más o menos 2 millones de hectáreas de superficie y es el tercero en México en extensión superficial. Es aquí donde queremos iniciar una cruzada nacional para la conservación, la restauración, el desarrollo rural permanente o sustentable

de nuestros recursos naturales, llámense monte, agua, suelos, plantas, animales o nosotros mismos.

Entiéndase desarrollo permanente o sustentable como aquel que permite la emancipación y desarrollo de los recursos vitales en una forma continua. De forma que podamos tener más suelos cubiertos, más variedad de vegetación, más volumen de vegetación, mayor penetración y menos escurrimiento acelerado del agua, mayor capacidad de carga animal, mayor tasa de crecimiento y regeneración de los árboles, mayores y más diversas formas de generar riqueza y generar actividades y proyectos productivos que buscan la integración y la formación de unidades de producción eficientes en términos y en relación a la reconstrucción, restauración de capital biológico o natural que nos sustentan. Conservación es la acción planeada para proteger, administrar, mantener y cuidar de los ciclos y los procesos vitales que sustentan a la comunidad o población.

Nuestro esfuerzo se basa en que somos una entidad u organización cimentada en la ganadería y estamos asociados en una empresa rural, familiar, con el propósito del manejo común de nuestros ranchos. Somos una organización con una clara visión holística con respecto a sus objetivos o procedimientos operativos. Creemos en la participación ciudadana como una forma efectiva de coger, para crear acuerdos y cooperar. Promovemos el crecimiento y la diversidad de alternativas económicas rurales. Entre algunas de las actividades productivas que promovemos en el rancho están la cría de ganado bovino, cría de caballos de trabajo, operación de servicios de maquila y pastoreo de ganado, uso racional y selectivo de los montes para la producción de madera y productos terminados como piso y cubiertas para mesa. Otras actividades productivas incluyen la utilización de las vainas del mezquite, para su transformación a una dulce y deliciosa harina integral y el turismo cinegético como la cacería planeada del venado bura. Todas estas actividades generan una variedad de productos y servicios tanto domésticos como ambientales que aseguran la salud de nuestros escenarios naturales y son la base de la riqueza que nos sustenta. En nuestro carácter de rancheros, conservacionistas, educadores, y sobre todo como administradores de pastizales y agostaderos, estamos estrechamente comprometidos a continuar facilitando la implementación de procesos administrativos alternativos a los tradicionales, ya que reconocemos

que existe un gran vacío en el conocimiento práctico contemporáneo.

También reconocemos que existe una gran necesidad de que estos modelos alternativos sean transmitidos, comunicados, e implementados para adaptar y promover el crecimiento y el mantenimiento permanente de comunidades rurales, llámense ranchos, ejidos, rancherías, etc.

En otras regiones y en diferentes foros, hemos propuesto que para mejorar nuestros valores de calidad de vida es sumamente importante que todos nos involucremos en procesos educacionales y así fortalecer los esfuerzos intergeneracionales en materia de conservación ambiental. Hemos aprendido que no tenemos que comprometer el derecho de nuestras propiedades, ni nuestro estatus financiero, ni la salud y vitalidad y sustentabilidad de nuestros agostaderos. Para cristalizar lo que acabamos de mencionar, debemos avanzar científica y prácticamente a través de cambios de hábitos, tradiciones y cultura.

Todas nuestras acciones se derivan de una base de creencias, hábitos o costumbres. Hoy en día en la ganadería y el campo hay creencias que predominan en la toma de decisiones. Como algunos ejemplos tenemos la creencia que:

- La naturaleza es mecánica y lineal y su conocimiento se puede lograr por la suma de sus partes.
- El descanso de la tierra es una situación natural y de una u otra forma va a restaurar la diversidad biológica.
- El pastoreo severo normalmente es malo para las plantas.
- El sobrepastoreo es debido a que tenemos demasiados animales pastoreando en determinada área.
- El pisoteo es destructivo para el suelo y las plantas.

Sin embargo, a través del estudio, la práctica y los hechos, hemos aprendido que existe otra realidad. El mundo natural es holístico e integral y el conocimiento de la naturaleza lo vamos a entender por medio del estudio de sus comunidades, conjuntos, patrones, poblaciones, etc. Bajo esta perspectiva ahora sabemos que:

- El descanso de la tierra no es natural, en más o menos dos terceras partes de la superficie de la tierra, tierras áridas o semiáridas donde la precipitación pluvial es

errática, el descanso provoca la simplificación de la composición biológica.

- El pastoreo severo es requerido por las mayorías de las gramíneas, herbáceas y arbustivas en algún momento de su ciclo de vida.
- Los factores que llevan al sobrepastoreo no son la cantidad de animales, sino el tiempo de exposición de la planta al herbívoro.
- El pisoteo del ganado es restaurativo para los suelos y las plantas y el resto de la comunidad biótica.

La pérdida de nuestros activos naturales biológicos es remediable y restaurable. Para finalizar, quiero citar a un pensador agrarista norteamericano llamado Wendel Berry que dice así:

“Debemos dejar a un lado nuestras convicciones supersticiosas de que podemos encontrar soluciones tecnológicas a todos nuestros problemas, por ejemplo, la pérdida del suelo es un problema que pone en ridículo todas nuestras pretensiones tecnológicas, si todo el mundo, si todo el suelo de algún lugar lo estuviéramos perdiendo en una sola carga o evento, eso atraería grandemente a los posibles héroes de la ciencia y la tecnología, quienes concertarían una solución rápida de grandes dimensiones y glamorosa, aunque pudiera causar tantos nuevos problemas al hacerlo así. Pero generalmente el suelo no lo perdemos en grandes furgones de ferrocarril o en grandes barcos de tonelaje excepcional y magnífico, el suelo se está perdiendo poco a poco, sobre millones de hectáreas, principalmente por los actos descuidados de millones de personas. No se puede salvar por hazañas heroicas de alguna tecnología gigantesca, pero solamente con millones de pequeños actos y restricciones acondicionados por pequeñas fidelidades, habilidades y deseos. Finalmente, la pérdida del suelo es un problema cultural, será corregido solamente con soluciones culturales”.

Estamos totalmente convencidos que a través de la introducción de modelos alternativos de pensamiento y toma de decisiones, vamos a revertir este proceso degradante por la cual la mayoría de los terrenos ganaderos está pasando.

Voices From the Local Communities

(summary)

Ma. Elena Baca Gómez *Consejo Regional de Turismo, Chihuahua*

Jorge Cordero *Ejido Heroína, Chihuahua*

Carmela Wallace *Rancho el Sauiz, Chihuahua*

Alberto Lafón *Universidad de Chihuahua (in behalf of other ejidatarios)*

We would have liked to hear more talks about production issues and alternative modes of production, such as the one given about ecotourism activities. However, the examples and experiences from Sonora and the United States were very useful and interesting. In a subsequent meeting, we would like to hear more about legal and organizational issues and not so much about research.

For people in rural areas conservation is not a priority, it is important but is just not as imperative as making sure there is enough money to buy food or to be able to address health and other basic needs. Conservationists seem to be more concerned about prairie dogs than people. In Mexico, conservation will not be possible if people are not taken into account. To speak about Mexican rural areas is to talk about social issues.

Many of the problems suffered in rural areas are related to a general lack of information and education. It is not possible to ask people to act differently when they do not know any better. That is why these meetings are very useful. They allow us to see alternative ways in which to do things and learn about successful examples being done elsewhere. However, we need more governmental support to be able to implement some of these proposals that you have mentioned.

Finally, there is also a real need to share knowledge between producers and researchers in order to address these issues in a better way. We invite researchers to come to our ranches and learn first hand how we conduct our work and earn our living.

Voces de Las Comunidades Locales

(transcripción)

Ma. Elena Baca Gómez *Consejo Regional de Turismo, Chihuahua*

Jorge Cordero *Ejido Heroína, Chihuahua*

Carmela Wallace *Rancho el Sauiz, Chihuahua*

Alberto Lafón *Universidad de Chihuahua (en nombre de otros ejidatarios)*

Hay algunas cosas que se hubieran querido ver y quizá este no era el foro. Por ejemplo se hubieran querido ver más pláticas sobre actividades alternativas de producción como lo que se habló de ecoturismo, los ejemplos en Sonora, o los de los ranchos en Estados Unidos. De igual manera, se hubiera querido tener información sobre aspectos legales y de organización.

Se habla de conservar cosas que en realidad para la gente local no son prioritarias, no que no sean importantes, pero no son la prioridad. Lo primero para los productores a este nivel es obtener dinero para comer, para atender problemas de salud, para vestir y luego algunas otras cosas, antes de pensar en conservación. Se hablaba de los perritos llaneros como si fueran más importantes que las comunidades rurales. En México no se podrá lograr la conservación si no se toma en cuenta a las comunidades.

Por otro lado hay un verdadero problema de falta de información y educación en la gente del campo. No podemos exigirle al ejidatario que se dé cuenta de los

verdaderos problemas si no los conoce. Hay que hablarles de formas alternativas de hacer las cosas y el por qué son las cosas. Es por eso que este tipo de reuniones con ustedes son muy buenas, porque de ellas nacen precisamente las inquietudes que debemos de analizar y de plantear aquí mismo en la región o más arriba en el gobierno.

Finalmente, es necesario estrechar los lazos de colaboración entre la gente del campo y los investigadores. Nosotros somos ganaderos, productores de la región, y algunas ideas a lo mejor a simple vista estarán peleadas con las ideas de ustedes, pero tal vez si ustedes conocieran lo nuestro no pensarían lo mismo.

Nosotros los invitamos a conocer de primera mano lo que se hace en el campo, cómo es la producción rural, cómo es un rancho, qué es el trabajo de un ganadero, para que ustedes tengan una idea palpable de lo que nosotros también hacemos, en un esfuerzo personal muy importante y tan entregado como el de ustedes, para simplemente llevar a cabo nuestra vida y darle de comer a nuestra familia.

Section IV

Update

Actualizar

An Update on Conservation in the Janos-Casas Grandes Area

Rurik List, Ph. D.

We live in a rapidly-changing world, and the Janos-Casas Grandes region is no exception. Many changes have occurred between the fall of 2001 and the spring of 2005.

During these years, agriculture has undergone strong regional development. Each year, dozens of new agricultural tracts, watered by center-pivot irrigation systems, have appeared, increasing the production of cotton, potato, chile, cereals, and beans. This growth is not regulated nor planned, factors that have generated important problems. Foremost among them, agricultural tracts are developed on any location where land can be purchased, frequently in prairie dog colonies, where the absence of trees and brush facilitates conversion into farmland. Although because prairie dogs are a protected species in Mexico, the illegal practice of converting prairie dog colonies into farmland is very common, resulting in the loss of many hectares of prime prairie dog habitat. The simultaneous increase in the number of agricultural wells creates concern among residents about the adequacy of the domestic water supply, since agricultural wells are much deeper than the wells that provide water to settlements. Ascensión, Chihuahua is now experiencing a domestic water shortage, a result of excessive industrial agriculture within the *municipio*. Since the new agriculture is high-tech, it renders direct benefits to only a small number of individuals, increasing the area's socio-economic disparity.

Another notable change in the area was the installation in 2004 of an electrical transmission line between Nacozari, Sonora and Nuevas Casas Grandes, Chihuahua.

The transmission line transects the Janos-Casas Grandes prairie dog colony, and crosses an area north of the Sierra Madre Occidental, where until now there have been no infrastructure intrusions, apart from a few roads.

During 2002 and 2003, the area underwent two additional years of drought, which, in conjunction with excessive stocking rates for drought conditions, has led to a noticeable reduction in vegetative cover. The soil has been left exposed and is susceptible to erosion from wind and water - during the infrequent rains. The reduction in vegetation appears to have had a negative effect in many bird species and on the prairie dogs, whose population has diminished noticeably, particularly during the second half of 2003 and the first half of 2004. Since the summer of 2004, rains have been abundant, creating a rapid recuperation of vegetation.

The reintroduction of black-footed ferrets has had promising results. Following the initial releases on October 2, 2001, periodic investigations indicate significant survival for released animals. In the spring of 2002, the first ferret births in Mexico were recorded. Ferret captures, undertaken to determine the animals' condition and to mark the Mexican-born offspring, indicate a fully healthy population, despite a decline in numbers during the spring of 2004, a result of the decrease in prairie dogs, the ferrets' principal source of sustenance. It is hoped that recovery of the prairie dog population will be followed by an increase in the ferret population. In the meantime, reintroduction efforts continue, with the objective of establishing a viable population of black-footed ferrets in the Janos area.

Janos-Casas Grandes a 4 Años del Taller Ecosistemas de Pastizal, Especies en Peligro y Ganadería Sustentable en la Frontera México-EE.UU

Vivimos en un mundo que está cambiando rápidamente, y la región de Janos-Casas Grandes no ha escapado a esta tendencia. Son muchos los cambios que han ocurrido desde Septiembre 30 y Octubre 2, 2001.

La agricultura ha tenido un fuerte desarrollo en la región estos últimos años, docenas de nuevos cultivos irrigados por pivote central se suman cada año a la producción de algodón, papa, chile, cereales y frijol. Este crecimiento no está regulado ni planificado, lo que ha generado problemas importantes. En primer lugar, los cultivos se están realizando en cualquier sitio en el que se ha podido comprar tierra, con frecuencia en colonias de perros llaneros ya que la ausencia de árboles y arbustos facilita la conversión a tierras agrícolas. Este fenómeno, aunque ilegal al ser los perros llaneros una especie protegida en México, es muy común, resultando en la pérdida de muchas hectáreas del característico ecosistema de los perros llaneros. Simultáneamente, el creciente número de pozos está generando preocupación entre los pobladores de la región por el abasto de agua para uso doméstico. Esto se debe a que en muchos casos la profundidad de los pozos agrícolas es mucho mayor a la de los pozos que alimentan a los pueblos, por lo que éstos pueden quedarse sin agua antes de que el agua sea insuficiente para la agricultura. En el pueblo de Ascensión ya existe desabasto de agua causado por la gran superficie de agricultura industrial establecida en ese municipio. Al ser una agricultura altamente tecnificada, los beneficios directos de esta actividad son para un reducido número de personas, por lo que el contraste socio-económico es cada vez más considerable.

Otro cambio notable en el área fue la instalación en el 2004 de una línea de transmisión eléctrica de Nacozari en Sonora a Nuevo Casas Grandes en Chihuahua, la

cual atraviesa parte del complejo de perros llaneros de Janos-Casas Grandes y cruza el norte de la Sierra Madre Occidental en un área que hasta entonces carecía de obras de infraestructura aparte de algunos caminos.

El área vivió dos años mas de sequía, del 2002 al 2003, que combinada con el mantenimiento de más ganado que el que debería estar en los terrenos del área ante las condiciones de sequía, redujo notablemente la cubierta vegetal, dejando el suelo descubierto y susceptible a la erosión del viento y del agua durante las infrecuentes lluvias. La reducida vegetación parece haber tenido un efecto negativo en muchas especies de aves y en los perros llaneros, cuyas poblaciones disminuyeron notablemente, sobre todo en la segunda mitad del 2003 y primera del 2004. Desde el verano del 2004 las lluvias han sido abundantes, por lo que la vegetación se está recuperando rápidamente.

La reintroducción de hurones de patas negras iniciada el 2 de octubre del 2001 fue muy prometedora, el seguimiento periódico mostró una importante sobrevivencia de animales liberados y en la primavera del 2002 se registraron los primeros hurones nacidos en México. Las capturas realizadas para determinar el estado de salud de los hurones y marcar a los animales nacidos en México mostraron siempre animales sanos, sin embargo, a consecuencia de la reducción en el número de perros llaneros, alimento principal de los hurones, su número declinó para la primavera de 2004. Se espera que la recuperación de los perros llaneros sea seguida por un incremento en la población de hurones, por lo tanto continuarán los esfuerzos de reintroducción, con el objetivo de establecer una población viable de hurones de patas negras en Janos.



**Crossing the border at Antelope Wells NM, USA.
Cruzando la frontera en Antelope Wells, Nuevo México,
E.E.U.U.**



**Charles Curtin and visitors at the Gray Ranch, NM.
Charles Curtin y visitantes en el Gray Ranch, Nuevo
México, E.E.U.U.**



**Artificial prairie dog burrows at the Gray Ranch.
Excavaciones artificiales de perros llaneros en el
Gray Ranch.**



**Artificial prairie dog burrows at the Gray Ranch.
Excavaciones artificiales de perros llaneros en el Gray
Ranch.**



**Lunch at the Janos field station in Chihuahua, Mexico.
Comida en el campamento de Janos, Chihuahua, México.**



**Prairie dogs at el Cuervo prairie dog colony in Chihuahua, Mexico.
Perros llaneros en la colonia de El Cuervo, Chihuahua, México.**



**Gray Ranch prairies.
Praderas del Gray Ranch.**



**Sunset at the Gray Ranch.
Ocaso en el Gray Ranch.**



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Prairie Dog Decline Reduces the Supply of Ecosystem Services and Leads to Desertification of Semiarid Grasslands

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Abstract

Anthropogenic impacts on North American grasslands, a highly endangered ecosystem, have led to declines of prairie dogs, a keystone species, over 98% of their historical range. While impacts of this loss on maintenance of grassland biodiversity have been widely documented, much less is known about the consequences on the supply of ecosystem services. Here we assessed the effect of prairie dogs in the supply of five ecosystem services by comparing grasslands currently occupied by prairie dogs, grasslands devoid of prairie dogs, and areas that used to be occupied by prairie dogs that are currently dominated by mesquite scrub. Groundwater recharge, regulation of soil erosion, regulation of soil productive potential, soil carbon storage and forage availability were consistently quantitatively or qualitatively higher in prairie dog grasslands relative to grasslands or mesquite scrub. Our findings indicate a severe loss of ecosystem services associated to the absence of prairie dogs. These findings suggest that contrary to a much publicize perception, especially in the US, prairie dogs are fundamental in maintaining grasslands and their decline have strong negative impacts in human well – being through the loss of ecosystem services.

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Introduction

Grasslands, including pastureland, croplands sown with pasture and fodder crops, shrublands, and rangelands, covered around 3.5 billion ha in 2000, which represented 26% of the world land area and 70 percent of the world agricultural area [1]. Grasslands have been heavily impacted by agricultural and other kind of fragmentation, introduction of domestic livestock and non-native species, and the suppression of natural fire regimes, which have led to the loss of biodiversity and the increased abundance of invasive species [2–4]. With the rate of grassland transformations greatly exceeding their protection, most grassland biomes are classified as being critically endangered [5]. These large-scale, land use changes are reducing the capacity of these ecosystems to maintain biodiversity [6–8].

Direct anthropogenic impacts interact with drought into driving desertification. Desertification is defined by UN as 'land degradation in arid, semiarid, and dry sub-humid areas resulting from various factors, including climatic variations and human activities' [9] and is characterized by the loss of grasses and forbs and the rapid expansion of shrubs such as mesquite (*Prosopis glandulosa*) [10]. Land degradation is dependent on biophysical and socioeconomic factors, the interactions between them, and their spatial and temporal scales of influence. Some of the biophysical

factors that play a key role in worldwide grasslands are the spatial distribution, soil fertility and stability, seed viability, species diversity, shrub encroachment, irrigation water, gully formation, soil erosion and composition of functional groups. On the other hand, the principal socioeconomic factors involved are labor needs, access to irrigation water, crop storage, education, access to government aid programs, selling or renting lands, conflict resolution, access to drinking water, population size, land planning, overexploitation of the resources, livestock and crops market, and migration [9].

The direct and indirect anthropogenic degradation of grasslands is likely to have paramount impacts on societies through the decline of their ability to supply key ecosystem services that are relevant to local, regional and global stakeholders. Grasslands play a key role in food production, through beef livestock production, which was 58 000 million tons in 2008 [1] as well as their transformation to agriculture, which accounts 20% of the historical area covered by world's native grasslands [11]. Grasslands are also important for ecosystem services such as carbon storage and sequestration, estimated at approximately 34% of the global stock of carbon in terrestrial ecosystems; water infiltration and aquifer recharge; the provision of biofuels, as well as recreation [12].

Changes in the ability of grasslands to supply fundamental ecosystem services depend on complex interactions between their abiotic and biotic components, as well as their interactions with societies. Such changes are likely linked to changes in the presence of keystone species, those that have a much larger role in the structure and function of the ecosystem than expected by their abundance [13]. One of such species is the black-tailed prairie dog (*Cynomys ludovicianus*) which its geographic range once extended from southern Canada to northern Mexico; however, the species has disappeared from 98% of their original distribution range [14].

Prairie dogs are keystone species and an ecosystem engineer and are essential in maintaining grasslands at three levels: a) as ecosystem engineers they have a great impact on the physical, chemical and biological soil properties; through the construction of their burrows they aerate the soil, redistribute nutrients, add organic matter and increase the water infiltration [15,16], b) with their foraging and burrowing activities they create unique islands of grassland habitat by maintaining a low, dense turf of forbs and grazing-tolerant grasses, contributing to the maintenance of the open grassland habitat and preventing the growth of woody plants [17–21], and c) they provide key habitat for many grassland animals, enhance the nutritional quality of forage, which attracts large herbivores to their colonies, and provide important prey for predators [18,19,22,23]; as a component in the food chain ensure the existence of certain carnivores that depend on it, such as the black-footed ferret (*Mustela nigripes*). In addition, their burrows are important refuges for species of amphibians, reptiles, birds and other mammals [15,16,24]. The negative impacts of prairie dogs extirpation are, among many others, the regional and local biodiversity loss [24,25], the increased seed depredation [26], and the promotion, establishment and persistence of invasive shrubs [10].

One of the largest black-tailed prairie dog complex have persisted in the grasslands of Janos biosphere reserve, northwestern Chihuahua, Mexico, which is one of the most important sites for conservation of the grasslands of North America [27–29]. These colonies survived because until the late 1990's the region lacked electricity and the local communities dominated by fundamental Mennonite communities refused to use modern technological methods for agriculture [30,31]. Unfortunately, that changed and grassland degradation in the Janos region has been accentuated in recent years, due to the acceptance of modern agricultural methods that have led to encroachment by agriculture and livestock overgrazing, the illegal exploitation of aquifers, suppression of fire regimes, and wildlife eradication [2]. Despite these anthropogenic pressures on the ecosystem, there are still large areas with prairie dogs colonies that have become the most important element for the conservation of this ecosystem and its species. The large extension of the prairie dog complex in the Janos region has provided us with a unique opportunity to evaluate the role of prairie dogs in the structure, function, and conservation of semiarid grasslands [2,15,27]. In this work we assess the role played by the black-tailed prairie dog in the supply of the key ecosystem services from grasslands.

We carried out our study in the Janos Biosphere Reserve because it supports a large prairie dog population, but also harbors areas in which the species has been recently extirpated giving rise to pastures and to areas dominated by mesquite. We investigate the effect of prairie dogs on five ecosystem services, including groundwater recharge, regulation of soil erosion, regulation of soil productive potential, soil carbon storage and forage availability. Specifically, we address the following questions: 1) What is the scope of the ecosystem services in the prairie dog grasslands? 2) How does supply of such ecosystem services change when prairie

dogs have become locally extinct and grasslands or mesquite scrub have developed? 3) What are the conservation implications of the presence (or absence) of prairie dogs and ecosystem services to human well being?

Methods

Study Site

The study was conducted in the black-tailed prairie dog complex located in the Janos Municipality in northwestern portion of the Mexican state of Chihuahua. The arid grasslands supporting these colonies extend northeast of the Sierra Madre Occidental to 75 km south of the U.S.-Mexico border (30° 50'N, 108° 24'W; Figure 1). The elevation is 1400 m above the sea level with the topography characterized by expansive arid plains with slopes of less than 5% and bounded by ridges and hills with 12 to 30% slopes [32]. According to the Köppen climate classification, modified by Garcia [33] the climate is arid (BSokw (e')). The temperatures range from 15°C in winter to 50°C in summer, with a mean annual temperature of 15.7°C [33]. The mean annual precipitation for this region is 307 mm [33] and displays bi-modal patterns, raining during the winter and summer growing season (July through September). The area receives occasional snowfall during the winter, with the spring (March–June) being characteristically dry with frequent high winds from the southwest. Humidity is low during most of the year [33].

The vegetation is dominated by a mixture of forbs and annual grasses with patches of perennial grasses in grasslands with and

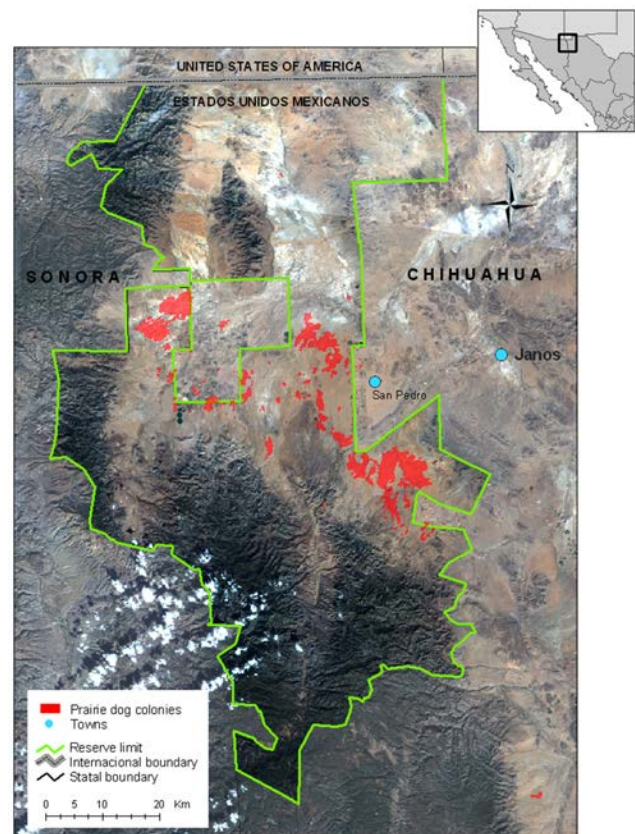


Figure 1. The study area was located in the Janos Biosphere Reserve, in northern Chihuahua, close to the Mexico – US (New Mexico) international border.

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without prairie dogs, and by mesquite shrubs in shrubs sites. Dominant species across the region include *Aristida adscensionis*, *Aristida divaricata*, *Bouteloua aristoides*, *Bouteloua gracilis*, *Bouteloua eriopoda*, *Prosopis glandulosa*, *Festuca imbricata*, *Pleuraphis mutica*, *Opuntia imbricata*, *Yucca canerosana* and *Ephedra trifurca* [32].

Characterization of the study area. Sites with similar soil and landform features but contrasting land cover resulting from prairie dog extirpation were identified, by analyzing topographic (Carta topografica Nacozari H12-6 1:250,000) and soil maps (Carta edafologica Nacozari H12-6 1:250,000) of the area. To assess the physical soil features of selected sites 36 soil drillings and 12 pits (2 m depth, 3 m length) were made. Soil samples were taken in each horizon for laboratory analyses. The dominant landform in the study area is the arid alluvial fans with sporadic runoff and little deposition. The dominant soil in the region, according to the classification of the Soil Survey Staff [34], is the Mollisol represented by two main groups: Argiustols and Haplustols.

Treatments and local plots. Three contrasting conditions (hereinafter called “treatments”) were identified along a successional continuum associated to prairie dog extirpation: grasslands currently occupied by prairie dog (prairie dog grasslands); grasslands occupied by prairie dogs 10 years ago (grassland), and grasslands previously occupied by prairie dogs (roughly 10 years ago) and currently dominated by mesquite (mesquite). Six 50×50 m plots were established for each treatment within the continuum for a total of 18 plots; all of them were in mollisols at the lower margins of the alluvial fan and with a minimum distance between them of one kilometer to ensure the plots were independent. Within each plot, three 50×1 m transects length were systematically positioned at 16 m intervals. Measurements were collected during the spring of 2010.

Evaluation of Ecosystem Services

The ecosystem or environmental services evaluated were groundwater recharge, regulation of soil erosion, regulation of soil productive potential, soil carbon storage and forage availability. We evaluated them as follows:

Groundwater recharge. Water infiltration was defined as the rate at which water enters the soil and is relevant to groundwater recharge. Groundwater is the main source of water for agricultural activities in the area [2]. Water infiltration was measured using the single-ring infiltrometer method [35]. A fixed volume of water (50 mm) is poured on a soil area under saturated conditions and the time needed for the total amount of water to enter the soil is recorded. The infiltrometers were systematically positioned every 10 m along the 3 transects within each plot, in a total of 15 points of measurement per plot. In the case of the mesquite treatment and according to the transects, the infiltrometers were randomly placed both under shrubs and interspaces between mesquites.

Regulation of soil erosion. Regulation of soil erosion was defined as the absence of evidences of soil erosion, and is a key service to owners of the plots. Soil erosion was assessed based on two evaluations:

a) Soil erosion indicators

- The presence or absence and intensity of nine qualitative soil erosion indicators were assessed following the Pellant et al. protocol [36]. The indicators included the presence of: a) rills, b) water flow patterns, c) pedestals and/or terracettes, d) bare ground, e) gullies, f) wind depositional areas, g) litter movement, h) soil surface resistance to erosion, and i) soil

surface loss or degradation. For each of the indicators a rank value was provided based on their qualitative intensity: none to slight (ranking value = 1), slight to moderate (2), moderate (3), moderate to extreme (4), extreme to total (5). A synthetic index was built with the sum of all ranking values for each of the nine indicators. Lower values indicated greater soil stability.

b) Soil protection through land cover

- Four classes of land cover were evaluated: plant, litter, rocks, and bare ground using a 50 m line-point-intercept [35] with point observations obtained every 50 cm, for a total of 100 readings per line and 300 readings per plot. Plant life-forms cover was also evaluated; the frequency of observations for each species was recorded with each one assigned to a specific life-form group (annual herbs, perennial herbs, annual grasses, perennial grasses and shrubs). The amount of grasses and herbs is a measure of habitat condition, with the greater the abundance of grasses, the better the habitat quality.

Regulation of soil productive potential. Regulation of soil productive potential was defined as the inverse of soil compaction; this is a key service to plot owners and to the inhabitants of the regions as it is associated to the regulation of soil productive potential, in particular to the development of radicular systems [37], as well as to the role played by soils in the regulation of runoff and infiltration [38].

Regulation of soil structure was measured using a static cone penetrometer Rimik CP20. Ten lectures, randomly established per plot, were taken to measure the resistance to penetration in KPa and to a maximum depth of 60 cm. In the case of the mesquite treatment, five lectures were taken under the shrubs and the other five in the interspaces. The higher the penetration the smaller the compaction.

Soil carbon storage. Soil carbon storage was defined as soil carbon content per unit volume of soils; this is a key service to the global community, given that grasslands are an important reservoir of carbon according to their worldwide extension.

Soil carbon content was assessed in three soil pits (2 m depth and 3 m length) per treatment. Soil samples (150 gr.) from the different horizons of each profile were taken and then analyzed with the Elemental Analyzer CHNS/O Perkin Elmer 2400 series II. An edaphoecological evaluation was conducted to obtain additional information of soils physical features to calculate carbon sequestration [39].

Forage availability. Forage was defined as the amount of forbs and grass biomass per unit area; the amount of total potential biomass to be consumed by cattle is a key ecosystem service to local ranchers.

To determine the amount of forbs and grass biomass for each class, six $\frac{1}{4}$ m² (50×50 cm) quadrants were clipped by species along each transect at a height of 1 cm of above the soil surface, placed in labeled paper bags, dried in a forced air oven at a temperature of 58°C for 48 hours, air equilibrated, then weighed. Dr. Toutha Lebgue Keleng, curator of the University of Chihuahua (UACH) herbarium, verified plant identification.

All the permissions and permits required for the fieldwork were requested and authorized by the private landowners, Janos municipality, communal land owners, and by the administration of The Nature Conservancy Ecological Reserve “El Uno”.

Data Analysis

The assumptions of data normality were assessed using the Shapiro-Wilks modified test. Data were analyzed using InfoStat program [40]. To determine differences in water infiltration and soil productive potential between treatments, a Kruskal-Wallis test was used followed by post-hoc multiple comparison test (Dunn's method) [41]. For differences in soil erosion between treatments a contingency table was used followed by a correspondence analysis. For soil carbon storage Friedman two way non parametric test was used to determine differences between treatments and also a Kruskal-Wallis test was used to determine differences in soil carbon storage between horizons. To determine the differences between treatments in terms of soil protection through land cover an ANOVA test was performed followed by Tukey post-hoc multiple comparison test; also, Kruskal-Wallis test was performed to test differences according to plant life-forms cover followed by post-hoc multiple comparison test [41]. Finally, for test differences in forage biomass between treatments an ANOVA followed by Tukey post-hoc multiple comparison tests were performed.

Results

In summary, our results indicate that black-tailed prairie dogs played an important role in providing ecosystem services. Grasslands with populations of prairie dogs (prairie dog grasslands hereafter) showed a higher supply of all the ecosystem services assessed here relative to areas devoid of prairie dogs that are now dominated by grasses (grasslands hereafter) or scrublands dominated by mesquite (mesquite hereafter). Prairie dogs had a very strong positive effect on the supply of groundwater recharge, regulation of soil erosion, regulation of soil productive potential, soil carbon storage, and forage (Figure 2).

Groundwater Recharge

Prairie dogs were associated to habitats with higher water infiltration. Water infiltration rates were highest in prairie dog grasslands (357 ± 288.45 mm/hour), followed by those of

grasslands (283 ± 194.36 mm/hour), and mesquite (97 ± 77.82 mm/hour; Kruskal-Wallis $H = 108.48$ d.f. = 2 $P < 0.0001$; Figure 3). Mesquite differed significantly from prairie dog grasslands and grasslands but these two did not differ between each other (multiple comparison: $D_{i,j} = 9.790$, $D_{i,j} = 7.973$, $D_{i,j} = 1.817$).

Regulation of Soil Erosion

a) Soil erosion indicators. Soil stability and erosion indicators, such as bare ground, litter movement, and water flow patterns, showed that mesquite scrubland soils were the least stable and more prone to soil erosion (overall ranking value = 55 points) than prairie dog grasslands (overall ranking value = 22) and grasslands (overall ranking value = 14; Table S1). The differences in erosion indicators (e.g. bare ground) were statistically significant among treatments ($X^2 = 25.14$ $P = 0.0015$). A correspondence analysis also showed that grasslands with and without prairie dogs were classified in the slight to moderate rating category, indicating that those plant communities are better in preventing soil erosion and had greater soil stability than mesquite scrubs, which were classified in the extreme categories (Figure S1).

b) Soil protection through land cover. Plant cover within the prairie dog grasslands (66%) and grasslands (64%) tended to be greater than mesquite scrubs (51%); however, these values were not significantly different (ANOVA $F = 1.51$ d.f. = 2 $P = 0.2534$; Figure 4). A related metric (percentage of bare ground) was significantly different between grasslands (13%) and the other treatments, prairie dog grasslands (18%) and mesquite scrub (33%), but the latter were not statistically different (ANOVA $F = 4.67$ d.f. = 2 $P = 0.0265$; multiple comparison: Tukey $MSD = 47.51196$; Figure 4). Percentage cover by class of plant life-forms (annual forbs, perennial forbs, shrubs, annual grasses and perennial grasses) varied across the treatments (Kruskal-Wallis $H = 18.54$ d.f. = 2 $P < 0.0001$). Annual forbs was the most abundant plant-life form (multiple comparison: $P = 0.03$), being statistically different within grasslands (80.2%; Kruskal-Wallis $H = 7.21$ d.f. = 4 $P = 0.0154$; multiple comparison: $P = 0.03$) and

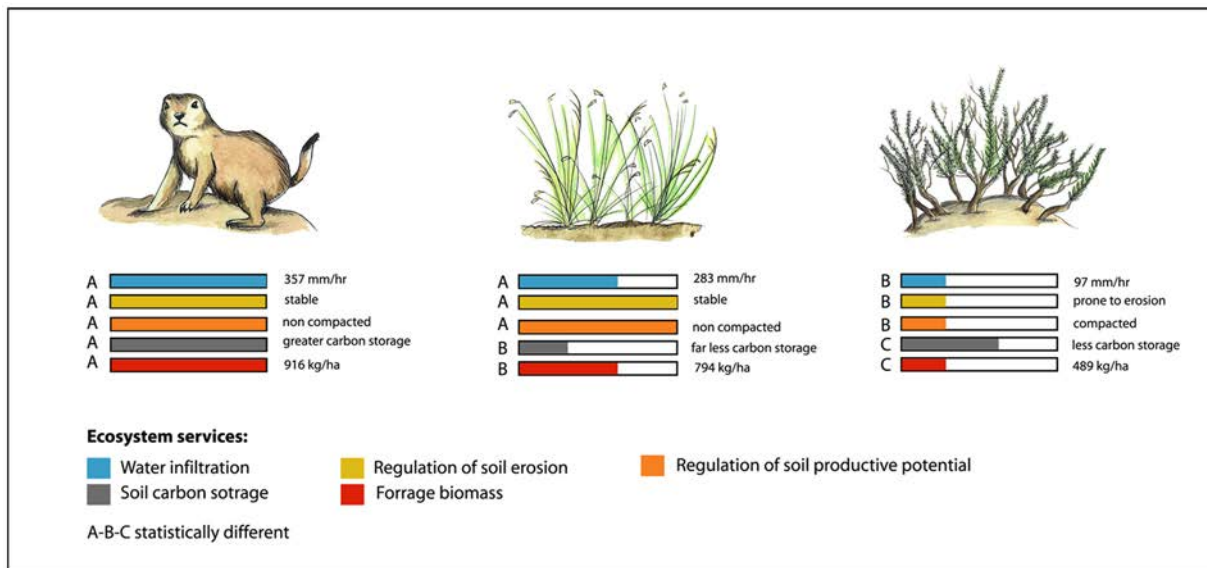


Figure 2. Ecosystem services were evaluated in grasslands with prairie dogs, grasslands and mesquite scrubs that have lost prairie dog colonies in the last 10 years, in the Janos region, Chihuahua, Mexico. Our results clearly show the positive effect of prairie dogs on the provision of these ecosystem services. Color bars indicate the relative magnitude of each of the services in the different treatments with respect to grasslands with prairie dogs.
 doi:10.1371/journal.pone.0075229.g002

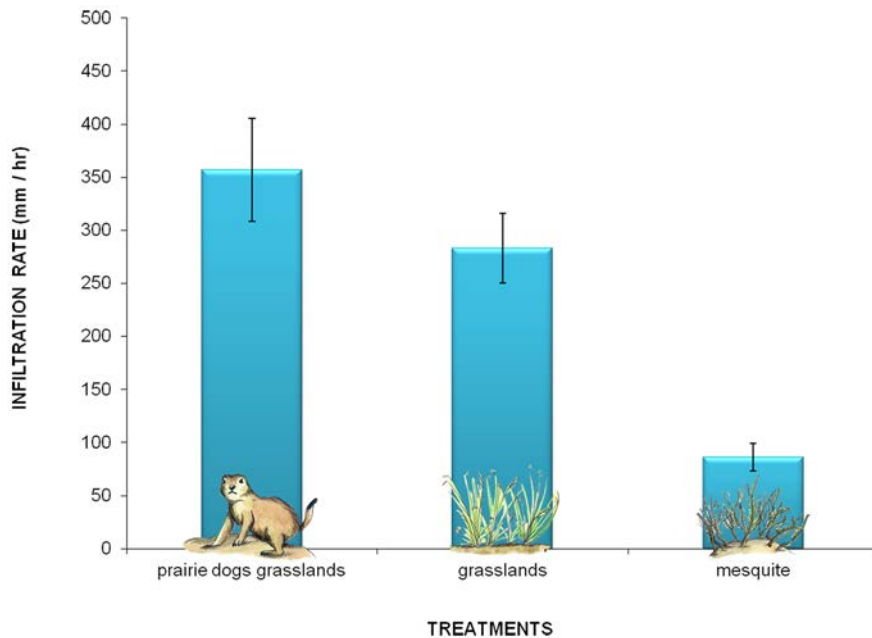


Figure 3. Groundwater recharge variation among treatments in the Janos region, Chihuahua, Mexico. Related to the foraging and burrowing activities of prairie dogs, among other physical and biological factors, the supply of this service was statistically higher in grasslands with prairie dogs than in grasslands and mesquite.
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prairie dog grasslands (85.5%; Kruskal–Wallis $H = 21.76$ d.f. = 4 $P < 0.0001$; multiple comparison: $P = 0.002$) but not within mesquite treatment (60.4%). Perennial grass cover was minimal in all treatments with average estimates of 1% of total plant cover for prairie dog grasslands and grasslands, and 7% of the mesquite scrubs. The low values for perennial grasses may be due to a 15-year drought and overgrazing [42]. Finally, shrub cover was much greater in mesquite treatment (15%) compared to the prairie dog grasslands and grasslands where prairie dogs were absent (Figure S2).

Regulation of Soil Productive Potential

Soil productive potential was negatively affected in mesquite scrubland, which had soils that were more compacted up to a depth of 60 cm compared to grasslands and prairie dog grasslands. These two treatments were statistically different from the mesquite treatment (Kruskal–Wallis $H = 68.35$ d.f. = 2 $P < 0.0001$; multiple comparison: $P < 0.0001$; Figure 5).

Soil Carbon Storage

Carbon storage is related to soil productivity and carbon emissions. In our study, soil carbon storage was greater in prairie dog grasslands followed by mesquite scrubs and then by grasslands (Kruskal–Wallis $H = 6.26$ d.f. = 2 $P = 0.0436$). Within treatments, carbon concentrations were statistically larger in deeper horizons in prairie dog grasslands (Kruskal–Wallis $H = 9.83$ $P = 0.0433$). However mesquite scrub and grasslands had similar values in all horizons (Kruskal–Wallis $H = 3.40$ $P = 0.1394$ $H = 1.56$ $P = 0.6676$, respectively; Table S2). We used a two-way ANOVA to evaluate the interactions between treatments and depth effect and we found no differences between them (Friedman $T^2 = 1.34$ $P = 0.2855$). When the prairie dog grasslands are converted into grasslands carbon storage is reduced. Carbon storage in mesquite scrubland was slightly smaller than prairie dog grasslands, indicating that mesquite scrublands may also mitigate carbon

emission but this service is negatively affected because of the presence of empty soil interspaces that have minimum carbon storage.

Forage Availability

Standing biomass, available to cattle as forage, was greater in prairie dog grasslands (916 ± 932.60 kg/ha) when compared with grasslands (794 ± 766.04 kg/ha) and mesquite scrubs (489 ± 524.45 kg/ha) (ANOVA $F = 6.80$ d.f. = 2 $P = 0.0013$; multiple comparison: Tukey MSD = 254.56; Figure 6).

Discussion

Our results clearly demonstrate a strong link between prairie dogs and the provision of ecosystem services. In general, prairie dogs influenced the structure and function of the plant communities as an outcome of their feeding and burrowing activities and such impact positively affects the provision of a wide range of ecosystem services linked to both abiotic and biotic characteristics. Some of these effects have been previously reported for a variety of habitats within the black-tailed prairie dogs' historic geographic range e.g. [13,24,25]. However, this is the first study that explicitly quantifies the effect of prairie dogs on specific ecosystem services. Prairie dogs support key regional socio-economic activities and are therefore directly related to human well-being. For instance, livestock benefits from cattle foraging on the edges of prairie dog colonies because of forage quality (Sierra, unpublished data). Thus, our study has strong implications for the conservation of the prairie dog in the grasslands of northern Mexico and adjacent southwestern USA.

The distribution of black-tailed prairie dogs has been greatly reduced because of habitat transformation into crops and by direct extermination by shooting and poisoning [17,43]. Black – tailed prairie dogs can reach high densities and are believed to compete with cattle for forage, but there is increasing evidence that under

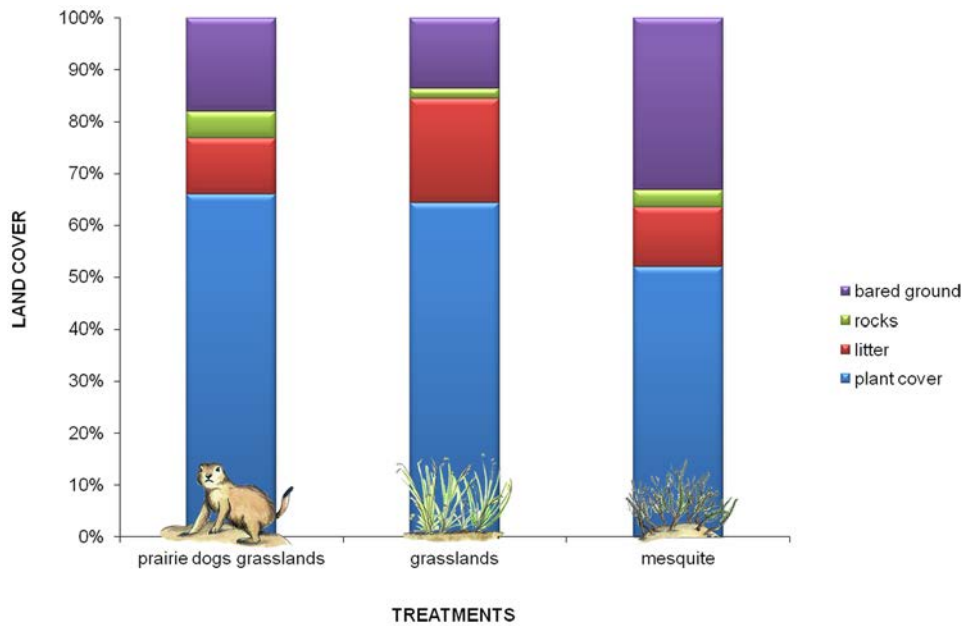


Figure 4. Variation in the regulation of soil erosion among treatments in the Janos region, Chihuahua, Mexico. Soils in prairie dog grasslands were less prone to erosion, because they showed more than 60% of plant cover, while mesquite soils had more than 30% bared and prone to erosion.
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suitable management both species can benefit. A similar case occurred with prairie dogs and bison (*Bison bison*) years ago. Bison prefers feeding on the edges of the colonies where forage quality was better, and at the same time their movements and foraging,

allowed prairie dogs to colonize other grassland areas [44; Sierra, unpublished data].

The ecosystem services related to prairie dog presence can be attributed to higher primary productivity that benefit cattle and

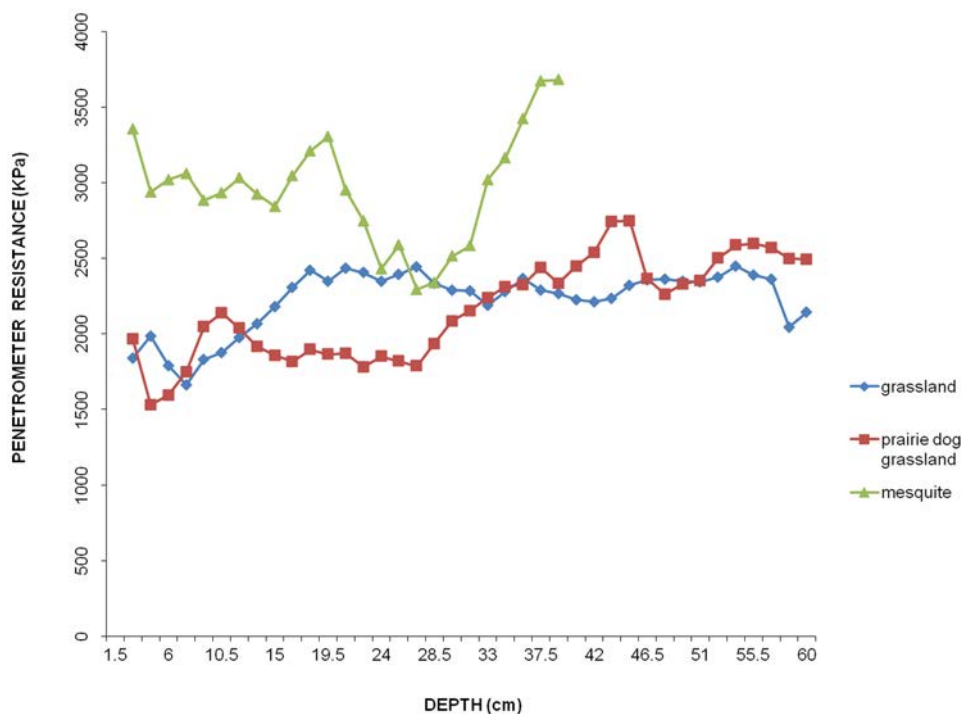


Figure 5. Regulation of soil productive potential service among treatments in the Janos region, Chihuahua, Mexico. Penetration resistance was higher in mesquite scrubs sites when compared with prairie dog grasslands and grasslands, indicating that soils are more compacted making more difficult the establishment of herbs and grasses.
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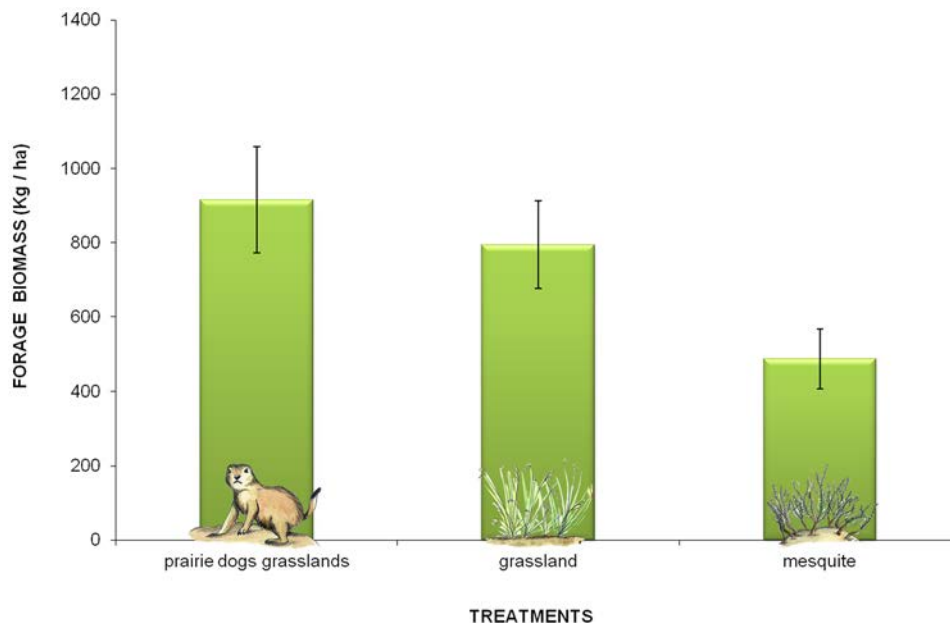


Figure 6. Forage availability among treatments in the Janos region, Chihuahua, Mexico. Contrary to a common lay and scientific assumption, forage availability was statistically higher in grasslands with prairie dogs than in grasslands and mesquite scrubs. doi:10.1371/journal.pone.0075229.g006

improved soil stability, with the attendant benefits of lower risk of erosion, flooding and desertification [see also 2, 20]. Recent studies have shown similar beneficial relationships by other small mammals, such as marmots and pikas, which act as keystone species in the maintenance of grasslands in different regions of the northern hemisphere [16,21,43].

The provision of ecosystem services by black-tailed prairie dogs is through complex interactions that we are only beginning to unravel. Soils within prairie dog grasslands are less compacted than soils within sites dominated by mesquite; they have more pore spaces needed for aeration and water movement within the soil profile, and have better conditions that improve their stability. These soil conditions increase water infiltration, a critical process in these semiarid grasslands where annual rainfall is less than 600 mm and ecological processes are governed by pulses of water [45]. The span of these pulsed inputs of water (summer rains are shorter than winter rains) affects nutrient cycles because the capacity of microbiota to decompose the organic matter and the ability of plants to use the nutrients depends on water availability [46]. Although nutrient turnover is a complex process depending on factors such as soil texture, vegetation patch structure, soil biota, and climate, the synchrony between nutrient availability and the capacity of plants to use available nutrients may be enhanced by prairie dog activities that increase infiltration.

The increase in soil water and prairie dog grazing improves forage production for cattle, which was demonstrated by our results on plant cover, and was consistent with data reported in the literature e.g. [47]. Aboveground plant production increases with moderate grazing because it accelerates the rates of mineralization of inorganic nutrients [47]. In addition, grazer like prairie dogs remove senescent leaves that decrease light and soil water for younger and more active tissues that also have greater nutrient concentrations for herbivores. Then herbivores can improve harvesting efficiency in terms of available nutrients per bite, and bites per minute, and increase the diversity and productivity in the grasslands [17,48]. In contrast, mesquite encroachment affects water infiltration and drainage, and limits the soil's capacity to

support the grasses and forbs needed by native herbivores and economically important livestock species. Soils in mesquite scrubs are compacted and have crusts on the surface; such features are associated with land degradation, reduced yield of useable forage and increasing surface water runoff and flooding [10,49]. Increased provisions of forage benefit local people by reducing cost of supplemental feeds and for improving the vigor of forage species. In the Janos region, 78% of the land is used for grazing.

From a global perspective, the maintenance of prairie dog grasslands mitigates impending climate change by storing atmospheric carbon. Semiarid grasslands, which cover 9 million km² in temperate regions, store from 10 and up to 30% of world soil carbon [50]. Grasslands converted to agricultural practices typically release soil carbon to the atmosphere and continued tillage of grasslands for intensive agriculture can compound the existing problem of atmospheric carbon pollution.

The loss of the black-tailed prairie dog resulting in the transition to a desertified mesquite scrub, negatively impact the landscape's ability to provide ecosystem services essential for local and regional natural communities and human well-being. In the Janos region, over the last 10 years, grasslands have lost more than 47,000 ha of ground cover, bare ground with no plant cover has increased from 6,645 ha to 152,123 ha, 73% of the 55,000 ha of prairie dog colonies have been lost and mesquite and ephedra (*Ephedra trifurca*) shrubs have encroached grass areas [2,51].

The fact that some of the services evaluated did not show significant differences between treatments is likely explained due to the low densities of prairie dogs. The region has experienced an intense drought period (1995-to date), that accelerated land degradation processes and therefore the decline of prairie dogs. These conditions have diminished the role of prairie dogs in shaping the structure and function of their environment. Nevertheless, the differences in our data suggest that prairie dog populations within a given density are the main driver in the maintenance and improvement of the ecosystem services evaluated. Is clear that is necessary to preserve prairie dog populations ecologically functional for maintaining these services on the long term.

Our conservation work on the Janos grasslands focuses on developing strategies with local and state governments to maintain and restore grasslands, their biodiversity, and the ecosystem services they provide. Prairie dog management to prevent desertification resulting from mesquite replacement of native grasslands is cost-effective, relative to the high cost (US \$58 per ha) for the removal of mesquite and grassland restoration [52]. A major challenge for the long-term conservation of the prairie dogs is the implementation of adequate management practices with cattle grazing and agriculture. We are developing novel techniques to couple the management of prairie dogs and cattle to maintain the grasslands, the intensive agriculture, and to restore mesquite scrubland in to grasslands.

Today's environmental challenges require an understanding of the processes of ecosystems and wildlife populations and an ability to integrate scientific research into decision-making. Ecologists and conservation biologists must adopt this approach if we are to preserve the world's biodiversity. To this end, the Janos Biosphere Reserve in Mexico is a global modal of commitment to the conservation of grasslands and their biodiversity.

Supporting Information

Figure S1 Regulation of soil erosion service. Soil erosion indicators demonstrated that mesquite soils are more prone to erosion (extreme categories) when compared with prairie dog grasslands and grasslands (slight categories). (TIF)

Figure S2 Regulation of soil erosion service. Forbs are the predominant plant life-form in prairie dog grasslands, grasslands and mesquite scrubs, being prairie dog grasslands the treatment with more percentage of them. (TIF)

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Table S1 Presence and intensity of the qualitative indicators of soil erosion.

(DOC)

Table S2 Carbon sequestration in grasslands, prairie dog grasslands and mesquite scrubs.

(DOC)

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Author Contributions

Conceived and designed the experiments: LME PB GC. Performed the experiments: LME JP. Analyzed the data: LME PB JP GC. Contributed reagents/materials/analysis tools: LME PB JP GC. Wrote the paper: LME PB GC.

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Prairie Dogs: An Ecological Review and Current Biopolitics

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ABSTRACT In recent years, people have interpreted scientific information about the black-tailed prairie dog (*Cynomys ludovicianus*) in various, and sometimes conflicting, ways. Political complexity around the relationship among black-tailed prairie dogs, agricultural interests, and wildlife has increased in recent years, particularly when prairie dogs occur on publicly owned lands leased to private entities for livestock grazing. Some have proposed that estimates of prairie dog (*Cynomys* spp.) numbers from 1900 are inflated, that prairie dog grazing is not unique (other grazers have similar effects on vegetation), and that prairie dogs significantly reduce carrying capacity for livestock and wildlife. We address all these issues but concentrate on the degree of competition between prairie dogs and ungulates because this motivates most prairie dog control actions. We conclude that the available information does not justify holding distribution and numbers of prairie dogs at a level that is too low to perform their keystone ecological function. We further conclude that it is especially important that prairie dogs be sufficiently abundant on public lands to perform this function. (JOURNAL OF WILDLIFE MANAGEMENT 71(8):2801–2810; 2007)

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KEY WORDS black-tailed prairie dog, competition, *Cynomys ludovicianus*, dietary overlap, grazing, population trend.

In recent years, people have interpreted scientific information about the black-tailed prairie dog (*Cynomys ludovicianus*) in varying ways. We expect this in review papers, as the authors often interpret the work of others and base conclusions on inconclusive historical data. With high-profile species, these differences can fuel contentious political battles. We discuss the ecological role of a politically charged species, the black-tailed prairie dog, and the relationship between prairie dogs, other wildlife species, and livestock. As conservation biologists, we seek a broader scientific understanding for use by resource managers.

In recent years the political complexity has increased over the relationship among black-tailed prairie dogs, agricultural interests, and wildlife (see Hoogland 2006). This is particularly true on publicly owned land leased to private entities for livestock grazing. Biologists agree that prairie dogs greatly declined in numbers over the last 2 centuries but disagree over the magnitude of the decline (Vermeire et al. 2004, Forrest 2005, Proctor et al. 2006). Interests responsive to agricultural concerns tend to emphasize evidence that minimizes the level of decline, whereas interests concerned with the ecological role of prairie dogs frequently emphasize evidence supporting higher levels of decline (up to 98%; Proctor et al. 2006). Some advocates of

the agricultural industry actively promote management of public lands in ways designed to benefit the livestock industry (South Dakota Department of Game, Fish, and Parks and South Dakota Department of Agriculture 2002, Johnson-Nistler et al. 2004, Cooper and Gabriel 2005). Conversely, conservationists propose reduced livestock grazing on public lands in the interest of conservation of native wildlife species.

Vermeire et al. (2004) concluded that estimates of prairie dog (*Cynomys* spp.) numbers from 1900 are inflated because of overgrazing by cattle and drought during the 1880s and 1890s. Because tall, dense vegetation impedes prairie dog colony expansion (Snell and Hlavacek 1980, Cable and Timm 1988), these conditions permitted prairie dog colonies to grow given the low vegetation cover. These authors contend that lower (uninflated) estimates justify maintaining lower numbers of prairie dogs today, that prairie dog grazing is not unique among herbivore species (i.e., other herbivores could substitute for prairie dog grazing), and that prairie dogs reduce carrying capacity for livestock and other wildlife. In rebuttal of the first point, Forrest (2005; see also Proctor et al. 2006) provided evidence that historical estimates of prairie dog numbers were not inflated. Several researchers convincingly contradicted the second point, that prairie dog grazing is not unique (Whicker and Detling 1988, Sharps and Uresk 1990, Kotliar et al. 1999, Kotliar 2000, Miller et al. 2000).

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Resolutions adopted by the Society of Conservation Biology (1994) and the American Society of Mammalogists (1998) also acknowledge the importance of prairie dogs. We mainly address the third point, the level of competition between prairie dogs and large ungulates, and we offer some information on costs vs. benefits of poisoning. Additionally, we also discuss the first 2 points primarily as they refer to the issue of competition.

COMPETITION BETWEEN PRAIRIE DOGS AND LARGE UNGULATES

Ecological Effects of Competition

We follow Ricklefs and Miller (2000:384) in defining competition as resulting “when many species seek the same resources, and the depressing effect that each one has on the availability of the shared resources adversely affects the others.” Cattle and black-tailed prairie dogs exhibit a high dietary overlap—up to 60% in a mid-grass prairie and 64% in a short-grass prairie (Hansen and Gold 1977; Uresk 1984, 1986). Competition, however, does not necessarily occur simply because 2 species use the same resource. Competition exists when species A is worse off because of the activities by species B, and vice versa. Thus, cattle and prairie dogs may seek the same resources, but diet overlap alone does not prove that either species is adversely affected.

Demonstrating competition is difficult in natural systems. First, there is an issue of scale. High competition may occur in localized cases (e.g., a single ranch), but when considering larger landscapes the actual level of competition may become insignificant. Second, although prairie dogs clearly reduce plant biomass, debate remains about the impact to other grazers because of increases in forage quality as a result of prairie dog activities. It appears that the degree of compensation is highly situational (see Curtin 2006, Derner et al. 2006, Detling 2006). Third, presence and level of competition among species can vary across geographical area (e.g., differences in productivity), across vegetation types (mid-grass, short-grass, or desert grasslands), among seasons, and among years (by variation in rainfall). Because we often lack data over the full range of these conditions, a useful guideline may be that in areas of low biomass productivity, competition is more likely than in areas of high biomass productivity (Detling 2006). Competition is also more likely at higher stocking levels than at light levels (see review by Holechek et al. 2004). The larger public policy question is whether competition justifies poisoning prairie dogs on publicly owned lands to benefit cattle grazing by private leasees.

Proponents of holding prairie dogs at low numbers claim such management is necessary to maintain wild ungulates and economically viable numbers of domestic livestock (Stoltenberg et al. 2004, Vermeire et al. 2004). They frame competition around a negative effect on large ungulates by prairie dogs, and typically define competition as overlapping resource use. Even if prairie dogs compete with large ungulates, the fact remains that coexistence is possible as millions of bison (*Bison bison*), pronghorn (*Antilocapra*

americana), and elk (*Cervus elaphus*) lived for millennia with prairie dogs before European settlers introduced domestic livestock to the Great Plains.

In North America, individual bison cows and yearlings appear to benefit from grazing on prairie dog colonies, as opposed to grazing only away from those colonies (Vanderhye 1985, Detling 2006). Seasonal weight gain of bison varies directly with the time they spend grazing on prairie dog colonies (Detling 2006). For wild ungulates, competition with high densities of livestock may present a larger problem than competition with prairie dogs. When researchers calculated livestock competition based on diets, cattle grazing reduced bison numbers by 72% and elk numbers by 40% (Wydeven and Dahlgren 1985, Uresk 1986, Holechek et al. 1989).

At the beginning of the 20th century, Merriam (1902) estimated the effects of prairie dogs on grazing lands. Some people cite his work as justification for poisoning prairie dogs to benefit cattle grazing (see Vermeire et al. 2004). Furthermore, Merriam used an unstated formula to claim that 256 prairie dogs consume as much grass as one cow, and failed to correct for dietary overlap or to account for prairie dog food that is not livestock forage (Koford 1958). Merriam (1902:258) concluded “Hence, it is no wonder that the annual loss from prairie dogs is said to range from 50 to 75 per cent of the producing capacity of the land.” Modern standards of evidence cannot support this assertion, which recent studies contradict.

O’Meilia et al. (1982) estimated competition between cattle and prairie dogs in Oklahoma, USA, and found no statistical difference in weight gain between steers raised on and off of prairie dog colonies. A reanalysis by Vermeire et al. (2004) of O’Meilia’s data agreed with the original conclusion that no statistical difference in weight gain of steers occurred over the entire year, but they found a difference during winter. However, reduced winter weight gains are irrelevant for most western ranchers, because cattle typically do not free-range during winter (particularly on public lands) and ranchers supplement cattle in winter with stored foods. The O’Meilia et al. (1982) study comprised small sample sizes, so we should cautiously interpret both the original conclusion and the reanalysis (Detling 2006).

After reintroducing black-tailed prairie dogs to the Gray Ranch in southwestern New Mexico, vegetation was shorter on the prairie dog colony (Brown 2003; Curtin 2003, 2006). Vegetation diversity was lower on the colonies, but biomass was slightly higher than on random control plots, perhaps because grasses became more bunched (Curtin 2006). Soils probably played some role in the biomass results because prairie dogs colonized the richer areas (C. Curtin, Massachusetts Institute of Technology–United States Geological Survey Science Impact Collaborative, personal communication). Most importantly, large grazers do not find the tabosa grass (*Hilaria mutica*) of the region palatable, so livestock did not use the grass away from prairie dog colonies; livestock only ate tabosa grass after prairie dogs clipped it (C. Curtin, personal communication).

A study in New Mexico also reported that cattle walked miles from water across open terrain to graze on prairie dog colonies (Brown 2003, Curtin 2003). Curtin (2003:91) observed, "In short, prairie dogs have a positive interaction with native and non-native grazers." We should not extrapolate this example from southwestern grasslands across the prairie dog's range. In short-grass steppe habitat in northeastern Colorado, USA, cows showed no preference for grazing on or off colonies (Guenther and Detling 2003, Detling 2006). In a northern mixed-prairie, bison showed a decided preference for grazing on prairie dog colonies (Coppock et al. 1983b, Detling 2006).

Using actual data and linear programming Uresk and Paulson (1988) estimated competition between cattle and prairie dogs at 4% to 7% in South Dakota, USA. Data included diets, consumption rates, plant production, stocking rates (20% to 80% forage utilization), densities of black-tailed prairie dogs (up to 40 ha of prairie dogs at 44 prairie dogs/ha in a 2,100-ha pasture), and plant seral stages. They analyzed vegetation from 4 treatments: 1) neither cattle nor prairie dogs, 2) prairie dogs only, 3) both cattle and prairie dogs, and 4) cattle only (Uresk and Bjugstad 1983; Collins et al. 1984; Uresk 1985, 1987).

Many ranchers follow the adage "take half and leave half" of the vegetation (Lacey and Van Poolen 1981). When reviewing studies of stocking rates, Holechek et al. (2004) reported that heavy grazing used an average of 57% of primary forage species, moderate grazing used 43%, and light grazing used 32%; over long time frames, moderate grazing levels maintained vegetation productivity for arid and semi-arid grasslands. Using Uresk and Paulson's (1988) model, Detling (2006) suggested that when cattle consume 60% of the vegetation in a pasture and prairie dogs occupy 2% of that pasture, cow-calf capacity declines by 3.3%. Looking at different scales, individual pastures may include more than 2% of their area occupied by prairie dogs, but prairie dogs still occupy about 2% of their former range (Proctor et al. 2006). Holechek et al. (2004) promoted a moderate stocking rate (about 45% utilization) for range health, and stocking at that rate should also reduce competition between livestock and prairie dogs.

More recently, Derner et al. (2006) looked at interactions between cattle and prairie dogs on the short-grass steppe of the Pawnee National Grasslands, Colorado. Over 6 years, the weight of cattle declined with increasing area occupied by prairie dogs, but at a rate proportionately lower than the increasing percentage of pasture occupied by prairie dogs ($Y = 98.71 - 0.21X$). When prairie dogs occupied 20% of the pasture, cattle weight gain declined by 5.5%; when prairie dogs occupied 60% of the pasture, cattle weight gain declined by 13.9% (Derner et al. 2006). Annual precipitation was below average in 4 of the 6 years, and mean weight gain of cattle on and off of colonies was significantly different (which the authors defined as $P < 0.10$) in 3 of 5 years (2 of which experienced below average precipitation) for which the authors analyzed weight gain (Derner et al. 2006). One of those years demonstrated highly significant

differences ($P < 0.001$) and that year involved the pasture with a prairie dog colonization level of 63% and below average precipitation. During the wet year, only one site with prairie dogs (4.3%) was lower in cattle weights than other sites with and without prairie dogs (Tukey's Multiple Comparison Procedure, $\alpha = 0.01$). Over the entire study, mean seasonal weight gain of cattle on pastures without prairie dogs was 6% higher than on pastures with prairie dogs; mean area occupied by prairie dogs was 24%, with a range from 4% to 63% (Derner et al. 2006).

Contrary to statements by Vermeire et al. (2004:692), Uresk and Paulson (1988) did not "limit" prairie dogs to an early seral stage. Prairie dogs simply did not occur on the 58% of the 2,100-ha pasture that occurred at or near climax; the authors did not assume this (Uresk and Paulson 1988). Prairie dogs inhabited areas of the pasture that fell within the remaining 3 seral categories: early, early-intermediate, and a few in late-intermediate seral condition. Due to many years of heavy livestock grazing, areas of the grasslands existed in early seral stages of plant succession with buffalo grass (*Buchloe dactyloides*) being the dominant plant (Johnson et al. 1951, Lewis et al. 1956). However, with livestock reductions and poisoning of black-tailed prairie dogs, plant succession progressed to later seral stages (Uresk 1987, 1990). We recognize that plant succession does not always proceed in an orderly fashion; when disturbance is severe enough to push a system across a threshold, nonlinear responses can dominate.

All prairie dog towns sampled in the Badlands National Park, Buffalo Gap Grasslands, Thunder Basin Grasslands, and Ft. Pierre Grasslands contained prairie dog colonies in early or intermediate seral stages of plant succession (Koford 1958, Uresk 1985, Cincotta et al. 1989, Severson and Plumb 1998). In mixed-grass and tall-grass prairie, managing for a long-term, climax stage by reducing livestock-grazing increases vegetation height, and thus reduces the number of prairie dogs, which do not colonize in climax vegetation (Koford 1958, Snell and Hlavachick 1980, Snell 1985, Uresk 1987). Disturbance is indeed equated with seral status, and prairie dogs seek areas of disturbance or early seral condition (Koford 1958; Uresk 1987, 1990; Uresk and Paulson 1988; Cincotta et al. 1989). Prairie dogs do alter the vegetation for structure and composition, generally in association with another large herbivore, but the short grasses and the mid grasses are well adapted to herbivory (Uresk 1987, Winter et al. 2002).

Researchers estimate dietary overlap at 60% and 64% for cattle and prairie dogs in a mid-grass and short-grass prairie, respectively (Hansen and Gold 1977; Uresk 1984, 1986). Both livestock and prairie dogs independently and synergistically induced changes in plant species composition. Koford (1958) and Knowles (1982) found that prairie dogs began clipping mid grasses at approximately 15 cm or higher. Without grazing by livestock, or with light livestock grazing, clipping by prairie dogs generally occurs to maintain the colony in short vegetation (Koford 1958, Snell and Hlavachick 1980, Snell 1985, Uresk 1987). However,

Heady and Child (1994) reported that plant biomass can decline by 1% to 5% from the hoof action of cows and soil compaction, and this decreases plant biomass available for livestock. The negative effects of soil compaction increase as stocking rates increase (Holechek et al. 2004).

Vermeire et al. (2004) concluded that the presence of prairie dog burrow-mounds reduced vegetation, which reduced livestock carrying capacity. Mounds account for 2.5% to 6% of the ground area on a prairie dog colony (Farrar 2002, Detling 2006). However, as moisture runs off these mounds, the adjacent areas harvest the water and nutrients for plant growth. As a result, the aboveground biomass of plants associated with mounds increases in native vegetation (Gold 1976, Severe 1977). This increase in aboveground biomass can variably offset the loss of vegetation on the prairie dog burrow-mounds.

Vermeire et al. (2004:694) also stated "...habitat occupied by prairie dogs shifts, over time, from one suited for grazers to one better suited for browsers." Johnson-Nistler (2004) reported the opposite. In some grasslands where woody plant encroachment is a problem, prairie dogs limit woody species and help maintain the dominance of herbaceous species. Everett (2002) found shrub cover was 7.5 times higher outside of prairie dog colonies than inside of colonies on Thunder Basin National Grassland in Wyoming, USA. Similarly, mesquite (*Prosopis* spp.) increased from 27% to 61% of the cover in the first 23 years after prairie dogs were removed from an area in Texas, USA (Weltzin et al. 1997). In Chihuahua, List (1997) documented a 14% increase in mesquite in the first 8 years after a prairie dog colony was poisoned. When prairie dogs were reintroduced on the Gray Ranch in southwestern New Mexico, USA, they clipped and girdled mesquite plants immediately after release (Brown 2003, Curtin 2003).

Economic Effects of Competition

Stoltenberg et al. (2004) indicated that total forage removed on prairie dog colony-sites (cattle + prairie dogs) was nearly 2 times greater than the forage removed by cattle (based on a forage estimation study). Stoltenberg et al. (2004) stated that prairie dogs removed an average of 852 kg/ha (760 pounds) of forage in June and July. Achieving this amount of forage consumption would require 457 prairie dogs/ha (185 prairie dogs/acre). One prairie dog consumes about 0.93 kg (2.05 pounds) of forage per month (Hansen and Cavender 1973). Furthermore, prairie dogs should have engaged in minimal clipping to enhance visibility on the study sites. Stoltenberg (2004) reported average vegetation heights ranging from a low of 7.4 cm to a high of 9.7 cm, but clipping for visibility does not generally occur until heights reach approximately 15 cm or greater (Koford 1958, Knowles 1982). The results of this study are difficult to evaluate with the limited information that Stoltenberg et al. (2004) and Stoltenberg (2004) presented. Prairie dogs and cattle apparently removed nearly equal amounts of forage during the 2 months, even though prairie dogs colonized 7.9% of the 701-ha study site. The authors do not describe stocking rates of livestock and prairie dog densities, and the

methods used to estimate and compare forage weight are unclear. We could not calculate forage disappearance (consumption + clipping) based on the information available.

Vermeire et al. (2004) analyzed the effect of prairie dogs on livestock using a 1:1 competition rate via direct forage reduction, but livestock and prairie dogs do not compete for forage at a 1:1 ratio. Furthermore, the calculations of Vermeire et al. assume a full year of grazing by prairie dogs, cows, steers, and sheep, but livestock generally graze public lands over a 6-month period (or less), and prairie dogs do not always come aboveground during the winter months (Hoogland 1995). Thus, Vermeire et al. (2004) estimated that, at prairie dog densities ranging between 8/ha and 46/ha, 12 and 67 cow-days were lost and 76 and 435 sheep-days were lost, respectively. We estimated forage reduction for cows and sheep based on 6 months of grazing, and we adjusted for dietary overlap with prairie dogs using information from Alexander et al. (1983) and Uresk (1984, 1986). At the same prairie dog densities as above (8/ha and 46/ha), over 6 months 4 and 20 cow-days were lost and 8 and 48 sheep-days were lost, respectively (Table 1). Similarly, we estimated reduction in numbers of cows and sheep on a 1,000-ha grazing allotment (Table 2). Eight prairie dogs per hectare (low densities) would require a reduction of one cow or 3 sheep on a 1,000-ha allotment (carrying capacity of 2.4 ha per 1 animal-unit-month [AUM] for cows). Eighteen prairie dogs per hectare ($\bar{x}$ densities on the prairie) would require a reduction of 2 cows or 7 sheep on the allotment. Extreme densities of 46 prairie dogs per hectare required a reduction of 6 cows or 18 sheep on a 1,000-ha allotment.

Trying to increase forage by poisoning prairie dogs adds to expense borne by the public. In 2004, the South Dakota Game, Fish, and Parks poisoned prairie dogs on 3,110 ha of United States Forest Service lands at a cost to taxpayers of \$24.58/ha (State of South Dakota 2005). Prorated over a 3-year period, at a stocking rate of one cow-calf pair per 2.4 ha—stocking rates in the general area ranged from 2 ha/AUM to 8.7 ha/AUM, depending on conditions (Uresk and Paulson 1988)—poisoning prairie dogs cost the taxpayers \$19.40/AUM. An economic analysis by Collins et al. (1984) looked at prairie dog control in Conata Basin, South Dakota, where the 2004 poisoning was focused. They based their results on harvesting vegetation under 4 treatments: 1) neither cattle nor prairie dogs, 2) prairie dogs only, 3) both cattle and prairie dogs, and 4) cattle only (Uresk and Bjugstad 1983; Collins et al. 1984; Uresk 1985, 1987). Removing prairie dogs gained 51 kg/ha of forage, rendering it uneconomical to poison prairie dogs for additional livestock forage (unless subsidized by the public sector).

Similarly, Derner et al. (2006) found that declines in weight gain of cattle grazing on pastures with 20% occupancy by prairie dogs resulted in \$14.95 less per steer. This translates to a 5.5% reduction. On pastures with 60% of the area in prairie dogs, the amount was \$37.91 less per steer, a 14% reduction (Derner et al. 2006). In terms of

Table 1. Direct reduction of forage (grazing d for 6 months) for cows and sheep relative to forage consumption by density of black-tailed prairie dogs.^a

Prairie dogs/ha	Grazing d/ha lost for 6 months to prairie dog grazing ^b	
	Cow	Sheep
8	4	8
18	8	19
46	20	48

^a Data based on corrected diet similarities (dry wt composition) among the 3 herbivores.

^b Colony area required for the given densities of prairie dogs (31 g daily dry matter intake/prairie dog; Hansen and Cavender 1973; Uresk 1984, 1986) to consume one grazing-yr equivalent of forage for cows (11.9 kg daily dry matter intake/cow; National Research Council 1984) and sheep (1.3 kg daily dry matter intake/sheep; Church 1972, Alexander et al. 1983).

profit per unit of area, this translates to a loss of about \$2.23/ha (\$0.88/acre) at 20% occupancy by prairie dogs and about \$5.58/ha (\$2.20/acre) at 60% occupancy (Derner et al. 2006). According to Buhler (2006), an agronomy specialist with the Colorado State University Cooperative Extension, poisoning 76 burrows/ha (30 burrows/acre) would cost about \$3.81 (\$1.50/acre) using zinc phosphide and about \$10.67 (\$4.20/acre) using aluminum phosphide tablets. One must also consider labor, and Buhler (2006) stated that commercial applicators charge about \$178/ha (\$70/acre). Such large expenditures for so little gain are not profitable.

Factors that limit prairie dogs include soil types, slope, aspect, vegetation, and plague (Koford 1958, Reading 1993). Within those physical limits, reproductive success varies with social and demographic factors, such as population numbers, and maternal body mass (Hoogland 1995). High population levels or low maternal body mass inhibit reproductive success and thus make prairie dog numbers somewhat self-limiting. Historically, prairie dogs covered about 20% of the short and mixed-grass prairie (Summers and Linder 1978), and prairie dog colonies occupy about the same percentage of a prairie dog complex (Miller et al. 1996). More recently, Cooper and Gabriel (2005) estimated that 1.1% of the Great Plains managed by the United States Forest Service holds prairie dogs. Thus, there is little detriment to the livestock industry as a whole. We contend that it is scientifically and economically irresponsible to further reduce prairie dog populations on publicly owned lands because of competition with livestock.

HISTORICAL NUMBERS AND POLITICS

Historical estimates for numbers of prairie dogs help guide present management goals. Virchow and Hygnstrom (2002) and Vermeire et al. (2004) suggested that an estimate of 40,000,000 ha of prairie dogs in 1900 was unnaturally high because prairie dogs expanded in the face of drought and overgrazing by domestic livestock during the 1880s and 1890s. If the presence of roughly 23,000,000 cattle around 1900 led to inflated numbers of prairie dogs, what would have prevented prairie dogs from becoming equally numerous in the early and mid-1800s, when 30,000,000

Table 2. Estimated stocking rate of cows and sheep (grazing d for 6 months) for a 1,000-ha grazing allotment at different densities of black-tailed prairie dog.^a

Colony area (ha)	Prairie dogs/ha					
	8		18		46	
	Cow	Sheep	Cow	Sheep	Cow	Sheep
0	69.0	483.0	69.0	483.0	69.0	483.0
20	68.8	482.2	68.5	481.3	67.6	478.5
40	68.5	481.4	67.9	479.5	66.1	474.1
60	67.9	480.7	67.3	477.8	64.7	469.6
80	67.9	479.9	66.8	476.0	63.2	465.1

^a Carrying capacity of cows is estimated at 69 based on 2.4 ha per animal unit month (11.9 kg daily dry matter intake/cow; National Research Council 1984). Seven sheep are considered equivalent to one cow (1.3 kg daily dry matter intake/sheep; Church 1972, Alexander et al. 1983). Cow and sheep numbers are based on direct consumption of forage with a dietary overlap of 60% and 22%, respectively (31 g daily dry matter intake/prairie dog; Hansen and Cavender 1973; Uresk 1984, 1986). Forage utilization levels and plant standing crop for the allotment are not considered.

bison inhabited the plains and similar environmental conditions prevailed (Forrest 2005)?

We suggest that Vermeire et al. (2004) misinterpreted Smith (1899) when stating that overgrazing in the 1880s set the stage for unnaturally high numbers of prairie dogs in 1900. Vermeire et al. (2004:690) stated “Smith (1889) described the grasslands as a ‘pastoral paradise’ with luxuriant growth before the 1880s.” Smith’s (1889:8) statement about a “pastoral paradise” referred to a period from 1874 to 1884 in central and western Texas after the near extermination of the southern buffalo herd by 1873 and after an act of Congress removed Native Americans in 1874:

“The disappearance of the buffalo was nearly coincident with that of the Indian, and there was a period of fully ten years after the destruction of the buffalo herds before the number of cattle and sheep on any portion of the ranges equaled the great herds of game. These years, from 1874 to 1884, may be called the ‘golden period’ of the Southwestern stockman. ... There were also abundant rains and the seasons were mild. ... Grasses and forage plants, ungrazed, grew and thrived, reseeded themselves, and increased to a wonderful degree of luxuriance, so the stockmen on entering this pastoral paradise thought that it was not possible to put enough cattle and sheep on the land to eat down all of the rank growth of vegetation.”

Smith (1889:9) also wrote:

“Newcomers who had not seen the land when it was possessed by the Indian, the buffalo and mustang, at the time when the herbage was eaten down, or kept in check by fires or drought, naturally thought that this rich profusion of vegetation was the normal condition and that the saying that it was impossible to put enough cows on the land to eat all the grass was literally true.”

The more complete statement by Smith (1889) offers a different picture than indicated by Vermeire et al. (2004).

The argument that prairie dogs were expanding at the beginning of the 20th century did not consider the huge numbers of bison that were already exterminated (as mentioned in Smith 1889) or the extensive prairie dog poisoning that already occurred (Knowles et al. 2002). Furthermore, the relevant point is that the declining trends in prairie dog populations are clear. Using the United States Fish and Wildlife Service's (2004) current estimates for black-tailed prairie dogs, the prairie dog species with the greatest historical range, the declining population trend is clear whether there were once 40,000,000 ha, 30,000,000 ha, 20,000,000 ha, or 10,000,000 ha of that species. Respectively, these figures indicate declines of roughly 98%, 97%, 96%, or 92%.

A quarter century ago, prairie dogs covered only 1.6% of the Forest Service lands on the Great Plains (Schenbeck 1982). Prairie dogs currently occupy <2% of the land within the species' range in South Dakota; yet despite such low numbers, implementing the South Dakota Black-Tailed Prairie Dog Conservation and Management Plan could result in a further reduction. The Plan recommends a statewide population goal of 80,726 ha of prairie dog colonies. Surveys completed in accordance with the Plan documented that prairie dogs currently inhabit 166,503 ha in South Dakota (Cooper and Gabriel 2005). We do not mean to single out South Dakota. The situation is similar in other states throughout the range of the prairie dog; we simply had access to better documentation for South Dakota. Considering the benefits of prairie dogs to the grassland ecosystems they inhabit (e.g., sustaining wildlife, soil nutrients, and vegetation; Campbell and Clark 1981, Agnew et al. 1986, Sharps and Uresk 1990, Bevers et al. 1997, Lomolino and Smith 2003), 1.1% occupancy by prairie dogs on federally owned land seems extremely modest.

The criteria the United States Fish and Wildlife Service uses to list species under the United States Endangered Species Act are 1) the present or threatened destruction, modification, or curtailment of its habitat or range; 2) overutilization for commercial, recreational, scientific, or educational purposes; 3) disease or predation; 4) the inadequacy of existing regulatory mechanisms; and 5) other natural or human factors affecting its continued existence (see Manes 2006 for a discussion of all 5 criteria). A species must only meet one of these criteria to merit listing. Interestingly, the sparse occupancy of prairie dogs throughout their range appears to counter one of the arguments the United States Fish and Wildlife Service used to remove prairie dogs from the candidate list in 2004 (Manes 2006), at least on federal lands where the government controls management. The United States Fish and Wildlife Service argued that prairie dogs increased over the last 40 years (Manes 2006). Proctor et al. (2006) analyzed the present area inhabited by prairie dogs and found that of the 2% of their original range that prairie dogs still occupied, 1.5% occurred on tribal lands, 0.33% occurred on federal lands, and only 0.08% occurred on private lands.

UNIQUENESS OF PRAIRIE DOG ACTIVITIES

Proponents of reducing prairie dogs argue that prairie dog grazing does not produce unique effects and stated "Long-term, intensive use by any grazer will cause comparable changes in plant communities" (Vermeire et al. 2004:692). Scientific research does not support this claim on the mixed-prairie. For example, bison grazing alone produced a small impact on plant biomass, plant species composition, and plant or soil nitrogen, but prairie dog grazing led to a large effect on these same factors (Fahnestock and Detling 2002). Indeed, no additive effect occurs when bison and prairie dogs grazed together versus when prairie dogs grazed alone (Fahnestock and Detling 2002). Bison often create conditions necessary for prairie dogs on mixed grass prairies, but prairie dogs exert the larger effect on soil and plants.

Any grazer creates more succulent and nutritious regrowth than ungrazed forage, and large herbivores often select those previously grazed patches (McNaughton 1984, Knapp et al. 1999). At a macro-ecological scale, grazing represents a natural disturbance to the landscape. At a local scale, however, not all grazing is the same. Different species of grazers prefer different types of plants, and they eat those plants in different ways. Some species are opportunistic, some are selective, and some are intermediate between those 2 extremes. Even for a given species of grazer, seasonal differences exist. Cattle are grazers, but confinement produces a landscape with less diversity than one grazed by wandering ungulates (Benedict et al. 1996). Bison, in contrast, wander over an immense region and particular patches of grass may have as much as a 2-year rest before the bison return (Lott 2002). Perhaps the major difference between grazing by native herbivores and domestic livestock comes when some livestock managers promote killing predators and competitors, building fences unfriendly to wildlife, making unnecessary roads, increasing exotic plants, using chemicals, altering fire regimes, or managing in ways that degrade riparian areas (Freilich et al. 2003).

For cattle to serve as an ecological substitute for bison at some level on federal lands (see Tohill and Dollerschell 1990, Thomas 1991), they should mimic the pattern of wild bison—no prairie dog poisoning and avoidance of areas with drought. The lower rate for leasing federal lands and compensation programs can compensate for not poisoning. Turning an existing, negative subsidy (poisoning) into a positive incentive for not poisoning can fund compensation (Miller et al. 1996, Miller and Reading 2006). The National Wildlife Federation followed this pattern to provide incentives to leaseholders on National Forest lands around Yellowstone National Park that retire their leases to reduce conflict between livestock and grizzly bears (*Ursus arctos*) or wolves (*Canis lupus*). This program increases habitat security for wildlife, financially benefits the rancher, and reduces management headaches for the Forest Service. Similar options may exist for National Grasslands. The Malpai Borderlands Group, and others in New Mexico and Arizona, USA, stress the need to destock an area during

drought, and they use grass banks or land held in reserve for ranchers affected by drought (Sayre 2001; <http://www.malpaiborderlandsgroup.org/gb.asp>).

Like cattle, prairie dogs graze, but prairie dogs represent much more than just grazers (Kotliar et al. 2006). They also move soil (Detling and Whicker 1988, Detling 1998), influence nutrient cycling (Coppock et al. 1983a; Detling and Whicker 1988; Whicker and Detling 1988, 1993; Detling 1998), increase nitrogen content of soil and plants (Holland and Detling 1990, Detling 1998), change vegetation structure and community dynamics (Coppock et al. 1983a, Whicker and Detling 1988, Weltzin et al. 1997, Detling 1998, Fahnestock and Detling 2002), aerate the ground (Whicker and Detling 1988, Outwater 1996, Detling 1998), alter soil chemistry (Munn 1993), and deepen water penetration (Outwater 1996, Detling 1998). They provide a ready source of prey to many predators and burrows for shelter to other animals and insects (Goodrich and Buskirk 1998, Kotliar et al. 1999, Shipley and Reading 2006). This combination of effects gives the prairie dog its role as a highly interactive (keystone) species in the ecosystem, creating a matrix of different habitats that increases diversity across the grassland (Kotliar et al. 1999, 2006; Miller et al. 2000).

Vermeire et al. (2004:689) cited Kotliar et al. (1999) as saying that the role prairie dogs play in influencing other vertebrate species is “greatly overstated.” Vermeire et al. (2004:689) added the word “greatly”; Kotliar et al. (1999) did not use it. The following quotes accurately reflect the assessment by Kotliar et al. (1999:177 and 178, respectively):

“Despite our conclusion that some prairie dog functions may be smaller than previously assumed, collectively these functions are quite large compared to other herbivores in the system. We suggest that prairie dogs also provide some unique functions not duplicated by any other species and that continued decline of prairie dogs may lead to substantial erosion of biological diversity and landscape heterogeneity across prairie and shrub-steppe landscapes.”

“We conclude that although some aspects of their role have been overstated in the literature, the available science clearly indicates that prairie dogs function as a keystone species.”

The Society of Conservation Biology (1994) and the American Society of Mammalogists (1998) also advanced resolutions that support the view of Kotliar et al. (1999, 2006) that prairie dogs fit the definition of a keystone species (significantly affects ecosystem structure, function, and composition in ways not wholly duplicated by other species). Vermeire et al. (2004:695) stated that just as early interests in eradication were an overreaction, interests for conservation “may be an equally extreme reaction based on exaggerations of the prairie dogs’ positive role in grassland systems.” However, they offered no detailed discussion about that role and why it is exaggerated, and they ignore a growing body of literature (cited above) that suggests prairie dogs play key roles in the ecological processes of grasslands.

CONCLUSIONS

The issue of how much competition exists between prairie dogs and livestock is hotly disputed. In general, competition is more likely in areas of low productivity than in areas of high productivity, and light to moderate stocking rates produce less competition than high stocking rates (Detling 2006). Some members of the agricultural industry have framed the argument of competition in terms of how prairie dogs hurt cattle and large ungulates. They have not explored the effect that cattle can have on other grazers, large and small. We agree that more research is clearly required. We disagree, however, with the conclusions of Vermeire et al. (2004). We do not think the available evidence justifies holding distribution and numbers of prairie dogs at levels too low for them to perform their ecological function (Soulé et al. 2002, 2005).

We propose that the politics of the agricultural community only serve to cloak an important conservation issue. The prairie dog, a highly interactive species of grassland ecosystems, has declined greatly throughout its range to a level and distribution at which it can no longer serve its historical ecological function (Soulé et al. 2002, 2005; Proctor et al. 2006). Some people suggest that holding prairie dogs at low numbers is necessary to maintain livestock and wild ungulates. Yet, wild ungulates thrived for millennia with prairie dogs before European settlers. And, setting goals for prairie dogs based on the real or perceived needs of domestic livestock means we favor an abundant exotic species at the expense of a declining native species. In this case, the native species helped drive the evolution of the grassland system over thousands of years. To label such a species as a pest is not ecologically sound.

The best example of a species benefiting from prairie dogs is the black-footed ferret (*Mustela nigripes*). As obligate associates of prairie dogs, ferrets rely on them for about 90% of their prey and use their burrows as den sites and refugia (Miller et al. 1996). Because prairie dogs declined, black-footed ferret numbers collapsed. At one point, only 10 known individuals represented the entire species; they survived because of an intensive, and expensive, captive breeding effort (Miller et al. 1996, Biggins et al. 2006). Reintroductions of captive-raised black-footed ferrets began in 1991, but the black-footed ferret recovery effort is stalling because too few prairie dog complexes of sufficient size exist to meet the goals of the 1988 Black-Footed Ferret Recovery Plan (United States Fish and Wildlife Service 1988, Miller and Reading 2006). Bevers et al. (1997) estimated that an adult population of 200 black-footed ferrets requires a black-tailed prairie dog complex of 6,500 ha to support it. Because it takes 3 individual black-footed ferrets to make a genetically effective population (N_e) of 1 (United States Fish and Wildlife Service 1988), 200 individuals would reduce the consequences of inbreeding over the short term (by surpassing the guideline of needing an N_e of ≥ 50), but that number falls short of an N_e of 500, a number proposed for adaptive evolution in the long term (Frankel and Soulé 1981).

Constraining prairie dogs to low numbers in small, widely distributed colonies may allow them to persist, but low densities and scattered distribution will preclude them from performing their ecosystem functions (Miller et al. 2000, Soulé et al. 2005, Proctor et al. 2006). In other words, prairie dogs are functionally extinct (Soulé et al. 2005).

The day the United States Fish and Wildlife Service announced that they would remove the black-tailed prairie dog from the protection of their candidate list, the Governor of South Dakota announced a federal–state plan to “control the infestation of prairie dogs” on federal lands (Stein 2004:7). Thus 3,110 ha of prairie dogs were poisoned on the Buffalo Gap National Grasslands, parts of which occurred on the Conata Basin prairie dog complex, home to one of the most successful reintroduced populations of the endangered black-footed ferret. Other states took similar actions to poison prairie dogs. Given that prairie dogs occupy 1.1% of Forest Service lands on the Great Plains (Cooper and Gabriel 2005), how much more prairie dog control on our publicly owned lands does the livestock industry require? Kotliar et al. (1999) stated that continued decline of prairie dogs can lead to an erosion of biological diversity. What is considered an acceptable loss of biological diversity? Should we draw the line before black-footed ferrets go extinct, or should we wait for other species to become imperiled?

MANAGEMENT IMPLICATIONS

If society wants to conserve prairie dogs, the species should exist in densities and distribution that allows them to perform their evolutionary and ecological function on the grasslands. Black-footed ferret recovery could function as a benchmark for measuring the ecological function of prairie dogs. Recovering ferrets requires large complexes of prairie dogs distributed throughout their former range (United States Fish and Wildlife Service 1988). Because prairie dogs occupy 1.1% of Forest Service lands on the Great Plains (Cooper and Gabriel 2005), because poisoning is not economically feasible (Collins et al. 1984, Derner et al. 2006), and because prairie dogs support biodiversity and ecosystem processes (Kotliar et al. 1999), the implications of continued poisoning programs are clear. For cattle to serve as an ecological substitute for bison at some level on federal lands (see Tohill and Dollerschell 1990, Thomas 1991), management should strive to mimic the pattern of wild bison—no prairie dog poisoning and avoiding areas with drought. Policy makers could convert tax dollars currently allocated to a negative subsidy (poisoning) into a positive incentive for prairie dog conservation (Miller et al. 1996, Miller and Reading 2006). A grassbank system, perhaps created by holding some retired federal leases open, could help mimic bison moves during drought.

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The Keystone-Species Concept in Ecology and Conservation

Management and policy must explicitly consider the complexity of interactions in natural systems

L. Scott Mills, Michael E. Soulé, and Daniel F. Doak

Will the extinction of a single species in a community cause the loss of many others? Can we identify a set of species that are so important in determining the ecological functioning of a community that they warrant special conservation efforts? The answer to these questions hinges on the existence of a limited number of species whose loss would precipitate many further extinctions; these species have often been labeled keystone species.

The term *keystone species* has enjoyed an enduring popularity in the ecological literature since its introduction by Robert T. Paine in 1969: Paine (1969) was cited in more than 92 publications from 1970 to 1989; an earlier paper (Paine 1966), which introduced the phenomenon of keystone species in intertidal systems but did not use the term, was cited more than 850 times during the same period.

As used by Paine and other ecologists, there are two hallmarks of keystone species. First, their presence is crucial in maintaining the organization and diversity of their ecological communities. Second, it is implicit that these species are exceptional, relative to the rest of the community, in their importance.

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The term *keystone species* is poorly defined and broadly applied

Given the assumed importance of keystone species, it is not surprising that biologists have advocated that key or keystone species be special targets in the efforts to maximize biodiversity protection (e.g., Burkey 1989, Frankel and Soulé 1981, Soulé and Simberloff 1986, Terborgh 1986) and as species in need of priority protection (e.g., Cox et al. 1991). Management to protect keystone species has been suggested to resolve general policy and land-use dilemmas. For example, it has been proposed that management for individual keystone species should be a focus for the management of whole communities (Rohlf 1991, Woodruff 1989). Further, Carroll (1992) argues that managed keystone species could be used to support populations of other species in reserves that would otherwise be too small to contain viable populations. Conway (1989) suggested that, for restoration, keystone species are necessary to help reestablish and sustain ecosystem structure and stability.

Such policy recommendations imply that a clear operational definition exists for *keystone species*. In contrast, we argue that the term is broadly applied, poorly defined, and nonspe-

cific in meaning. Furthermore, the type of community structure implied by the keystone-species concept is largely undemonstrated in nature, although it has fundamental implications for conservation and food-web theory. These ambiguities and uncertainties motivate this discussion of the implications of the keystone-species concept for ecology and conservation, as well as the dangers inherent in shaping conservation strategies around keystone species.

The varied meanings of the term *keystone species*

The term *keystone species* was originally applied to a predator in the rocky intertidal zone:

[T]he species composition and physical appearance were greatly modified by the activities of a single native species high in the food web. These individual populations are the keystone of the community's structure, and the integrity of the community and its unaltered persistence through time...are determined by their activities and abundances (Paine 1969).

Subsequently, the term has been applied to many species at many trophic levels. For heuristic purposes, we have collapsed the usages of *keystone species* into five types (Table 1). This categorization is not meant to imply mutually exclusive groups or an exhaustive review of the term's application, but rather to show the diversity of keystone effects referred to in the literature.

Keystone predator. Paine (1966, 1969) noted that experimental removal of some rocky intertidal carnivores (such as the starfish *Pisaster*) led to nearly complete dominance of the substrate by one or two sessile species (mussels), resulting in greatly decreased species diversity. In this and other cases, the importance of the keystone predator derived from two requisites (Paine 1969, Pimm 1980): the predator preferentially ate and controlled the density of a primary consumer, and the consumer was capable of excluding (through competition or predation) other species from the community. Essentially, then, the early connotation was that keystone predators are important because they control the densities of important competitor or predator species.

Predators have also been labeled *keystone* when they control the densities of other types of ecologically significant prey species. For example, sea otters (*Enhydra lutris*) have often been referred to as keystone predators (e.g., Duggins 1980, Estes and Palmisano 1974) because they limit density of sea urchins (*Strongylocentrotus* spp.), which in turn eat kelp and other fleshy macroalgae that form the basis of a different community than is present in their absence (VanBlaricom and Estes 1988). Thus, otter removal has community-level influences, by releasing from predation a primary consumer that eats a plant that harbors other organisms.

Other authors have ignored the original requisites for the keystone-predator label and merely require that the species in question has a major effect on community composition. Risch and Carroll (1982) described fire ants (*Solenopsis geminata*) as keystone predators because their absence increases the number of individuals and species of arthropods potentially harmful to agriculture. The ants are generalist species preying on herbivores, which in turn are not highly competitive; hence, neither of the original requisites for keystone predators apply.

Keystone prey. In a theoretical analysis that assumed no competitive interactions between prey species, Holt (1977, 1984) demonstrated that a preferred-prey species that is able to maintain its abundance in the face of pre-

Table 1. Categories of presumed keystones and the effects of their effective removal from a system.

Keystone category	Effect of removal
Predator	Increase in one or several predators/consumers/competitors, which subsequently extirpates several prey/competitor species
Prey	Other species more sensitive to predation may become extinct; predator populations may crash
Plant	Extirpation of dependent animals, potentially including pollinators and seed dispersers
Link	Failure of reproduction and recruitment in certain plants, with potential subsequent losses
Modifier	Loss of structures/materials that affect habitat type and energy flow; disappearance of species dependent on particular successional habitats and resources

dation (via a high reproductive rate) can affect community structure by sustaining the density of a predator, thus reducing the density of other prey. Holt (1977) called such a predator-tolerant prey a *keystone species* "inasmuch as its properties control the density of the predator and restrict the range of parameters open to other prey." As an anecdotal example, Holt describes the contraction of habitat use of arctic hares after the introduction of snowshoe hares on Newfoundland, indicating that the snowshoe hare may have increased lynx populations, which then heavily preyed on the more vulnerable arctic hare. As the term *keystone prey species* was used by Holt, removing the keystone prey species would increase, not decrease, overall species diversity in the community.

However, Noy-Meir (1981) suggested that Holt's model involving a predation-tolerant keystone prey could be modified so that the removal of keystone prey would decrease species diversity. If the predator switches to the keystone prey when numbers of other prey species are low, then sensitive prey that otherwise would have been driven to extinction may coexist in the presence of the predator-tolerant keystone prey. Thus, we again see that the label *keystone* has been applied to species whose removal would either increase or decrease species diversity in their communities.

Keystone mutualists. Some species have been considered to be keystone because they are critical to mutualistic relationships. Gilbert (1980) introduced the term *mobile links* to describe "animals that are significant factors in the persistence of several plant species which, in turn, support otherwise separate food webs." The implication was that mobile links are a kind of keystone species, and mobile links have since been frequently cited as examples of keystone species. In addition to the mobile-link pollinators and seed dispersers described by Gilbert (1980), other examples of this type of keystone species include hummingbird pollinators and mammalian dispersers of mycorrhizal fungi (Wilcox and Murphy 1985).

Keystone hosts. If mobile links, or keystone mutualists, depend critically on ecologically important host plants, then it follows that these hosts also receive the label *keystone*. Included in this group are those plants that support generalist pollinators and those fruit dispersers that are considered critical mobile links (Gilbert 1980). Terborgh (1986) considered palm nuts, figs, and nectar to be keystone resources because they are critical to tropical forest nectar or fruit eaters, including primates, squirrels, rodents, and many birds. Together, these vertebrates account for as much as three-quarters of forest bird and mammal biomass.

Keystone modifiers. The activities of many species greatly affect habitat features without necessarily having direct trophic effects on other species. If the modified habitat affects the survival of many other species, the modifying species has been considered a keystone species. The North American beaver (*Castor canadensis*) was described as a keystone species because its dams alter hydrology, biogeochemistry, and productivity on a wide scale (Naiman et al. 1986). Likewise, the Brazilian termite (*Cornitermes cumulans*) has been called a keystone species because loss of its large, abundant, and uniquely structured mounds would likely precipitate loss of obligate and possibly opportunistic users of the mounds (Redford 1984).

Many species have been called key-

stone herbivores because their foraging causes drastic habitat modification. Based on the observation that large herbivores (more than 1000 kg) can readily convert closed thicket or forest into open grassy savanna, Owen-Smith (1987) posited a keystone-herbivore hypothesis to explain the late Pleistocene extinction of approximately half of the mammalian genera with body masses of 5–1000 kg. This theory posits that the elimination of large herbivores initiated vegetational changes that were deleterious to the fauna.

A keystone-herbivore hypothesis was also advanced to describe red-naped sapsuckers (*Sphyrapicus nuchalis*), which create sap wells in tree bark, thereby providing resources for other herbivores (Ehrlich and Daily 1988). Sea urchins have been called keystone because their grazing prevents the change from a system dominated by encrusting algae to a system dominated by large, fleshy algae (Fletcher 1987, see also VanBlaricom and Estes 1988). Similarly, pocket gophers (*Thomomys bottae*) were described as keystone because they maintain mountain meadow communities by slowing down aspen invasion of the meadows (Cantor and Whitham 1989). After the removal of what they called a “keystone guild” of kangaroo rats (*Dipodomys* spp.), Brown and Heske (1990) documented drastic changes in vegetation type and accompanying changes in the rodent community. Clearly, the distinction between keystone predation and keystone modification becomes fuzzy for those species that modify habitat through predation on plants.

Useful contributions of the keystone-species concept

We have seen that the label *keystone* has been applied to a plethora of species with very different effects—both qualitative and quantitative—on their communities. Given the diversity of the usages of the term *keystone species* in the ecological literature, what are the contributions and liabilities of this concept for ecological and conservation research?

One fundamentally important contribution is the attention these studies have drawn to differing interaction strengths in community food webs.

Table 2. Predicted or observed effect of removing presumed keystones, based on articles in which authors called a species *keystone* and predicted a community composition change upon removal.

Author	Presumed keystone (community type)	Effect of removal
Paine (1966, 1969)	Starfish (rocky intertidal)	Observed reduction of system from 15 to 8 species
Fletcher (1980)	Sea urchins (subtidal)	Observed takeover of large fleshy algae, resulting in loss of approximately one-half of grazers
Terborgh (1986)	Palm nuts, figs, and nectar (tropics)	Predicted loss of one-half to three-quarters of total bird and mammal biomass
Owen-Smith (1987)	Herbivores more than 1000 kg (Pleistocene)	Hypothetical mechanism for loss of approximately half of mammalian genera during late Pleistocene

Robert MacArthur (1972) first advocated close scrutiny of interaction strengths, defining a strong interactor simply as a species whose “removal would produce a dramatic effect.” Studies of presumed keystone species have certainly demonstrated the presence of strong interactors in many systems.

To gain some quantitative feel for the extent to which the removal of presumed keystone species may decrease overall species diversity, we reviewed all published studies we could find that refer to a species as a keystone and that predict or describe specific community composition changes occurring on removal of the presumed keystone. Despite the fact that investigators encountered enormous methodological problems and employ different trophic and taxonomic criteria to circumscribe the relevant assemblage, an interesting consistency is revealed (Table 2). Ecologists identify as keystone those species whose removal is expected to result in the disappearance of at least half of the assemblage considered. For reasons we will detail below, however, we hasten to warn against the use of a 50% loss rule as an operational criterion for identifying a species as keystone.

The second important contribution of the keystone paradigm is its implication that only a small minority of species have strong interactions that affect community composition. In other words, reference to a particular species as keystone implies that it is unusual, standing out from the majority of the other species in its effects on community structure or function. If we define the community importance of a given species as the percentage of

other species lost from the community after its removal, we can illustrate this assumption by plotting, for a hypothetical community, the relative community importance of each species (Figure 1). The keystone concept assumes that frequencies of community-importance values are strongly skewed, with only a few species having large effects on the composition or structure of the community (Figure 1a).

In contrast to this assumption, food-web theorists have generally assumed either that species-by-species interaction strengths are drawn from symmetrical distributions (e.g., Figure 1b, normal distributions; Cohen and Newman 1988) or else are uniform (Figure 1c, an implicit assumption of static food webs; see Pimm and Kitching 1988). Although species-by-species interaction strengths are unlikely to directly correspond to community-importance values as defined here, there is likely to be considerable correlation between the two. In particular, it is difficult to imagine a species having a large effect on species diversity (community importance) without having strong interactions with other species. Thus, the keystone concept’s implicit assumption about interaction strengths appears to be in conflict with the more explicit, but not necessarily more realistic, food-web models (Lawton 1992).

This apparent dichotomy between food-web theory and the keystone-species concept is certainly worth exploring. The two conceptualizations imply different patterns of community structure and hence require different conservation strategies. If many or most species are of similar importance (Figure 1b,c), any efforts to save

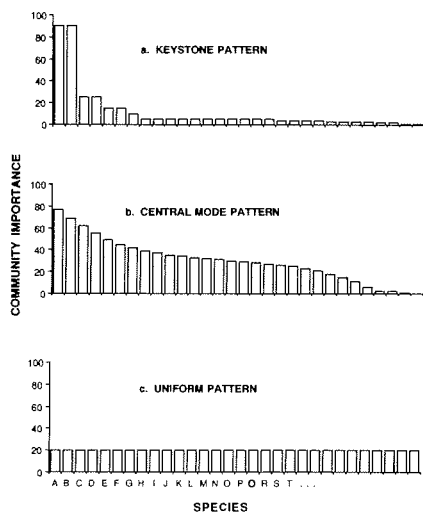


Figure 1. Expected distributions of community importance values (percent of species lost from a community upon removal of a given species) for a hypothetical community based on the keystone-species model (a) and based on food-web theory (b and c). Axes are arbitrarily scaled to demonstrate the general shape of the distributions.

only a few keystones will inevitably fail to protect the rest. Conversely, if only a few species have strong interactions/community effects, then detailed understanding and protection of the few important taxa would be critical to the well-being of the overall community.

What do the data say about this conflict? To date, only one study has addressed the distributions of interaction strengths in part or all of an ecological community. Paine (1992) developed an index of per capita interaction strength and found that only two of seven species of intertidal grazers strongly affect brown algae, which are their major food and also a profound modifier of the local environment. These results indicate "a few strong interactions embedded in a majority of negligible effects" (Paine 1992), supporting an assumption of highly skewed interaction strengths (Figure 1a). Although suggestive, it is premature to generalize this result: Paine looked at only one type of interaction for each species (herbivory of brown algal sporlings) and he looked at only a subset of the grazers within a single community. Indeed, his finding that 29% of the species were strong interactors could be interpreted as indicating that a large fraction of species have strong effects. Clearly, more

studies of this type are needed in many more communities.

Keystones and conservation

What role should the keystone-species concept play in conservation efforts? Currently, implementation of the Endangered Species Act often amounts to emergency-room conservation (Scott et al. 1987), whereby the bulk of conservation resources are spent on single species that are on the brink of extinction. In the absence of comprehensive biodiversity legislation and/or increased funding and support for the Endangered Species Act, it has been suggested that "The Act could serve as an extremely useful tool for preserving keystone species, thus indirectly benefiting the many other life forms in some way dependent upon those species" (Rohlf 1991; see also Burkey 1989, Westman 1990).

We see both technical and philosophical liabilities associated with reliance on keystone species in a conservation context. (See Landres et al. 1988 for a parallel critique regarding labeling certain species "indicator species.") The overriding technical difficulty is one of definition. Before keystone species become the centerpiece for biodiversity protection or habitat restoration, we must be able to say what is and is not a keystone species.

Lacking any a priori definition, the best way to identify keystone species would be perturbation experiments whereby the candidate keystone species are removed and the responses of a predefined assemblage of species are monitored. Such tests would require adequate experimental replication and careful attention to defining the relevant assemblage (MacMahon et al. 1978 give a useful organism-centered definition of community), as well as consideration of time scales over which responses should be measured.

Bender et al. (1984) evaluated mathematical approaches for evaluating the consequences of the inevitable omission of certain species in perturbation experiments and the impact of lumping together the interactions of related groups of organisms (e.g., combining data for related ant species to measure the effect of removing a granivorous rodent). Extraordinary difficulties await researchers attempting such experiments (see Bender et

al. 1984, Carpenter et al. 1985). The problem of objectively defining which species are keystone makes it likely that subjectively chosen subsets of species will be so labeled, whereas other species of similar importance will be ignored.

Even if keystone species could readily and reliably be identified for a given location at a given time, several philosophical dangers arise. First, the term is burdened with historical connotations that, as shown earlier, mean different things to different people. The lack of a clear operational definition hinders any political or legal implementation. Second, the term *keystone species* is misleading because it indicates the existence of a species-specific property of an organism, when in actuality the keystone role is particular to a defined environmental setting, the current species associations, and the responses of other species (Gautier-Hion and Michaloud 1989, Jackson and Kaufmann 1987, Levey 1988, Palumbi and Freed 1988). Thus, it is exceptionally difficult to confidently define a priori which local populations (not to mention species) are keystone (Elner and Vadas 1990, Foster and Schiel 1988). Another problem is that removal of combinations of nonkeystone species could have effects as large as removal of a keystone.

Finally, a conservation criterion that favors the maintenance of keystone species—and with them the majority of species in a community—may fail to protect other species of interest to conservationists or the public at large. For example, spotted owls, wolverines, grizzly bears, and California condors may have little role in the maintenance of species richness in their respective habitats, yet the protection of these charismatic species has been advanced because their fates are thought to indicate the integrity or health of their habitats, or because the viability of many such species requires large areas; these areas may ensure, in turn, sufficient habitat heterogeneity and space for large numbers of other species, some of which may have specialized requirements.

In sum, both the complexity of ecological interactions and ignorance of them militates against the application of the keystone-species concept for practical management recommen-

dations. Despite its heuristic value, we see more harm than good in the formalization of the term in laws and policy guidelines that have rigid practical implications.

Conclusions

The lack of data addressing both the range of interaction strengths within communities and the generality of trends across communities leads us to suggest that neither the science of ecology nor the protection of biodiversity is advanced by continuing to label certain species as keystone. Instead, we advocate the study of interaction strengths and subsequent application of the results into management plans and policy decisions. Emphasizing strengths of interactions instead of a keystone/nonkeystone dualism is more than a semantic improvement; it recognizes the complexity, as well as the temporal and spatial variability, of interactions.

Although Paine's 1992 study is compelling in its demonstration of the existence of just a few strong interactors for the rocky intertidal zone, no data address whether other systems have similarly distributed interaction strengths. Paine's tantalizing results should inspire theoreticians to explore the implications of assemblages structured with many weakly interacting species and only a few strong interactors. At the same time, further empirical studies could assess, at the level of both short- and long-term effects (Carpenter and Kitchell 1988), the generality of skewed interaction strengths and trophic cascades (e.g., Carpenter et al. 1985, Paine 1980, Power 1990) or mesopredator release in the absence of a larger predator (Soulé et al. 1988).

If they abandon the keystone-species concept and the rigid structure it imposes on species interactions, investigators are less likely to assume that interactions or their strengths and distributions are constant in space and time. The concept has been useful in demonstrating that under certain conditions some species have particularly strong interactions, and we recognize that in recommending the abandonment of a popular and evocative concept there is a danger of making it more difficult for biologists to communicate with policy makers, manag-

ers, and the public. We think, however, that the inconvenience caused by the dropping of the label *keystone species* will, in the long run, be compensated by the development of management and policy guidelines that more explicitly accounts for the complexity of interactions in natural systems.

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Research Article

Lesser Prairie-Chicken Space Use in Relation to Anthropogenic Structures

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ABSTRACT The Southern Great Plains has been altered by conversion of native grassland to row-crop agriculture, which is considered the primary cause of declining lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations. However, recent analyses indicate that direct loss of grassland has slowed while lesser prairie-chicken populations continue to decline, suggesting that remaining grasslands potentially suffer from degradation by various land uses (e.g., increased anthropogenic disturbance). Understanding the spatial ecology of lesser prairie-chickens relative to anthropogenic structures is important for conservation planning, habitat management, and infrastructure mitigation. We investigated effects of proximity to anthropogenic structures on home range and nest placement (second-order selection) and within home range space use (third-order selection) of radio-marked lesser prairie-chickens ($n = 285$) at 2 scales of selection using resource utilization functions and resource selection functions. We collected data from birds marked in the Mixed-Grass Prairie and Short-Grass Prairie ecoregions of Kansas, USA, from 15 March 2013 to 14 March 2016. Home range placement did not vary by region or season, and lesser prairie-chickens placed home ranges farther from powerlines and roads than would be expected at random. As distance increased from 0 to 3 km away from roads and powerlines, the relative probability of home range placement increased 1.66 and 1.54 times, respectively. Distance to powerline was the single most consistent variable negatively affecting nest placement. As the distance from powerline increased from 0 to 3 km, the relative probability of nest placement increased 2.19 times. Distance to oil well did not influence placement of home ranges or nests. When pooled across regions, lesser prairie-chickens exhibited behavioral avoidance of powerlines, roads, and oil wells within their home range. Lesser prairie-chickens, on average, used space at greater intensities within their home range farther from wells, powerlines, and roads than available. Across breeding season phases, we found no evidence of increased behavioral avoidance of anthropogenic structures during the nesting or brooding phases compared to the lekking or post-breeding phases. Within home range space use during the brooding phase was not related to powerlines, wells, or roads. Our results indicate that avoidance of anthropogenic structures may result in functional habitat loss and continued fragmentation of remaining grassland habitat. Reduction or elimination of anthropogenic development in quality lesser prairie-chicken habitat and concentrating new development in already altered areas that are avoided by lesser prairie-chickens and no longer considered available habitat may reduce continued habitat degradation throughout the species' range and aid in population persistence. © 2018 The Wildlife Society.

KEY WORDS anthropogenic, Kansas, lesser prairie-chicken, management, mitigation, *Tympanuchus pallidicinctus*.

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Demand for domestic oil, natural gas, and wind energy within the United States has spurred increased anthropogenic disturbance in the Great Plains, which can negatively affect wildlife populations (Pruett et al. 2009a, Hagen et al. 2011, Allred et al. 2015). Development of energy infrastructure can result in direct habitat loss from the development footprint, behavioral responses to development-related activities, or fragmentation by way of infrastructure needed for exploration, development, or extraction (Northrup and Wittemyer 2013, Hovick et al.

2014, Winder et al. 2014). Infrastructure development can cause direct mortalities from collisions with the structures themselves or vehicles, exacerbate fragmentation by providing access to further development, and provide travel corridors and perching sites for mammalian and avian predators (Wolfe et al. 2007, Naugle et al. 2011, Northrup and Wittemyer 2013, Allred et al. 2015).

The lesser prairie-chicken (*Tympanuchus pallidicinctus*) is an endemic prairie grouse that resides in the southern Great Plains of Texas, New Mexico, Oklahoma, Kansas, and Colorado, USA, and has experienced significant declines in population size and occupied range during the last several decades (Hagen et al. 2013, Boal and Haukos 2016). Range-wide declines have been associated with the loss of habitat quantity and quality resulting from conversion of native prairie to cropland, energy development, invasive species, and unmanaged grazing (Hagen et al. 2004, Boal and Haukos 2016, Rodgers 2016, Van Pelt 2016). The lesser prairie-chicken has been petitioned for protection under the 1973 Endangered Species Act twice since 1995 but remains under review in response to a petition following a 2015 judicial ruling and subsequent removal of the species from the Federal List of Endangered and Threatened Wildlife in 2016. Despite the species' contentious legal status, threats to population persistence continue with increasing pressure from energy exploration and development, necessitating continued investigation of anthropogenic effects on lesser prairie-chicken populations.

In 2017, an estimated 88% of the remaining range-wide population of lesser prairie-chickens occurs in the Sand Sagebrush Prairie (SSPR), Short-Grass Prairie-Conservation Reserve Program Mosaic (SGPR), and Mixed-Grass Prairie (MGPR) ecoregions of Kansas (McDonald et al. 2014). Strategies for protection of the lesser prairie-chicken and its habitat are inherently complex because much of the species' range is rich with energy resources and widely used for fossil fuel exploration and extraction (Hagen and Giesen 2005, Bartuszevige and Daniels 2016, Van Pelt 2016). Research on multiple species of prairie grouse, including the lesser prairie-chicken, has demonstrated that these species are sensitive to anthropogenic disturbance on the landscape (e.g., Hagen 2010, Hovick et al. 2014). Most research investigating effects of anthropogenic disturbance on lesser prairie-chicken ecology has focused outside of their core area in the Sand Shinnery Oak Prairie (SOPR) ecoregion of Texas and New Mexico (Grisham et al. 2014, Godar 2016, Griffin 2016) and the southernmost portion of the MGPR ecoregion in Oklahoma (Pruett et al. 2009a,b; Dusang 2011). Contemporary research of anthropogenic disturbance on lesser prairie-chicken space use ecology is lacking in the core area of their range in Kansas. Only one study, occurring in the SSPR of southwest Kansas, has occurred in the lesser prairie-chicken's core area (Robel et al. 2004, Pitman et al. 2005, Hagen et al. 2011). Researchers have not investigated the effects of anthropogenic disturbance on lesser prairie-chicken ecology in either the northern portion of the MGPR or the SGPR in south-central and northwest Kansas, respectively, or investigated if these effects vary regionally.

Additionally, researchers have examined the apparent avoidance of anthropogenic disturbance, but true avoidance, based on behavioral observations, has not been quantified for the genera, except in the congeneric populations of greater prairie-chickens (*Tympanuchus cupido*; Winder et al. 2014, Hovick et al. 2014, Bartuszevige and Daniels 2016).

Habitat, or "the resources and conditions present in an area that produce occupancy—including survival and reproduction—by a given organism" (Hall et al. 1997:175), varies in quality based on the accessibility of resources, whereby selection is an active process in which individuals can assess the quality of each habitat patch and are free to move to the highest quality patch (Haukos and Zavaleta 2016). Initial declines in lesser prairie-chicken populations were associated with direct habitat loss from conversion of native prairie to row-crop agriculture (Boal and Haukos 2016). However, for the last 2 decades, direct loss of grassland in the northern extent of the species range has been minimal (Ross et al. 2016, Spencer et al. 2017). Current lesser prairie-chicken populations have continued to decline despite grassland quantity remaining stable, suggesting that degradation of remaining grassland habitat may be the culprit. If increased anthropogenic development within the lesser prairie-chicken range results in behavioral displacement, avoidance, or a reduction in the probability of selection of otherwise quality habitat, especially for nesting and brooding, then the grassland habitat has either been degraded or functionally lost (Robel et al. 2004). Pitman et al. (2005), for example, estimated that in the SSPR of southwest Kansas anthropogenic features reduced their field site 53% from 13,380 ha of available habitat to 7,114 ha through avoidance behavior. Alternatively, if females select habitat near anthropogenic structures (e.g., oil wells), which results in failed nests, broods, or increased female mortality, then the habitat would become an ecological trap (Aldridge and Boyce 2007). Reduction in the availability or quality of grassland habitat could have severe negative effects on reproduction, recruitment, and population persistence, especially when coupled with an already fragmented landscape. Relating the impact of anthropogenic development on lesser prairie-chicken-habitat relationships is vitally important to understanding potential negative population consequences and directing appropriate mitigation strategies for industrial development.

We assessed lesser prairie-chicken space use and nest site selection to anthropogenic structures in the northern portion of the MGPR and the SGPR in Kansas at 2 scales of selection: second order (i.e., home range and nest placement) and third order (i.e., differential space use within a home range; Johnson 1980). Our specific objectives were to quantify effects of anthropogenic structures on lesser prairie-chicken home range placement and space use between ecoregions for both 6-month seasons (i.e., breeding and nonbreeding), and within breeding season phases (i.e., lekking, nesting, brooding, post-breeding); investigate the influence of anthropogenic structures on nest-site selection; and provide distances that may buffer effects of these structures for use in development of future conservation and mitigation strategies. We predicted lesser prairie-chickens

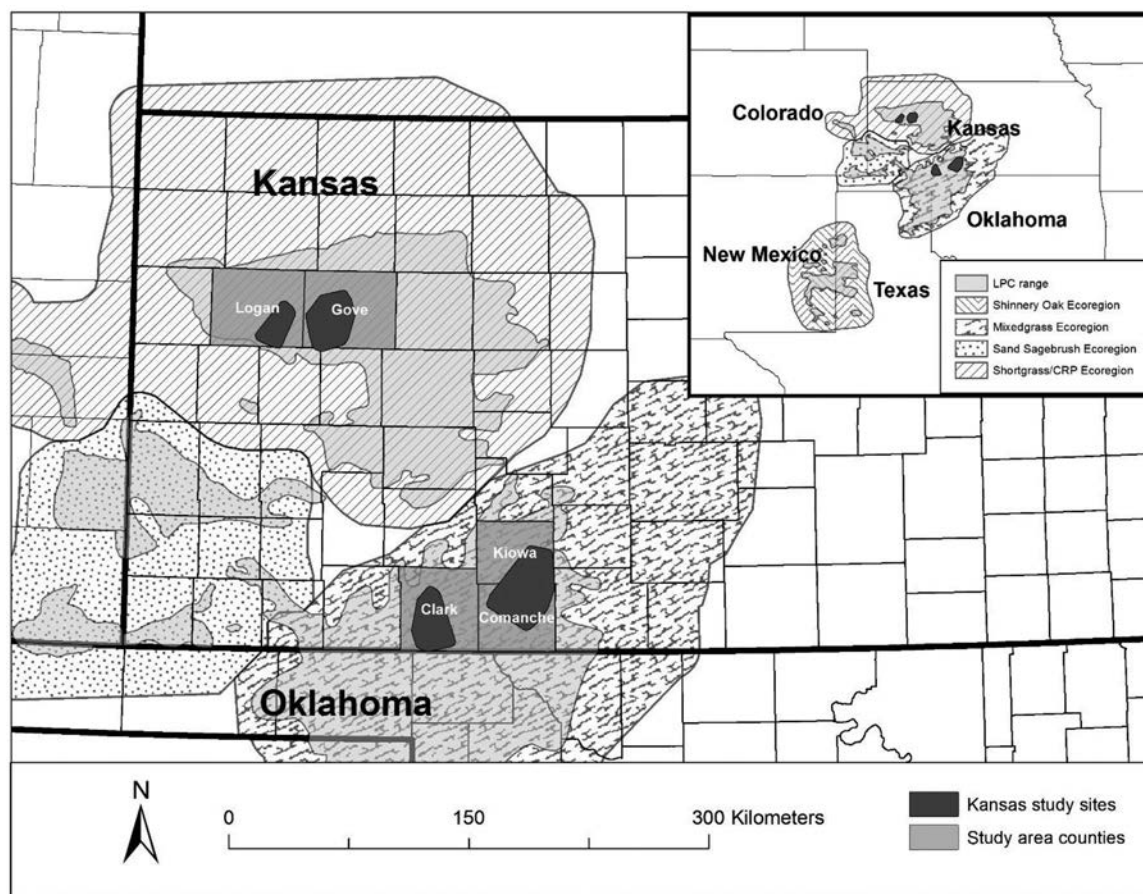


Figure 1. Study sites in northwest and south-central Kansas, USA, where we measured lesser prairie-chicken (LPC) space use, home range placement, and nest site selection in relation to anthropogenic structures, 2013–2016. Study areas in Kansas included northwest, with 2 sites (Logan in Logan County and Gove in Gove County), and south-central, with 2 sites (Red Hills in Kiowa and Comanche counties and Clark in Clark County).

would place home ranges, nests, and use space within their home range farther from structures than available; females would exhibit heightened avoidance of structures during the nesting and brooding phases of the breeding season; and lesser prairie-chicken home range placement and within home range space use would vary between ecoregions, with the magnitude of the effect of anthropogenic structures being greater in south-central Kansas (more intact landscape) than in northwest Kansas (fragmented landscape). Additionally, we predicted that the influence of anthropogenic structures would not differ between the 2 6-month breeding and nonbreeding season because anthropogenic structures do not change between seasons.

STUDY AREA

Our research was conducted from 15 March 2013 to 14 March 2015 in the SGPR (i.e., northwest Kansas) and MGPR and SSPR ecoregions (i.e., south-central Kansas) of Kansas, which supported approximately 88% of the range-wide lesser prairie-chicken population in 2017 (McDonald et al. 2017). We collected data during 2 6-month biological seasons, the breeding season (15 Mar–15 Sep) and nonbreeding season (16 Sep–14 Mar; Winder et al. 2017, Robinson et al. 2017). We established study area boundaries

by creating minimum convex polygons around all very high frequency (VHF) and satellite platform transmitting terminal (SAT-PTT) locations generated from marked birds in each area, excluding dispersal events (unidirectional movements >5 km), using the minimum bounding geometry tool in ArcGIS 10.2 (Environmental Systems Research Group [ESRI], Redlands, CA, USA; Robinson et al. 2017). Each study area was comprised of 2 field sites in each ecoregion. The northwest Kansas study area was 1,714 km² and encompassed sites located in Gove and Logan counties (Fig. 1). Research in the Gove County site was conducted solely on private lands. Research in Logan County was centered on The Smoky Valley Ranch owned and managed by The Nature Conservancy and surrounding private lands.

The northwest study area was a mosaic of short-grass and mixed-grass prairies, land enrolled in the Conservation Reserve Program (CRP) with the United States Department of Agriculture, and row-crop agriculture on silt-loam soils (McDonald et al. 2014). Long-term average temperatures in the study area ranged between −8.5°C and 33.1°C (High Plains Regional Climate Center [HPRCC] 2017). Elevation ranged from 733 m to 961 m (U.S. Geological Survey [USGS] 2015). Long-term average annual precipitation in the northwest study area ranged from 46.7 cm to 56.6 cm and

the average frost-free period ranged from 132 days to 168 days (Kansas State University [KSU] 2018, HPRCC 2018). During the study period, annual precipitation was 56.6 cm, 65.3 cm, and 53.6 cm for 2013, 2014, and 2015, respectively. Annual temperatures ranged from minimums of -20.0°C , -23.9°C , and -20.6°C to maximums of 41.7°C , 38.3°C , and 38.9°C in 2013, 2014, and 2015, respectively (HPRCC 2018). Dominant vegetation in the region included blue grama (*Bouteloua gracilis*), hairy grama (*B. hirsuta*), buffalograss (*B. dactyloides*), little bluestem (*Schizachyrium scoparium*), sideoats grama (*B. curtipendula*), big bluestem (*Andropogon gerardii*), Illinois bundleflower (*Desmanthus illinoensis*), prairie sunflower (*Helianthus petiolaris*), annual buckwheat (*Eriogonum annuum*), sand milkweed (*Asclepias arenaria*), nine-anther dalea (*Dalea enneandra*), and western ragweed (*Ambrosia psilostachya*; Lauver et al. 1999). Some of the grass species originally planted within the CRP fields included little bluestem, sideoats grama, big bluestem, switchgrass (*Panicum virgatum*), blue grama, buffalograss, and Indian grass (*Sorghastrum nutans*; Fields et al. 2006). After original planting in the mid-late 1980s, some CRP fields were interseeded with forbs in the mid-1990s including white sweet clover (*Melilotus alba*), yellow sweet clover (*M. officinalis*), Maximillian sunflower (*Helianthus maximiliani*), Illinois bundleflower, purple prairie clover (*Dalea purpurea*), and prairie coneflower (*Ratibida columnifera*; Fields et al. 2006). Wheat, sorghum, and corn were the major crops in the region. Dominant fauna in northwest Kansas consisted of coyote (*Canis latrans*), swift fox (*Vulpes velox*), striped skunk (*Mephitis mephitis*), northern harrier (*Circus cyaneus*), Swainson's hawk (*Buteo swainsoni*), red-tailed hawk (*Buteo jamaicensis*), ring-necked pheasant (*Phasianus colchicus*), white-tailed deer (*Odocoileus virginianus*), and mule deer (*Odocoileus hemionus*; Robinson et al. 2017). The dominant land uses in this region were rotational and season-long livestock grazing, row-crop agriculture, CRP, oil extraction, electrical distribution, and rural towns.

The northwest Kansas landscape was comprised of 54.0%, 36.0%, and 7.4% grassland, crop, and CRP, respectively (Robinson et al. 2018). The northwest Kansas site was characterized as a fragmented grassland landscape (Robinson et al. 2018). The density of anthropogenic structures in northwest Kansas was 0.34 oil wells/km², 0.31 km of powerline/km², and 0.43 km of road/km², respectively.

The south-central Kansas study area was 1,203 km² and encompassed sites located on private lands in Kiowa, Comanche, and Clark counties (Fig. 1). This area consisted of mixed-grass prairie on loamy soils, with primary land uses of livestock grazing, oil and gas extraction, and limited row-crop agriculture in bottomland areas. Long-term average temperatures ranged from -7.5°C to 33.8°C (HPRCC 2017). Elevation ranged from 515 m to 703 m (USGS 2015). Long-term average annual precipitation in the south-central study area ranged from 56.6 cm to 72.5 cm and the average frost-free period ranged from 144 days to 225 days (KSU 2018, HPRCC 2018). During the study period, annual precipitation was 72.4 cm, 63.2 cm, and 70.6 cm for 2013,

2014, and 2015, respectively. Annual temperatures ranged from minimums of -18.9°C , -22.2°C , and -14.4°C to maximums of 42.2°C , 38.9°C , and 41.7°C in 2013, 2014, and 2015, respectively (HPRCC 2018). Dominant vegetation within the region included little bluestem, blue grama, hairy grama, sideoats grama, buffalograss, sand dropseed (*Sporobolus cryptandrus*), alkali sacaton (*S. airoides*), Louisiana sagewort (*Artemisia ludoviciana*), annual sunflower (*Helianthus annuus*), western ragweed, sand sagebrush, Russian thistle (*Salsola kali*), Kochia (*Kochia scoparium*), and eastern redcedar (*Juniperus virginiana*; Lauver et al. 1999). Dominant fauna in south-central Kansas consisted of coyote, striped skunk, American badger (*Taxidea taxus*), northern harrier, red-tailed hawk, ring-necked pheasant, and white-tailed deer (Robinson et al. 2017).

The south-central Kansas landscape was comprised of 86.7%, 8.9%, and 2.2% grassland, crop, and CRP, respectively. The south-central region of Kansas was characterized by large intact tracts of native mixed-grass prairie with minimal row-crop agriculture and was less fragmented than northwest Kansas (Robinson et al. 2018). The density of anthropogenic features in south-central Kansas was 0.21 wells/km², 0.29 km of powerline/km², and 0.39 km of road/km², respectively.

METHODS

Radio-Telemetry

We captured lesser prairie-chickens on leks sites during spring (Mar–May) and fall (Sep–Oct) of 2013–2015 using walk-in drift traps, rope-triggered drop-nets, and magnetic drop-nets (Haukos et al. 1990, Silvy et al. 1990, Schroeder and Braun 1991). We identified sex using the presence of air-sacs, greater pinnae length in males, and tail feather color (females have barred tail feathers and males have mainly black tail feathers; Copelin 1963).

We marked female lesser prairie-chickens with either a 15-g bib-style VHF transmitter (A3960, Advanced Telemetry System, Isanti, MN, USA) or a rump-mounted 22-g SAT-PTT global positioning system (GPS) transmitter (Solar Argos-GPS PTT 100, Microwave Telemetry, Columbia, MD, USA; Bedrosian and Craighead 2007, Wegge et al. 2007). We opportunistically equipped male lesser prairie-chickens with the remaining SAT-PTT transmitters after females stopped attending leks in May. We used male prairie-chicken data in nonbreeding season analyses because home range size and space use behavior did not differ between sexes (Robinson et al. 2018). We released captured individuals within 20 minutes of initial capture at the capture site. All capture and handling procedures were approved by the Kansas State University Institutional Animal Care and Use Committee (protocols 3241 and 3703) and Kansas Department of Wildlife, Parks, and Tourism scientific collection permit (SC-042-2013, SC-079-2014, SC-001-2015, SC-014-2016).

We located lesser prairie-chickens equipped with VHF transmitters 3–5 times/week and collected spatial locations via triangulation (Cochran and Lord 1963). We triangulated

individuals from 3–5 locations using a 3-element hand-held Yagi antenna and either an Advanced Telemetry Systems Receiver (R4000, R4500) or a Communications Systems 49 Receiver (R1000, Communications Specialists, Orange, CA, USA). We took bearings of locations ≥ 15 degrees apart and within 20 minutes to decrease error from bird movement. We used Location of a Signal (LOAS; Ecological Software Solutions LLC, Hegymagas, Hungary) to estimate the Universal Transverse Mercator (UTM) location and error polygon around the location of the individual. If individuals could no longer be located because of dispersal from the study area, we used a fixed-wing Cessna aircraft (Cessna, Wichita, KS) to locate the lost individual. Birds outfitted with a SAT-PTT transmitter recorded up to 10 GPS positions a day with 18-m accuracy between 0600 and 2200. We downloaded points weekly from the Argos satellite system (CLS America, Largo, MD, USA) to obtain UTM locations, locate nests, and find mortalities. We tracked marked lesser prairie-chickens from date of capture until they emigrated from the study area and we could no longer locate the lost individual, the radio failed, or the animal died.

Breeding Season Phases

Lesser prairie-chicken space use varies depending on the behavioral phase and season (Riley et al. 1994, Jamison 2000, Plumb 2015, Robinson 2015). Therefore, the probability of interaction with and the magnitude of influence from anthropogenic development on lesser prairie-chicken space use likely varies and should be investigated separately for each phase and season. During the breeding season, we categorized behavioral phases for each female using empirical data of reproductive status (e.g., lekking, nesting, brood rearing, post-breeding) to generate biologically relevant estimates of space use rather than using subjective calendar dates.

We defined lekking, the time when females were visiting leks, as the time from capture or start of the breeding season (15 Mar) to the start of nest initiation and the time between a failed nest and nest initiation of a re-nest attempt. We pooled the nesting phase across all nest attempts and began at the start of nest initiation until we determined the fate of the nest. At this juncture, females could enter the brooding phase if the nest was successful, enter back into the lekking phase for another breeding attempt, or omit from further breeding attempts and enter the post-breeding phase. Females that had successful nests entered the brooding phase until we determined the fate of the brood using brood flushes. If a brood failed between brood flushes, we used the median date as the transition from the brooding phase into the post-breeding phase. We determined the end of the breeding season as the average date of brood break up (15 Sep). Females could end the breeding season in either the brooding phase if the brood was still with the female until the average brood break up date, or in the post-breeding phase if all other breeding attempts failed.

Spatial Analysis

Space use.—We collected spatial locations using VHF and SAT-PTT transmitters at 2 different temporal resolutions: 3–5 locations/week for VHF and approximately 70

locations/week for SAT-PTT transmitters. Differences in data resolutions required us to use separate methods of space use estimation. We used a fixed-kernel density estimator within the function `kernelUD` in the program `adehabitatHR` (Calenge 2006) of the statistical program R (R Core Development Team, Vienna, Austria) to estimate space use for coarse temporal spatial data generated from VHF-marked individuals. We used the `dpik` function in the program `KernSmooth` (`KernSmooth` version 2.23-15, <https://cran.r-project.org/package=KernSmooth>, accessed 29 June 2015) to select a direct plug-in bandwidth for smoothing of the kernel estimation (Wand and Jones 1995). We created utilization distributions (UD) for all marked individuals that had ≥ 25 locations each for both breeding and nonbreeding seasons (Pruett et al. 2009b). We did not estimate VHF UD for specific breeding season phases because there were not enough locations collected within each phase to meet the minimum location requirement.

We estimated space use of SAT-PTT-marked individuals using the Brownian bridge movement model (BBMM; Horne et al. 2007) with the BBMM function in the BBMM package (Nielson et al. 2012) of the statistical program R. The BBMM is a continuous-time stochastic model of movement in which the probability of being in a specific space at a given time is conditioned on starting and ending locations, time elapsed between those 2 locations, error associated with the transmitter, and mobility of the organism (Horne et al. 2007). This methodology explicitly makes use of auto-correlated telemetry data and is well suited for GPS data (Bullard 1991, Walter et al. 2011). We limited the sample to only females that had > 90 locations (~ 10 days). We removed from the dataset birds that did not meet the location requirement. We did not use segments of the animal track that had starting and ending locations with elapsed time between them $> 2,880$ minutes (> 2 days) in the Brownian motion variance calculation. We estimated the biotelemetry error as 1 standard deviation from the average linear error calculated from a beacon test (5.7 m; Nielson et al. 2012).

For both methods of estimation, we used only female locations to estimate space use during the breeding season. Females influence population demography because they take sole parental care of the young and they were our focus during the breeding season (Hagen et al. 2008). To investigate nest site selection and female space use separately, we removed all repeat nest locations from female space use data during the breeding season so we would not bias the UD (Hagen et al. 2011). We conducted a separate analysis investigating the relationship between nest placement and anthropogenic structures.

Space use centroids.—We defined space use centroids as the geographic center of the 1% isopleth polygon of the BBMM and kernel UD. We choose the 1% percent isopleth polygon because it represents the area of greatest concentration of use within the UD (Winder et al. 2015). We generated isopleth polygons for each estimated BBMM and kernel UD by importing each bird's UD into the Geospatial Modeling Environment (Beyer 2012) and using the isopleth tool. We then imported isopleth polygons into ArcGIS 10.2 and used

the feature-to-point tool to estimate the center of gravity or centroid of each 1% percent isopleth polygon created. If multiple centroids were created for an individual UD because of large-scale movements, dispersal, or different areas selected within the home range as a result of behavioral state, we defined each centroid as an independent location of home range placement through time and used all created centroids for analysis.

Space use predictors.—We hypothesized that 3 different anthropogenic structures reported to negatively influence lesser prairie-chicken home range placement and nest site selection in other regions would influence lesser prairie-chicken selection in our study areas: distance to oil and gas wells (hereafter wells), distance to distribution powerlines (hereafter powerlines), and distance to roads (county gravel and paved; Pitman et al. 2005, Pruett et al. 2009b, Hagen et al. 2011). We did not include ranch roads (i.e., unimproved 2-tracks) because these have relatively low frequency of vehicle traffic. Additionally, we did not differentiate between gravel and paved roads or distribution and transmission lines because paved roads and transmission lines occurred in low frequency within our study sites and were not often encountered by marked lesser prairie-chickens. We were unable to determine the power source of all active wells on the landscape and therefore, did not distinguish among power sources operating wells. We included all roads (paved or gravel) and well pumping units (electric or gas powered) in the analysis as either well or road (Hagen et al. 2011). We collected active well and road layers from the Kansas GIS and Data and Support Center (www.kansasgis.org, accessed 9 Sep 2015). We obtained powerline layers from the Kansas Corporation Commission (<http://www.kcc.state.ks.us/>, accessed 16 Sep 2014).

Anthropogenic structures are likely spatially correlated because development of a region would require a clustering of basic infrastructure (e.g., roads and powerlines), especially for oil and gas exploration and extraction. Variables exhibiting multicollinearity can be problematic for coefficients in regression modeling (Belsley et al. 1980). We tested for multicollinearity among variables using condition indices and variance decomposition rates, as described by Belsley et al. (1980), where condition indices ≥ 30 coupled with ≥ 2 variables with variance decomposition proportions $> 50\%$ indicate collinearity issues. If variables were indicated as being highly correlated, we chose the variable we felt had the greatest biological meaning according to the current knowledge of anthropogenic avoidance in published literature (Doherty et al. 2008). Further, when variables were moderately correlated, we checked for stability and consistency of regression coefficient estimates as we added predictor variables to models. If a regression coefficient switched signs when correlated variables were in the same model, we removed one variable from the analysis if the other was an important predictor (Doherty et al. 2008).

We were also interested in investigating regional and season variation in the effects of our anthropogenic predictors. We included 2 categorical variables for region and season and an interaction term to determine if the effect

of the anthropogenic variables changed as a function of either region (northwest or south-central), season (breeding or nonbreeding), or both.

Statistical Analysis

Second-order selection.—We used a resource selection framework (i.e., used [1] vs. available [0] study design) to test the effects of distance to anthropogenic structures on lesser prairie-chicken home range and nest placement on the landscape (Boyce et al. 2002, Manly et al. 2002). We considered the area within a 3-km buffer of home range centroids and nests as the maximum perceived area available in which a lesser prairie-chicken could place their home range or nest. We selected 3 km as the area available for home range and nest placement because the average distance of non-dispersing lesser prairie-chickens who traveled from initial marking to the last location generated within either the 6-month breeding or nonbreeding season was 2.78 km (95% CI = 2.13, 3.42). Additionally, the average distance from lek of capture to nest location was 3.35 km (95% CI = 3.12, 3.58; R. T. Plumb, Kansas State University, unpublished data). To reduce the effect of landcover type on selection and isolate the effects of anthropogenic structures, we generated cover type polygons within all 3-km buffered areas for grassland and crop using the Playa Lakes Joint Venture landcover classification layer (McLachlan 2012). We then randomly distributed 3 times the number of home range centroids in direct proportion to the number of centroids witnessed in grassland ($\sim 93\%$) and crop ($\sim 7\%$) cover types to generate an estimate of distances to anthropogenic structures that would be available at random (Northrup and Wittemyer 2013). Unlike home range centroids, all nests were located within grassland cover types. Therefore, we randomly distributed 3 times the number of nest site locations only in grassland patches found in the 3-km buffered areas. We did not evaluate the influence of other landscape characteristics (e.g., landscape composition, terrain ruggedness, microhabitat) because we were interested in exploring only the spatial response of lesser prairie-chickens to anthropogenic structures. In doing so, we acknowledge that this approach is assuming that our disturbance metrics were not confounded by other latent sources of landscape heterogeneity. However, by using general landcover categories (i.e., grassland, crop) to constrain our placement of available locations, in relation to witnessed locations, we accounted for coarser resolution habitat selection, which allowed us to explicitly isolate effects of anthropogenic structures.

As a result of using 3 times the number of available locations compared to observed locations, our models were potentially biased toward the larger sample of available locations. We used an importance weight, which gives full weight to used locations but a fractional weight proportional to the ratio of observed locations to available locations (0.33) to reduced potential bias with our larger available sample. Weighting effectively adjusts the standard errors of the estimates and allows for traditional inferences of standard errors and *P* values for coefficient estimates (Aldridge and Boyce 2007, Carpenter et al. 2010).

For home range placement analysis, we assigned variables into 1 of 2 model categories: distance to anthropogenic structures and regional or seasonal effects. We then created models for each possible combination within each category and ranked models using Akaike's Information Criterion corrected for small samples sizes (AIC_c ; Burnham and Anderson 2002). We carried over models that were equally parsimonious ($\leq 2 \Delta AIC_c$) within each category to the next hierarchy of model selection and allowed models to compete across categories to test if the additional information increased model fit (Doherty et al. 2008). For nests, we created a set of models with each possible combination of anthropogenic variables and a categorical variable for region and ranked models using AIC_c (Burnham and Anderson 2002). We selected the model with the lowest AIC_c value and greatest model weight (w_i). We considered models with $\Delta AIC_c \leq 2$ to be equally parsimonious. For both analyses, if beta (β) coefficient estimates from the top model differed from zero (95% CI did not overlap 0), then we considered the variable to be influential. We estimated the relative probability of home range and nest placement in relation to the distance from each influential variable (0–3 km) using the predict function and plotted the relative probability of use curve while holding all other variables at their mean. We conducted all resource selection functions in Program R.

Third-order selection.—We measured differential space use relative to anthropogenic structures within the home range of each female marked with a SAT-PTT during the 6-month breeding season and both males and females during the 6-month nonbreeding season. During the breeding season, we also estimated differential space use for each of the breeding season phases. We did not use male prairie-chicken data during the breeding season because of differential space use behavior between sexes during the breeding season. We combined male and female UD's because space use behavior is similar between sexes during the nonbreeding season (Robinson et al. 2017). We did not use UD's estimated from VHF data in the third-order analysis because the BBMM estimation creates a more representative estimate of individual space use when compared to the kernel method (Horne et al. 2007). If we monitored individual lesser prairie-chickens in multiple seasons or years, we considered each 6-month breeding or nonbreeding season and breeding season phase to be independent for use of our complete data set (Winder et al. 2014). We used UD's to represent space use as a continuous, probabilistic variable. We estimated the Brownian motion variance ($\hat{\sigma}_m^2$), which is related to the animal's mobility, separately for each individual.

The spatial extent of space use and availability of variables of interest were defined by the 99% isopleth of the BBMM UD boundary for each lesser prairie-chicken's home range (Kertson and Marzluff 2011, Winder et al. 2014). We created a raster surface with 30-m² cells within the UD, where we assigned use values, bounded from 1 to 99, to each cell based on the relative volume (height) of the UD for that cell. We then log_e transformed space use data to meet

assumptions of multiple linear regression models (Kertson and Marzluff 2011). We used resource utilization functions (Marzluff et al. 2004) in the RUF.fit package (Handcock 2007) for Program R to relate the effect that distance to well, road, and powerline have on lesser prairie-chicken within home range space use. Resource utilization functions are based on relative space use, where the unit of study is the individual utilization distribution. A resource utilization function relates the intensity of use to the resources available within the 99% isopleth on a cell-by-cell basis in a multiple linear regression framework to obtain β coefficients. These coefficients indicate the relative importance or influence of each variable to the variation in the utilization distribution of each lesser prairie-chicken (Marzluff et al. 2004, Kertson and Marzluff 2011). We developed population inferences by calculating a mean standardized β coefficient ($\bar{\beta}$) for each predictor and pooled across years for each 6-month seasonal period and breeding season phase (Winder et al. 2014). We investigated regional effects by pooling across seasons for each region specifically. If the standardized coefficients differed from zero based on the range of their 95% confidence intervals, we inferred that the influence of that variable was either greater (+) or less (–) than expected compared to the availability of that resource within the home range (Marzluff et al. 2004, Winder et al. 2014).

Distance to anthropogenic structures.—We quantified distances of all estimated home range centroids to anthropogenic structures using the near tool in ArcMap 10.2. The near tool measures the shortest linear distance between locations and anthropogenic structures. Hagen et al. (2011) indicated that distance metrics that are averaged across all individuals may give spurious results because anthropogenic structures are not ubiquitously distributed across the landscape and, therefore, the distances may not produce a true representation of avoidance. To characterize distances for potential use in conservation planning and compare to Hagen et al. (2011), we used the lower tenth percentile of the distribution of observed distances because this represents the portion of the study population that occurred closest to the anthropogenic structures. Furthermore, the lower tenth percentile is not too extreme to be subject to excessive random variation in its estimation. We report all means with their associated 95% confidence intervals unless otherwise noted.

RESULTS

We captured 273 female and 341 male lesser prairie-chickens in northwest and south-central Kansas during spring 2013, 2014, and 2015. We deployed 170 SAT-PTT transmitters (female = 150, male = 20) and 115 VHF transmitters (all female) on captured lesser prairie-chickens. Of the 150 females marked with SAT-PTT transmitters, we successfully created 147 home range UD's during the 6-month breeding season and 87 UD's during the 6-month nonbreeding season. Within the 6-month breeding season, we created 138 UD's during the lekking phase, 124 UD's during the nesting (initial nests and re-nests) phase, 25 UD's during the brooding

phase, and 65 UD during the post-breeding phase. Using UDs generated from VHF- and SAT-PTT-marked birds, we estimated 764 home range centroids, 322 for northwest Kansas and 442 for south-central Kansas. Pooled across regions, we generated 359 home range centroids during the breeding season and 405 during the nonbreeding season. We located 235 lesser prairie-chicken nests across all study sites (northwest $n=99$, south-central $n=136$).

We calculated large variance decomposition proportions between our distance to road (87%) and distance to powerline (35%) variables as expected. However, the condition index for these variables (4.0) did not meet the suggested threshold (≥ 30) to suggest collinearity problems (Belsley et al. 1980). Therefore, for home range placement analysis, we retained all hypothesized variables in both modeling frameworks. However, for nest placement analysis, the addition of or removal of other variables switched the coefficient sign of distance to road, indicating its instability. Therefore, we removed the distance to road metric from the nest placement analysis.

Second-Order Selection

Home range placement.—Model evaluation of anthropogenic metrics indicated that distance to powerlines and distance to roads were the most influential predictors of home range placement and these variables composed the only parsimonious model ($\Delta AIC_c \leq 2.0$) with the greatest support ($w_i = 0.74$; Table 1). The top ranked model for regional and seasonal effects was the null model (Table 1). Univariate models for region and season were also parsimonious ($\Delta AIC_c \leq 2.0$); however, because the null model was the top-ranked model and held the greatest model weight

($w_i = 0.51$), we did not include regional or seasonal effects in our final model.

Lesser prairie-chickens placed home ranges farther from roads ($\beta = 0.00028$, 95% CI = 0.00017, 0.00039) and powerlines ($\beta = 0.00031$, 95% CI = 0.00021, 0.00042) than would be expected at random. As distance increased from 0 to 3 km away from roads, the relative probability of home range placement increased 1.54 times (Fig. 2). Similarly, as the distance from powerline increased from 0 to 3 km, the relative probability of home range placement increased 1.66 times (Fig. 2). Distance to well was not indicated as an important predictor of home range placement.

Nest placement.—There was no single top ranked model in the model set (Table 2). We made inference based on the top 4 models, all of which were parsimonious ($\Delta AIC_c \leq 2.0$) and had a combined model weight of 0.99. Distance to powerline was the single most consistent variable and was in all of the top models. Distance to well and region were not informative predictors of lesser prairie-chicken nest placement ($\beta = -0.00008$, 95% CI = -0.00027 , 0.00012; $\beta = -0.37$, 95%

Table 1. Rankings of models testing the influence of distance to anthropogenic structures and categorical variables of region (northwest and south-central) and season (breeding and nonbreeding) on lesser prairie-chicken home range placement in Kansas, USA, 2013–2016.

Model	ΔAIC_c^a	K^b	w_i^c	Dev ^d
Linear metrics				
Powerline+road	0.00	3	0.74	1,970.10
Powerline+well+road	2.20	4	0.25	1,969.95
Powerline	10.00	2	0.01	1,995.59
Powerline+well	10.90	3	0.00	1,993.25
Road	19.60	2	0.00	2,004.26
Road+well	21.60	3	0.00	2,004.26
Well	74.40	2	0.00	2,112.18
Null	75.60	1	0.00	2,118.26
Categorical variables				
Null	0.00	1	0.51	2,118.26
Region	2.00	2	0.19	2,118.26
Season	2.00	2	0.19	2,118.26
Region+season	4.00	3	0.07	2,118.26
Region $\times$ season	6.00	4	0.03	2,118.26
Region+season+region $\times$ season	6.00	4	0.03	2,118.26

^a Difference in Akaike's Information Criterion, corrected for a small sample size.

^b Number of parameters.

^c Model weight.

^d Deviance.

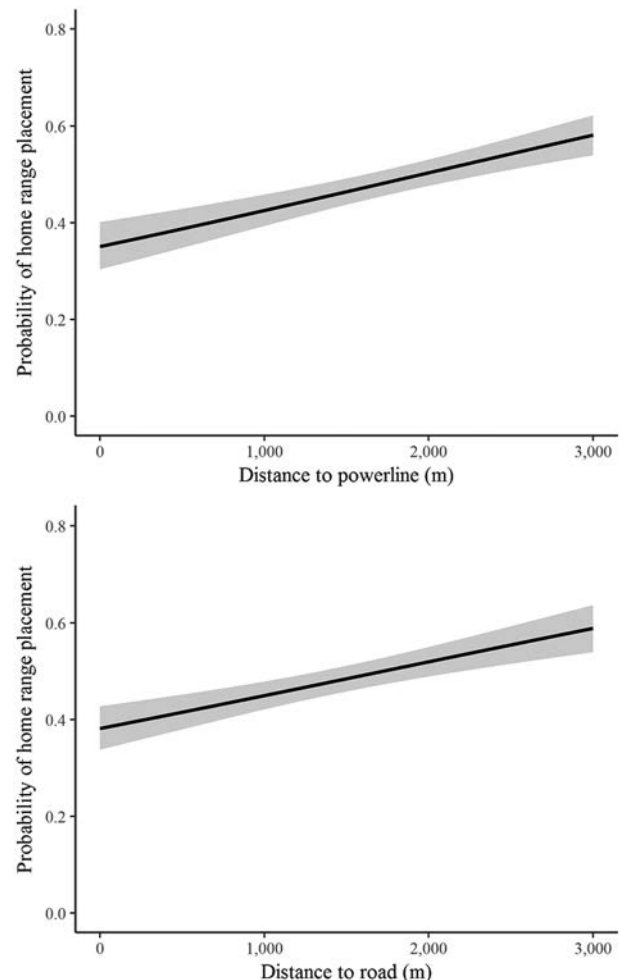


Figure 2. Relative probability of use curves depicting lesser prairie-chicken home range placement ($\pm 95\%$ CI) in relation to the nearest powerline and road in Kansas, USA, 2013–2016.

Table 2. Rankings of models testing the influence of distance to anthropogenic structures and categorical variables of region (northwest and south-central) and season (breeding and nonbreeding) on lesser prairie-chicken nest site selection in Kansas, USA, 2013–2016.

Model	ΔAIC_c^a	K^b	w_i^c	Dev ^d
Powerline	0.00	2	0.34	603.06
Powerline+region	0.10	3	0.32	600.20
Powerline+well+region	1.30	4	0.18	599.50
Powerline+well	1.60	3	0.15	602.70
Well	22.90	2	0.00	640.09
Region	23.10	2	0.00	640.47
Well+region	24.90	3	0.00	640.09
Null	740.00	1	0.00	1,039.20

^a Difference in Akaike's Information Criterion, corrected for a small sample size.

^b Number of parameters.

^c Model weight.

^d Deviance.

CI = −0.78, 0.035). Distance to powerline was the only significant predictor of lesser prairie-chicken nest placement with females placing nests farther from powerlines than expected at random ($\beta = 0.00046$, 95% CI = 0.00031, 0.00062). As the distance from powerline increased from 0 to 3 km, the relative probability of nest placement increased 2.19 times (Fig. 3).

Third-order selection.—For data pooled across both regions and seasons, all anthropogenic predictors were significant (Fig. 4A). Lesser prairie-chickens, on average, used space at greater intensities within their home range farther from wells ($\beta = 0.08$, 95% CI = 0.05, 0.17), powerlines ($\beta = 0.10$, 95% CI = 0.04, 0.16), and roads ($\beta = 0.11$, 95% CI = 0.05, 0.17).

Within home range space use varied regionally. In northwest Kansas, individuals exhibited behavioral avoidance of powerlines ($\beta = 0.18$, 95% CI = 0.10, 0.25; Fig. 4B), whereas in south-central Kansas individuals avoided oil and gas wells ($\beta = 0.12$, 95% CI = 0.06, 0.17; Fig. 4C). Roads were avoided in both regions (northwest $\beta = 0.11$, 95%

CI = 0.04, 0.19; south-central $\beta = 0.11$, 95% CI = 0.02, 0.20; Fig. 4B, C). Lesser prairie-chickens used space farther from wells during the breeding ($\beta = 0.06$, 95% CI = 0.01, 0.12; Fig. 4D) and nonbreeding seasons ($\beta = 0.10$, 95% CI = 0.02, 0.19; Fig. 4E). Lesser prairie-chickens used space at greater intensities farther from powerlines ($\beta = 0.14$, 95% CI = 0.07, 0.22; Fig. 4D) than was available within their home ranges during the breeding season but did not avoid powerlines during the nonbreeding season. Inversely, roads were not avoided during the breeding season but were avoided during the nonbreeding season ($\beta = 0.21$, 95% CI = 0.09, 0.32; Fig. 4E).

We did not observe increases in avoidance behavior during the nesting or brooding phases of the breeding season for either northwest or south-central Kansas. Females in northwest Kansas used space within their home range farther from powerlines and roads during the lekking ($\beta = 0.17$, 95% CI = 0.08, 0.26; $\beta = 0.11$, 95% CI = 0.02, 0.19) and nesting phases ($\beta = 0.26$, 95% CI = 0.12, 0.39; $\beta = 0.27$, 95% CI = 0.14, 0.40) and only powerlines during the post-breeding phase ($\beta = 0.08$, 95% CI = 0.01, 0.16; Fig. 5). Distance to well was not a significant predictor for any of the breeding season phases in northwest Kansas. In contrast, distance to well was the only significant predictor for females in south-central Kansas. Females in south-central Kansas avoided wells during the lekking phase only ($\beta = 0.11$, 95% CI = 0.02, 0.19; Fig. 5). No other predictors affected space use in the other breeding season phases for lesser prairie-chickens in south-central Kansas. Space use during the brooding phase was not related to any hypothesized predictors for either region, implying that the lack of predictive ability is a result of prairie-chickens using space in equal proportion to the resource availability within their home range (Fig. 5).

Distances

Though not all linear distance predictors affected female home range placement or within home range space use, the lowest tenth percentile of home range centroids, as described by Hagen et al. (2011), did suggest that lesser prairie-chicken's space use occurs at greater distances away from roads (355 m) and powerlines (587 m) than would be expected at random (183 m, 216 m; Table 3). Differences between the tenth percentile distances of observed (467 m) and available locations (428 m) for wells was negligible. Additionally, regional differences in the tenth percentile distances were negligible (Table 3).

DISCUSSION

Our study adds to the growing consensus that increased anthropogenic disturbance and development in grasslands negatively affects lesser prairie-chicken space use and results in behavioral displacement. We found that lesser prairie-chickens consistently avoided powerlines across all analyses, avoidance of structures was exhibited across 2 scales of selection, and within home range avoidance responses were not elevated during the nesting and brooding phases of the reproductive season compared to other phases. Although

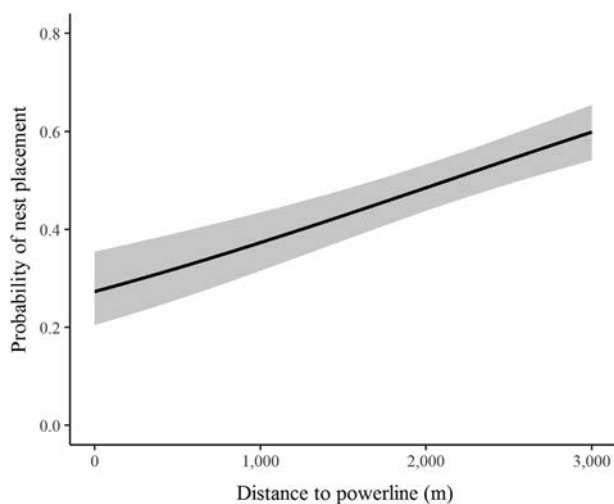


Figure 3. Relative probability of use curve depicting lesser prairie-chicken nest placement ($\pm$ 95% CI) in relation to nearest powerline in Kansas, USA, 2013–2016.

direct loss of grassland in the northern extent of the lesser prairie-chicken range has been minimal during the last 2 decades, current populations have declined (Ross et al. 2016, Spencer et al. 2017). Our results, combined with others (Robel et al. 2004, Pitman et al. 2005, Pruett et al. 2009_{a,b}, Hagen et al. 2011, Hovick et al. 2014, Winder et al. 2015), indicate that anthropogenic development, at a minimum, degrades lesser prairie-chicken habitat and may result in

functional elimination of available habitat. Anthropogenic development within remaining grassland patches further exacerbates effects of previous habitat loss and fragmentation, which may be a proximate reason for continued declines.

Powerlines are one of the few structures that have been a consistent negative factor on the landscape for lesser prairie-chickens and other species of prairie-grouse (Pitman et al.

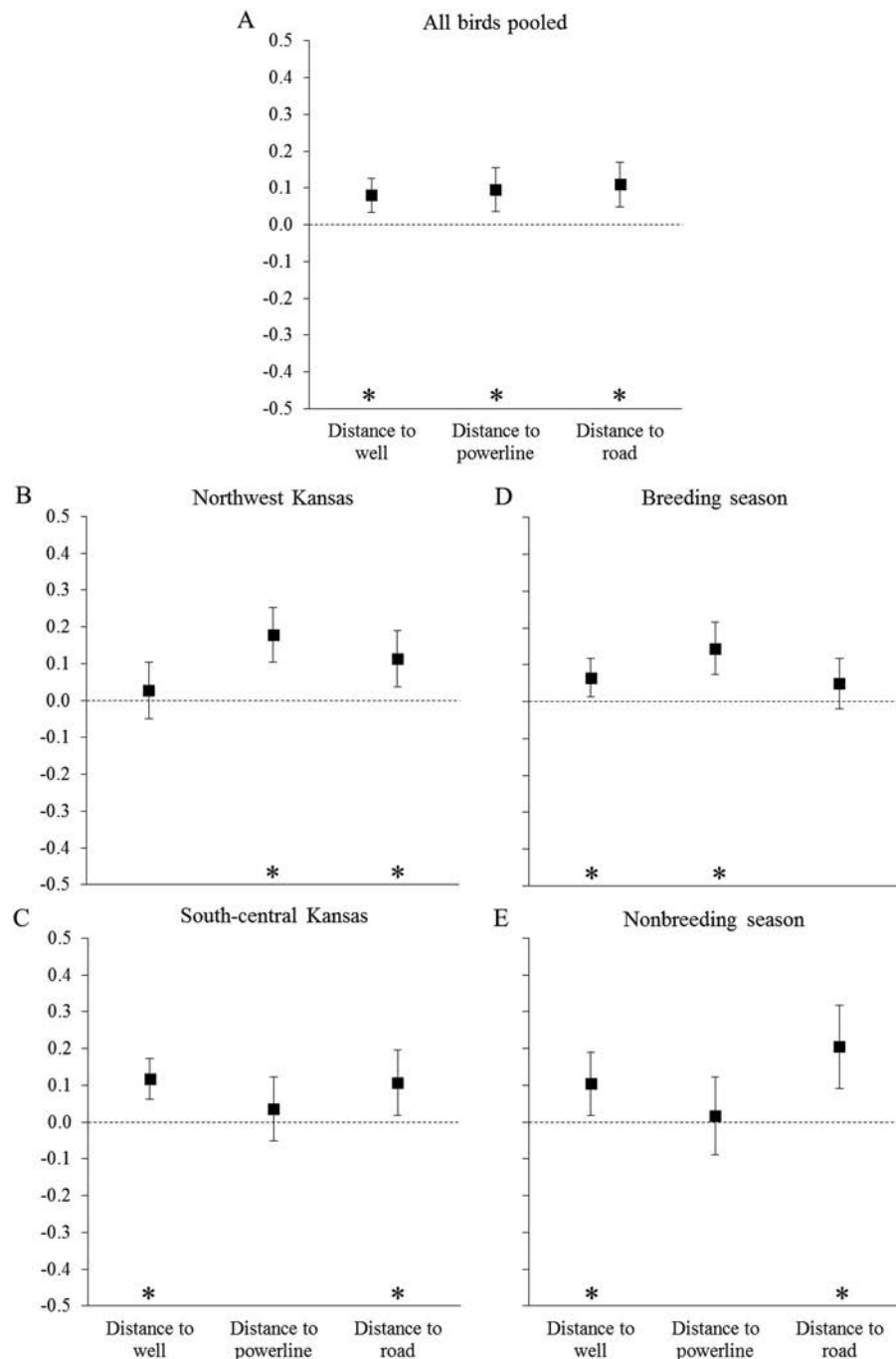


Figure 4. Mean standardized β coefficients ($\pm$ 95% CI) of lesser prairie-chicken resource utilization functions for all data pooled across region and season in Kansas, USA (A), for northwest (B) and south-central Kansas (C) pooled across season, and for the breeding (15 Mar–15 Sep; C) and nonbreeding (16 Sep–14 Mar; D) seasons pooled across region. Estimates represent all birds marked within each region and season regardless of fate. Asterisks denote a significant response at the population level ($\pm$ 95% CI of β s that do not overlap zero). A significant positive β coefficient signifies behavioral avoidance and a significant negative β coefficient signifies behavioral attraction.

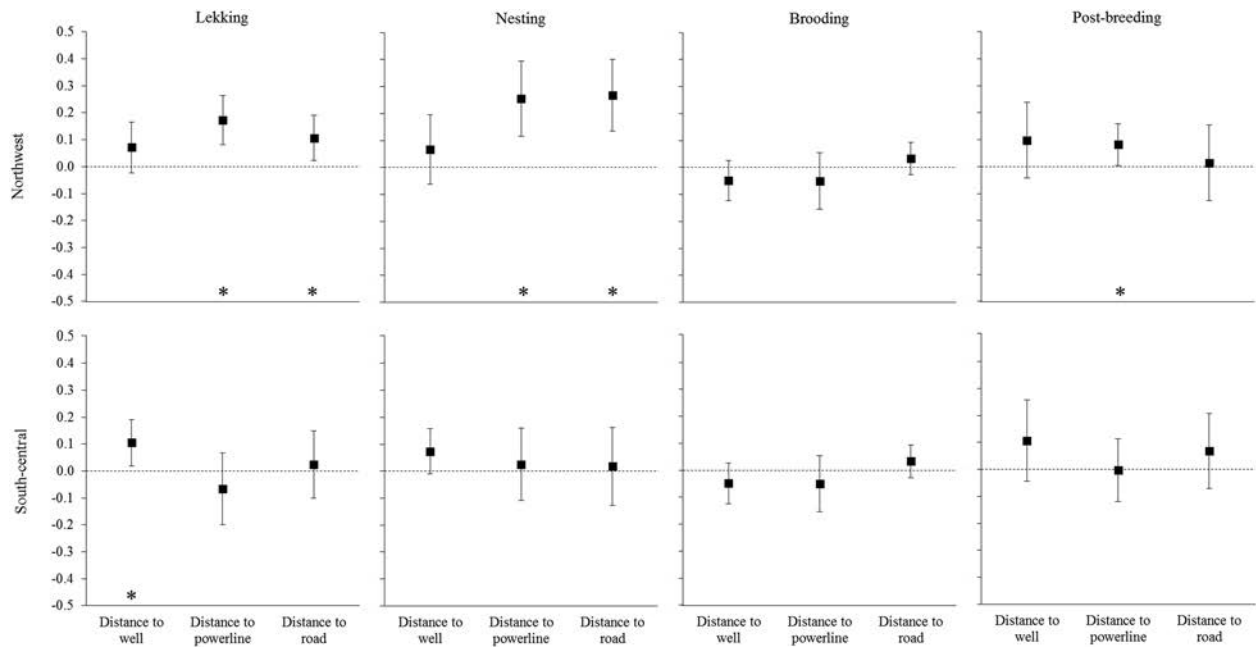


Figure 5. Mean standardized β coefficients ($\pm$ 95% CI) for female lesser prairie-chicken resource utilization functions within each region (northwest and south-central Kansas, USA, 2013–2016). Estimates are for each biological phase defined for the breeding season. Asterisks denote a significant response at the population level ($\pm$ 95% CI of β s that do not overlap zero). A significant positive β coefficient signifies behavioral avoidance and a significant negative β coefficient signifies behavioral attraction.

2005, Pruett et al. 2009b, Hagen et al. 2011, Grisham et al. 2014, Hovick et al. 2014). Powerlines have been implicated as obstructions to prairie grouse movement, nest site selection, and general habitat use (Pitman et al. 2005, Pruett et al. 2009b, Hagen et al. 2011, Grisham et al. 2014). Our results corroborate previous investigations; lesser prairie-chickens placed home ranges and nests farther from powerlines than would be expected at random and exhibited behavioral avoidance within their home ranges. Further, minimum avoidance distance of powerlines (587 m) was reasonably similar to those observed by other studies on lesser prairie-chickens (Pruett et al. 2009b, Hagen et al. 2011).

We posit that avoidance of powerlines may have been a product of 3 different mechanisms: increased predation attempts or perceived predation presence from raptors, a

general neophobic response to tall structures, or ultraviolet discharges from the powerline. In prairie landscapes, perch and wait raptors such as red-tailed hawks, Swainson's hawks, rough-legged hawks (*B. lagopus*), ferruginous hawks (*B. regalis*), great horned owls (*Bubo virginianus*), and golden eagles (*Aquila chysaetos*) use powerlines and other standing structures for perching to scan for potential prey (Behney et al. 2011, Boal 2016). These larger and less agile raptors lack the flight skills necessary to successfully take lesser prairie-chickens in the air. Their presence has been documented as inciting a flushing response from prairie-chickens but with little to no known success (Behney et al. 2011). Continued predation attempts from raptors using powerline structures may explain why lesser prairie-chickens place home ranges and use space within their home range farther from powerlines than would be expected at random.

Table 3. Summary statistics representing the mean ($\bar{x}$), lower and upper 95% confidence intervals (L95%, U95%), and the maximum distance of the nearest tenth percentile (10th %) of linear distances (m) between each anthropogenic structure and all observed and available home range centroids pooled across regions ($n = 764$), in northwest (NW) Kansas, USA, ($n = 322$), and south-central (SC) Kansas ($n = 442$), USA, 2013–2016. Sample sizes for random locations were 3 times the number of observed locations.

Feature type	Pooled				NW Kansas				SC Kansas			
	$\bar{x}$	L95%	U95%	10th %	$\bar{x}$	L95%	U95%	10th %	$\bar{x}$	L95%	U95%	10th %
Observed												
Well	1,826	1,743	1,908	467	1,987	1,834	2,140	437	1,708	1,621	1,795	501
Powerline	2,218	2,131	2,304	587	1,879	1,768	1,989	591	2,465	2,344	2,585	584
Road	1,925	1,832	2,017	355	1,622	1,501	1,743	317	2,145	2,016	2,275	391
Available												
Well	1,678	1,629	1,726	428	1,879	1,796	1,963	445	1,531	1,474	1,587	421
Powerline	1,512	1,462	1,562	216	1,344	1,274	1,414	208	1,634	1,565	1,703	237
Road	1,252	1,206	1,297	183	1,000	951	1,049	169	1,434	1,365	1,504	212

A female lesser prairie-chicken that is tending a nest may be a more susceptible target than a female that can move freely at will and is not tied to a reproductive input (Hagen and Giesen 2005, Behney et al. 2011). Adult female mortality tends to peak during the nesting period (Patten et al. 2005, Hagen et al. 2007, Wolfe et al. 2007, Plumb 2015). The majority of breeding season losses are due to predation, with roughly equal proportions attributed to mammals and raptors (Haukos and Broda 1989, Holt 2012). Cause-specific mortality results from this study indicated that the majority of predation-related mortalities came from avian predators and coincided with raptor migration peaks (46%; Plumb 2015). Increased susceptibility while nesting may explain why our results indicated an elevated negative response toward powerlines with the relative probability of nest placement increasing as the distance from nearest powerline increased.

Lesser prairie-chicken avoidance of powerlines may be a result of neophobia, or an extreme fear or dislike for something new (Walters et al. 2014). Lesser prairie-chickens evolved in prairie landscapes that were mostly devoid of tall natural structures such as trees, as a consequence of limited rainfall and fire. However, as fire was removed from the landscape, trees have begun to encroach into the grassland ecosystem. Lesser prairie-chickens avoid trees such as eastern redcedar (*Juniperus virginiana*) and honey mesquite (*Prosopis glandulos*) across their range (Boggie et al. 2017, Lautenbach et al. 2017). Our results, and others, provided clear evidence that lesser prairie-chickens avoided tall anthropogenic structures such as powerlines, poles, and frame towers (Pitman et al. 2005, Hagen et al. 2011, Hovick et al. 2014, Grisham et al. 2014).

Finally, avoidance of habitat near powerlines is a perplexing behavior because the lines and pylons are neither an impenetrable physical barrier nor always associated with human traffic (Pruett et al. 2009b, Tyler et al. 2014). Integrating information on visual function with the characteristics of powerline function provides evidence that avoidance may be linked with the ability of lesser prairie-chickens to detect ultraviolet light (UV; Tyler et al. 2014). Ultraviolet discharges occur as standing corona along cables and irregular flashes on insulators, with the discharge spectrum (200–400 nm) below the lower limit of human vision but within the visible range of birds, rodents, and reindeer or caribou (*Rangifer tarandus*; Maruvada 2000, Tyler et al. 2014). The ability for birds to see UV light emanating from powerlines may explain the lesser prairie-chickens avoidance rather than from physical or neophobic pressures. Further, during dark periods of the day, retinal sensitivity from lesser prairie-chickens could increase the effects of UV light associated with powerlines because, in darkness, lesser prairie-chickens may see powerlines not as dim, passive structures but, rather, as lines of flickering light stretching across the landscape (Tyler et al. 2014). This does not explain avoidance during daylight periods or when lines are not transmitting electricity but could be a classic example of conditioning where the events are perceived as threatening (Tyler et al. 2014). Unfortunately, potential avoidance

mechanisms are confounded with one another and are difficult to tease apart. Regardless, the negative response seen at the second- and third-order selection scales indicate that powerlines reduce the available habitat perceived by lesser prairie-chickens. Continued functional fragmentation of remaining habitat patches from powerlines in already fragmented landscapes may compound negative effects on lesser prairie-chicken movement, habitat availability and quality, and population connectivity.

Lesser prairie-chicken movements and home ranges frequently intersect roads, suggesting that roads are more permeable to lesser prairie-chickens than tall linear structures such as powerlines (Pruett et al. 2009b, Hagen et al. 2011). However, noise and disturbance associated with roads reduce habitat use and nest site selection of prairie grouse species (Lyon and Anderson 2003, Pitman et al. 2005, Hagen et al. 2011, Blickley et al. 2012). Our results indicate that lesser prairie-chickens place home ranges farther from roads than would be expected at random. Additionally, lesser prairie-chickens also exhibited behavioral avoidance of roads within their home range, supporting the hypothesis that disturbance associated with roads functionally eliminates otherwise available habitat. A novel finding from our study was the instability of distance to road as a predictor for nest-site placement. Previous research indicates nesting female lesser prairie-chickens place nest sites farther from paved roads than would be expected at random, even when vegetation characteristics are similar near these edges (Pitman et al. 2005, Hagen et al. 2011). Paved roads were rare in both study areas; only 23 km of 2-lane paved roads were within the 1,249-km² area we considered available for nesting. The limited exposure to paved roads may explain why distance to road was not a stable predictor.

The southern Great Plains is increasingly relied upon to produce energy for the country (Bartuszevige and Daniels 2016). Increased demand for domestic energy resources and advancements in mineral extraction has spurred an expansion in oil and gas development throughout the range of the lesser prairie-chicken. Presence of oil and gas wells has been documented as displacing multiple species of grouse through structure avoidance (Hovick et al. 2014). Results from our analysis indicated that the effect from wells varied among scales of selection. At the second-order selection scale, distance to well was not a significant predictor of home range or nest placement. However, lesser prairie-chickens did behaviorally avoid wells by disproportionately selecting areas farther from wells than available within their home range.

Well density (number of wells/unit area) has successfully been used to characterize the negative effects of energy development on habitat use of mule deer (*Odocoileus hemionus*), greater sage grouse (*Centrocercus urophasianus*), and lesser prairie-chickens (Sawyer et al. 2006, Walker et al. 2007, Doherty et al. 2008, Hagen et al. 2011). For example, the likelihood that greater sage grouse would use otherwise available winter range was diminished by 10% with the development of 1 well/4 km² (Doherty et al. 2008). We predict that well density would be a superior metric to use in future studies when compared to that of distance to well and

that lesser prairie-chickens will place home ranges and nests in areas with lower well density than available. Further, research investigating well density should also investigate the effect of well distribution and clustering to aid conservation decisions on mitigating the effects of oil and gas development.

Contrary to our prediction, we did not record heightened within home range avoidance of anthropogenic structures during critical nesting and brood-rearing phases. However, at the home range and nest site selection scale, lesser prairie-chickens exhibited heightened sensitivity when placing nests compared to home range centroids; females were more than twice as likely to place a nest 3 km from a powerline than 0 km, whereas the probability of home range placement increased by only 65% over the same distance. There was no measurable within home range avoidance of anthropogenic structures during the brooding phase, which was inconsistent with other breeding season phases.

Increased development of anthropogenic structures on the landscape, especially in grassland cover types, could have profound effects on population viability. Functional habitat loss, especially for nesting, from increased development could prove detrimental to demographic rates (Holloran 2005, Doherty et al. 2008). If females choose to use habitat with increased structure densities for reproduction, such decisions may lead to nest, brood, or female mortality greater than natural variability and the grassland habitat would become an ecological trap (Aldridge and Boyce 2007). Furthermore, if displacement or a resulting ecological trap affects productivity of the area, persistence of leks and the occupancy of these patches may diminish over time and lead to decreases in local populations (Hagen et al. 2011).

Reduction in habitat quality has been implicated as a contemporary mechanism for continued decreases in lek attendance, persistence, and associated population declines (Haukos and Zavaleta 2016, Rodgers 2016). Our results combined with others (Robel et al. 2004, Pitman et al. 2005, Hagen et al. 2011, Grisham et al. 2014) demonstrate the negative effects of anthropogenic development on home range placement, nest site selection, and space use by lesser prairie-chickens. Increasing evidence clearly supports the contention that disturbance and encroachment from anthropogenic structures continually degrade remaining habitat fragments that support lesser prairie-chicken populations.

MANAGEMENT IMPLICATIONS

Increasing buffer distances for distribution lines, secondary roads, and oil and gas pads to >550 m, >350 m, and >450 m, respectively, would maximize effectiveness of mitigation measures by management agencies. Grassland habitats within approximately 3 km of home range centroids and nest sites would benefit from protection from any initial or further anthropogenic disturbances. Removing or burying powerlines and decommissioning roads that penetrate or border remaining grassland patches, will likely reduce lesser prairie-chicken avoidance and increase habitat at multiple scales. Decommissioning and reclaiming retired

well structures and pads may mitigate lesser prairie-chicken avoidance, with the priority for well sites in intact grasslands. If constructing anthropogenic structures in lesser prairie-chicken habitat is necessary, efforts to reduce avoidance and increase home range and nest placement may include clustering structures together on the periphery of habitat patches or near already compromised areas such as heavily trafficked or paved roads, current standing structures, or agricultural fields.

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Effect of Energy Development and Human Activity on the Use of Sand Sagebrush Habitat by Lesser Prairie-Chickens in Southwestern Kansas

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Lesser prairie-chickens (*Tympanuchus pallidicinctus*) occupy xeric grasslands dominated primarily by sand sagebrush (*Artemisia filifolia*) or shinnery oak (*Quercus havardii*) in portions of southwestern Kansas, southeastern Colorado, western Oklahoma, northern Texas, and eastern New Mexico (Giesen 1998) and their populations have declined range-wide since the 1800s (Braun et al. 1994). In southwestern Kansas, lesser prairie-chickens are most abundant in mixed- and short-grass prairies dominated by sand sagebrush south of the Arkansas River. Population indices (lek counts) suggest lesser prairie-chicken numbers have declined since the 1970s (Jensen et al. 2000). Generally the decline has been attributed to the deterioration of the sandsage habitat and the conversion of suitable habitat to intensive agriculture, primarily center-pivot irrigated corn. Even though most of the large-scale conversion of sand sagebrush prairie to intensive agriculture ceased in the mid 1980s, lek indices to lesser prairie-chicken populations continued to decline in southwestern Kansas (Jensen et al. 2000).

A 6-year study initiated in 1997 examined factors that may have contributed to the 1980-2000 decline in numbers of lesser prairie-chickens in southwestern Kansas. Low nest success and poor chick survival were determined to be the most important factors contributing to the decline (Hagen 2003, Pitman 2003). The research was conducted in Finney County, an area of southwestern Kansas that historically supported a viable lesser prairie-chicken population. Lek survey indices to prairie chicken populations in that county averaged 12.1 birds per square mile (4.7 birds/km²) during the late 1960s (Church 1987). Between 1960 and 1975, approximately 60% of the native sand sagebrush prairie in Finney County was converted to intensive agriculture (Sexson 1980). That loss of habitat originally was thought to be the sole cause of the 33% decline (12.1 to 8.1 birds per square mile; 4.7 to 3.1 birds/km²) in the lesser prairie-chicken lek survey indices in Finney County during the 1980s and the 50% decrease (8.1 to 4.1 birds per square mile; 3.1 to 1.6 birds/km²) in the 1990s. However, these declines occurred even though large expanses of sand sagebrush prairie existed in the county through the 1980s and 1990s. During Hagen's (2003) and Pitman's (2003) studies, radio telemetry data disclosed avoidance by lesser prairie-chickens of what appeared to be suitable sand sagebrush habitat near anthropogenic features, e.g., roads, buildings, oil and gas wellheads, electric transmission lines, and center-pivot irrigation fields.

The human population of Finney County increased by over 25% between 1980 and 2000 (U. S. Census Bureau 2003), coincidental with the construction of a coal-fired electric generating station and associated transmission lines, road improvements, and an increased number of houses in rural settings. Petroleum exploration and production also increased in the county and compressor stations were constructed to move natural gas through underground pipelines. These anthropogenic changes in Finney County coincided with declines in lek survey indices to lesser prairie chicken populations in the 1980s and 1990s.

We conducted this study to assess the magnitude of the impacts of anthropogenic factors on use of sand sagebrush habitat by lesser prairie-chickens. We focused our efforts on the remaining sand sagebrush habitat in Finney, Kearny, and Hamilton counties of southwestern Kansas, the three counties supporting 25 to 50% of the lesser prairie-chicken population in Kansas during the early 2000s (assuming lek survey data are a realistic reflection of lesser prairie-chicken numbers).

Methods and Procedures

Data used to determine use of sand sagebrush habitat by lesser prairie-chickens were obtained from transmitter-equipped birds on two 12,500 acre (5,070 ha) study sites in Finney County during a 1997-2003 field study. Lesser prairie-chickens were captured on leks using walk-in funnel traps (Haukos et al. 1990) primarily during March and April. Captured birds were fitted with < 0.4-ounce transmitters (< 2% of each bird's body mass) and released within 15 minutes at capture sites. Birds were located daily by triangulation using a truck-mounted null-peak twin-Yagi telemetry system. The influence of anthropogenic features on the use of sand sagebrush habitat was estimated from these data, and its impact was extrapolated to the remaining sand sagebrush habitat in Finney, Kearny, and Hamilton counties during 2003-2004.

Study Area

The sand sagebrush prairies of Finney, Kearny, and Hamilton counties exist primarily on undulating sand dunes south of the Arkansas River (Kuchler 1974). Two soil types are typical across the sand sagebrush vegetation complexes, Tivoli fine sand and Tivoli-Vona loamy fine sands (Harner et al. 1965). The long-term average annual precipitation for the area was 19 inches with 75% of it occurring between March and August; the mean annual temperature was 55°F, ranging from 21°F for January to 79°F for July (U. S. Department of Commerce 2003).

Sand sagebrush dominated the vegetative community and was interspersed with grasses including six-week fescue (*Vulpia octoflora*), blue grama (*Bouteloua gracilis*), sand dropseed (*Sporobolus cryptandrus*), prairie sandreed (*Calamovilfa longifolia*), sand bluestem (*Andropogon halii*), and little bluestem (*Schizachyrium scoparium*). Other plants common on the area included western ragweed (*Ambrosia psilostachya*), annual erigeron (*Erigeron annuus*), sunflowers (*Helianthus* spp.), plains yucca (*Yucca glauca*), prickly pear (*Opuntia polyacantha*), and Russian thistle (*Salsola kali*). Kuchler (1974) presents a detailed description of the vegetation of the sand sagebrush prairie of the three counties. Over 90% of the sand sagebrush rangeland was grazed annually by cattle at various intensities resulting in highly variable vegetation structure across the study area.

Determining Coverage of Sand Sagebrush Prairie

The historical distribution of sand sagebrush habitat in Finney, Kearny, and Hamilton counties was primarily defined by the extent of the Tivoli association soil complex and vegetation based landcover maps by Kuchler (1974). Defining natural habitat based on soil types has been successfully used in similar studies (Johnson et al. 1995). Two Landsat 1 Multispectral Scanner images (pixel resolution = 66 yards) were used to identify sand sagebrush acreage in the three counties for 1973 whereas two Landsat 7 Enhanced Thematic Mapper (ETM+) images (pixel resolution = 36 yards) and ground truthing were used for 2001 determinations.

Inventory of Anthropogenic Features in the Three Counties

Locations of anthropogenic features in the sand sagebrush habitat were entered into a GIS system for display and analysis. Road center lines from the U.S. Census Bureau were downloaded from the Kansas Data Access and Support Center. Point data for oil and oil/gas wellheads were downloaded from the Kansas Geological Survey Database. Locations of buildings (large houses, feedlots, ranch steads, compressor stations, and the power plant) were

identified on U.S. Geological Survey 1:24,000 topographic maps and Landsat satellite imagery and a polygon layer of building sites was created by digitizing feature boundaries. Paper maps of electric transmission line routes were provided by the Sunflower Electric Corporation, georeferenced to Landsat ETM+ satellite imagery, then digitized into ArcInfo 8.1 to create a transmission line layer. Center-pivot fields were identified by their distinctive spectral and textural properties and classified in ERDAS Imagine 8.7 (Leica Geosystems 2003).

The scale of satellite images and coarse pixel resolution limited our ability to identify small anthropogenic features (minor roads and trails, individual houses, trailers, and small outbuildings). Therefore, our assessment of the impacts of anthropogenic features on lesser prairie-chickens in the sand sagebrush habitat of the 3-county area must be interpreted as a conservative estimate.

Determining Areas Avoided by Nesting Lesser Prairie-chickens

The movements of transmitter-equipped female lesser prairie-chickens were monitored daily during April-June to locate 187 nests. From these data, Pitman (2003) determined the distances to anthropogenic features avoided by nesting lesser prairie-chickens. Lesser prairie-chicken nests were located farther from five of six features than would be expected at random. The presence of unimproved roads had the least affect on placement of nests, and buildings the greatest (Table 1).

Locations of nests were incorporated into a geographic information system of the two study areas created in ArcView 3.1 (Environmental Systems Research Institute 1998) along with locations of wellheads, buildings, transmission lines, improved and unimproved roads, and center-pivot irrigated fields. Distances from each nest to the nearest wellhead, building, transmission line, improved or unimproved road, and center-pivot irrigated field edge (hereafter center-pivot field) were calculated for each nest.

Wellheads were oil and oil/gas wells with pumping units powered primarily by diesel fuel. Buildings consisted of houses, gas compressor stations, and a 380 MW coal-fired electric generating station. Transmission lines primarily were 125, 138, and 345 kV double circuit conductors distributing electricity from the generating station. Improved roads were graveled or paved and carried up to 486 vehicles per day (vpd) whereas unimproved roads were 2-lane pasture trails and ungraded service roads to wellheads with traffic <3 vpd. Center-pivot fields covered 160 acres with a water pump in the center and a 13- to 16-foot high sprinkler boom extending from the center to the edge of the field. When in operation (generally from late April or early May through summer), the sprinkler boom irrigated the field by rotating circularly across the field on self-powered wheels.

We used Monte Carlo simulations (Manly 1998) to determine if any of the six anthropogenic features were related to distances to locations of lesser prairie-chicken nests. Because features far from nest sites were unlikely to impact nesting birds, we used only nests close to each feature (closest 10% of the nests) to assess the impacts of the six anthropogenic features. Probability distributions were used to determine if nests were significantly ($P = 0.05$) farther than expected from a particular feature. If nests were significantly farther than expected from a feature, that feature was determined to negatively effect lesser prairie-chicken nest location. The mean distance of the closest 10% of the nests to a specific anthropogenic feature

was determined, and that distance was used as the ‘avoidance distance’ of nesting lesser prairie-chickens for that feature.

Determining Areas Avoided by Adult Lesser Prairie-chickens

We quantified use and non-use areas of sand sagebrush habitat from telemetry locations of lesser prairie-chickens. Use areas were defined using a 95% fixed kernel home range (Worton 1989) of bird locations. Because multiple locations at nest or lek sites may have underestimated the size of the kernel, we used only one lek or nest location per bird for kernel home range calculations. Sand sagebrush habitat not within the 95% fixed kernel home range was considered as the non-use area.

Vegetation measurements from 42 random locations in areas of sand sagebrush habitat used by lesser prairie-chickens (use areas) and 42 in areas not used by the birds (non-use areas) were the basis of comparing vegetation structure of use and non-use areas (Hagen 2003). Sagebrush canopy cover did not differ between use and non-use areas, nor did forb or grass canopy cover. Neither sagebrush density nor mean diameter of sagebrush plants differed between use and non-use areas. The only vegetation variable that differed between use and non-use areas was litter cover; being significantly greater on non-use than use areas. Thus, based on the vegetation measurements made, the vegetation structure of the sand sagebrush habitat in areas used and not used by adult lesser prairie-chickens was virtually identical.

Lesser prairie-chicken location data from April to September 2000 to 2002 were analyzed for impacts of four anthropogenic features (roads, buildings, wellheads, and transmission lines) on their distribution by month and year. Negative impacts of roads and wellheads were less than those of buildings and transmission lines (Table 2). These distances were used in GIS models to estimate the effects of human activity on sand sagebrush habitat use by adult lesser prairie-chickens.

Quantifying the Acreage Impacted by Anthropogenic Features

Distance to anthropogenic features avoided by 90% of nesting and 95% of adult lesser prairie-chickens were entered into an avoidance buffer database. Avoidance buffers around/or along individual anthropogenic features were created in ArcInfo 8.1 (Environmental Systems Research Institute 2001) with the width of avoidance determined from previously described field data. Buffers around anthropogenic features often overlapped, i.e., transmission lines running adjacent to roads, wellheads lying within center-pivot fields, and so on. This overlap could result in overestimation of avoidance area. To eliminate bias associated with overlap, the Merge and Dissolve by Attribute functions in ArcInfo 8.1 were used to create one comprehensive avoidance buffer that apportioned duplicated areas of impact among overlapping features.

Results and Discussion

Extent of Sand Sagebrush Prairie Habitat

Historically, an estimated 339,645 acres (137,556 ha) of sand sagebrush habitat existed in Finney, Kearny, and Hamilton counties. By 1973, this acreage had been reduced to 298,806 acres (121,016 ha) primarily due to conversion of sand sagebrush habitat to center-pivot agriculture (Table 3). Another 81,994 acres (33,208 ha) of sand sagebrush habitat was lost to center-pivot agriculture between 1973 and 2001. That loss, and a commitment of 3,277 acres

(1,327 ha) to urban development (residences, golf courses, etc.) left only 214,183 acres (86,744 ha) of sand sagebrush habitat in the three counties by 2001; approximately 63% of the historical acreage. Most of the loss of sand sagebrush habitat occurred in Finney County (74,154 of 142,132 acres; 52%) and in Kearny County (48,625 of 67,321 acres; 72%), and least in Hamilton County (2,004 of 130,192 acres; 2%).

Nest Locations Relative to Anthropogenic Features

Lesser prairie-chicken nests were located farther from five of six anthropogenic features than would be expected at random. Essentially, the presence of anthropogenic features reduced the suitability for nesting of the surrounding sand sagebrush habitat.

We did not attempt to determine causative factors associated with nesting lesser prairie-chicken avoidance of anthropogenic features, however, it appears that movement and noise might be implicated. Wellheads had pump jacks with weighted extensions that moved up and down when pumping, with larger units on deeper wells. The sprinkler booms of center-pivot irrigation systems moved across fields when operating and water nozzles on the ends sprayed back and forth. Vehicles ranging from small sedans to large grain and tanker trucks moved along roads, and more vehicle movement occurred on improved than unimproved roads. All of the anthropogenic features were sources of noise. On calm nights, pumps of center-pivots could be heard at a distance of approximately 0.6 mile, gas compressor stations were audible at over 2 miles, and noise from the power plant could be heard from 1 to 2 miles. Low frequency sounds were audible from the electric transmission lines when high voltage charges were being moved through the lines. Truck traffic on improved roads was commonly heard at 1-1/2 miles, and farther when drivers geared the trucks down for curves or inclines.

Additional research is needed to determine why the anthropogenic features we examined deterred lesser prairie-chickens from nesting near them. Such answers may allow modification of those features to reduce their negative impacts on nest placement by lesser prairie-chickens, and possible other avian species sensitive to human activity.

Acreage of Avoidance Buffers Around Anthropogenic Features

The acreage of sand sagebrush habitat made less suitable for lesser prairie-chicken nesting and use by the presence of anthropogenic features is substantial. The area approaches the acreage of sand sagebrush habitat converted to center-pivot agriculture in Finney, Kearny, and Hamilton counties.

Our research, and that of Peterson and Silvy (1996) and Wisdom and Mills (1997), determined that nest success was one of the most critical demographic parameters regulating prairie grouse populations. Therefore, any negative impacts of anthropogenic features on nesting of lesser prairie-chickens is of great concern.

The presence of improved roads reduced nesting by lesser prairie-chickens in the 859-yard buffer on either side of the roads. In 1973, that buffer included 141,312 acres (57,231 ha) of sand sagebrush habitat (Table 3). That estimate may be high because not all of the roads identified on the Landsat imagery carried high volumes of traffic. However, even if only 50% of the roads carried high levels of traffic, the acreage negatively impacted would exceed 70,000 acres (28,000 ha). The amount of sand sagebrush habitat negatively impacted by roads in 2001

was less than in 1973 because the roads crossed areas that were sagebrush in 1973, but had been converted to center-pivot fields by 2001. Even so, and assuming that only 50% of the roads carried high traffic volumes, the negative impacts of roads in the three counties extended to over 40,000 acres (16,200 ha) of sand sagebrush habitat in 2001.

Oil and oil/gas wellheads negatively impacted lesser prairie-chicken nesting on an estimated 8,564 acres (3,468 ha) of sandsage habitat in 1973. This area increased to 17,562 acres (7,113 ha) by 2001.

The presence of buildings negatively impacted 8,974 acres (3,634 ha) of lesser prairie-chicken nesting habitat in 1973, and increased to 15,774 acres (6,388 ha) by 2001. Buildings included a coal-fired power electric generating station, at least three compressor stations, and numerous large houses and cattle feedlots.

There were few to no major electric transmission lines crossing the sand sagebrush habitat of Finney, Kearny, and Hamilton counties in 1973, but several lines were present in 2001. These transmission lines were distributing electricity primarily to the west and southwest of the power station 7 miles (11 km) southwest of Garden City, in Finney County. Lesser prairie-chickens seldom nested within 400 yards of the electric transmission lines. The avoidance buffer encompassed by the transmission lines in the early 2000s approximated 16,803 acres (6,805 ha) of sand sagebrush habitat (the estimate includes the impacts of a transmission line under construction in 2003).

The avoidance buffers on the edges of center-pivot fields negatively affected approximately 31,795 acres (12,472 ha) of sand sagebrush habitat in 1973, and 53,694 acres (21,746 ha) by 2001. We do not know if nesting female lesser prairie-chickens were avoiding the center-pivot fields themselves, the noise from the irrigation pump in the center of the fields, or the large sprinkler booms that rotated across the fields. What ever the reason, lesser prairie-chickens seldom nested within 336 yards of the edges of center-pivot fields.

Combined, the total avoidance buffer areas around anthropogenic features in the three counties reduced the suitability of 157,296 acres (63,705 ha) and 125,962 acres (51,015 ha) of sand sagebrush habitat for lesser prairie-chicken nesting in 1973 and 2001, respectively. These areas represent 52% of the sand sagebrush habitat remaining in the three counties in 1973, and 58% of that remaining in 2001.

The area of sand sagebrush habitat made less suitable for general use by adult lesser prairie-chickens was less than that made unsuitable for nesting. Avoidance buffers along roads encompassed 12,320 acres (4,990 ha) in 1973 and 9,739 acres (3,944 ha) in 2001. Oil and oil/gas wellheads negatively impacted 1,440 acres (583 ha) in 1973 and 3,183 acres (1,289 ha) in 2001. Avoidance buffers around buildings contained 3,034 acres (1,229 ha) in 1973, increasing to 7,399 acres (2,997 ha) by 2001. Adult lesser prairie-chicken seldom used sand sagebrush habitat within 693 yards of electric transmission lines, and that avoidance buffer area amounted to 6,615 acres (2,679 ha) in 2001. Although some of these totals appear large, their impacts on the lesser prairie-chicken population are minor compared to the impacts of the presence of anthropogenic features on nesting habitat.

Summary and Management Implications

The decline of lesser prairie-chicken numbers in southwestern Kansas has been attributed to the loss of suitable habitat during the 1960s through the 1980s, primarily sand sagebrush prairie. However, population declines continued after large-scale losses of sand sagebrush habitat ceased and large tracts of that habitat remained. A 6-year study disclosed that low nest success was one of the most important factors in the decline of lesser prairie-chicken numbers in southwestern Kansas and that the birds avoided otherwise suitable habitat near human activity, especially for nesting. Human activity (population numbers, oil and gas development, construction of a coal-fired electric generation station, etc.) increased in southwestern Kansas coincidental with the decline of lesser prairie-chicken numbers. To gain a better understanding of the relationship between human activity and the viability of lesser prairie-chicken populations, we assessed the impacts of the presence of anthropogenic features (roads, buildings, transmission lines, etc.) on the use of sand sagebrush habitat by the birds.

The distance to anthropogenic features avoided by nesting lesser prairie-chicken females were used to create 'avoidance buffers' around anthropogenic features in sand sagebrush habitat. Sand sagebrush habitat within the avoidance buffer was less suitable for nest locations of 90% of nesting females, and for use by 95% of adult birds. The area contained in these buffer areas was then estimated for the sand sagebrush habitat remaining in Finney, Kearny, and Hamilton counties of southwestern Kansas. These three counties were thought to support a significant portion of the Kansas lesser prairie-chicken population.

By 2001, approximately 125,462 acres (50,812 ha) of the historic 339,645 acres (137,556 ha) of sand sagebrush prairie in the three counties had been converted to intensive agriculture or used for urban development. Avoidance buffers around improved roads, oil and oil/gas wellheads, buildings, electric transmission lines, and center-pivot fields reduced the nesting suitability of an additional 125,962 acres (51,015 ha) of sand sagebrush habitat. Thus, the amount of sand sagebrush habitat suitable for nesting by lesser prairie-chickens was only 88,221 acres (35,729 ha) in 2001, approximately 26% of the historic amount.

The impact of the avoidance buffers is depicted in Figure 1. The historic range of sand sagebrush habitat in Finney County (A) was reduced to 214,183 acres (86,744 ha) by 2001 (B), and that area was further reduced to only 88,221 acres (35,729 ha) of suitable nesting habitat (C) by the presence of anthropogenic features in the sand sagebrush prairie landscape. We suspect that the poor nest success and low chick survival experienced by lesser prairie-chickens in Finney County (Hagen 2003, Pitman 2003) were the result of a shortage of suitable nesting habitat. The remaining patches of sand sagebrush habitat suitable for nesting in that county were small and isolated, potentially increasing the predator pressure on lesser prairie-chicken nests, the nesting birds, and any fledgling chicks.

In the future, the negative impacts of anthropogenic features should be considered when assessing the suitability of habitat for lesser prairie-chickens, purchasing or leasing habitat for those birds, or implementing management actions for the benefit of those populations. The avoidance buffers around oil and oil/gas wellheads, electric transmission lines, and buildings must be recognized and integrated into environmental assessments of the development of petroleum resources and the construction of industrial wind energy facilities. The results of our

research most likely apply to other prairie grouse, but specific studies are needed to determine the magnitude of the impacts on individual species in various landscapes.

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Table 1. Mean distance (yards $\pm$ SE) to anthropogenic features avoided by 90% of 187 nesting lesser prairie-chickens during 1997-2002 in sand sagebrush prairie habitat of southwestern Kansas.

Anthropogenic feature	Distance to feature
Oil or gas wellheads	193 $\pm$ 25
Center-pivot fields	336 $\pm$ 51
Unimproved roads	32 $\pm$ 15 ^a
Improved roads	859 $\pm$ 44
Buildings	1,371 $\pm$ 65
Electric transmission lines	397 $\pm$ 70

^a Not significantly different ($P > 0.05$) from zero; the distance was not used in estimate of less suitable sand sagebrush habitat for nesting by lesser prairie-chickens in the 3-county area.

Table 2. Mean distance (yards $\pm$ SE) to anthropogenic features across which 95% of 18,866 telemetry locations of lesser prairie-chickens were absent in sand sagebrush prairie habitat of southwestern Kansas.

Anthropogenic feature	Distance to feature
Improved and unimproved roads	51 Å 4 ^a
Oil or gas wellheads	79 Å 5
Buildings	659 Å 46
Electric transmission lines	693 Å 44

^a Not significantly different ($P > 0.05$) from zero; but distance was used in estimate of less suitable sand sagebrush habitat for use by lesser prairie-chickens in the 3-county area.

Table 3. Acreage of sand sagebrush prairie habitat converted to intensive agriculture or made less suitable as lesser prairie-chicken nesting areas by the presence of anthropogenic features in Finney, Kearny, and Hamilton counties, Kansas, in 1973 and 2001.

	1973	2001
Historical acreage of sagebrush habitat	339,645	339,645
Converted to intensive agriculture	40,191	122,185
Converted to other uses (urban, recreation, etc.)	649	3,277
Sagebrush habitat remaining	298,806	214,183
Remaining sagebrush habitat made less suitable by presence of:		
Improved roads	141,312	89,297
Oil and oil/gas wellheads	8,564	17,562
Buildings	8,974	15,774
Electric transmission lines	nil	16,803
Center-pivot fields	30,795	53,694
Total acreage made less suitable by anthropogenic features	157,296	125,962
Remaining sagebrush habitat suitable for nesting by lesser prairie-chickens	141,570	88,221

[Note: figure not available electronically.]

Figure 1. Map showing changes in sand sagebrush prairie in Finney County, Kansas. A = historic coverage of sand sagebrush vegetation (black), B = sand sagebrush prairie remaining in 2001 (black), and C = sand sagebrush prairie in 2001 suitable for nesting by lesser prairie-chickens (black), and unsuitable for nesting (gray) due to presence of anthropogenic features.

RESEARCH ARTICLE

Black-Tailed Prairie Dogs, Cattle, and the Conservation of North America's Arid Grasslands

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Abstract

Prairie dogs (*Cynomys* spp.) have been eliminated from over 95% of their historic range in large part from direct eradication campaigns to reduce their purported competition with cattle for forage. Despite the longstanding importance of this issue to grassland management and conservation, the ecological interactions between cattle and prairie dogs have not been well examined. We address this issue through two complementary experiments to determine if cattle and prairie dogs form a mutualistic grazing association similar to that between prairie dogs and American bison. Our experimental results show that cattle preferentially graze along prairie dog colony edges and use their colony centers for resting, resembling the mutualistic relationship prairie dogs have with American bison. Our results also show that prairie dog colonies are not only an important component of the grassland mosaic for maintaining biodiversity, but also provide benefits to cattle, thereby challenging the long-standing view of prairie dogs as an undesirable pest species in grasslands.

Introduction

Grasslands cover approximately 55 million km² (43%) of the terrestrial Earth surface, providing livelihoods for nearly 800 million people, being the most important ecosystem for the provision of the global food supply, and are considered biodiversity hotspots [1]. Yet, grasslands have been subject to intense human pressure due to increasing demand for the expansion of agricultural lands, urbanization, water extraction, and mineral exploitation, causing declines in grassland ecological health and economic productivity [2,3]. Climate change is also important, causing increases in the duration and frequency of droughts, and exacerbating widespread invasion of shrubs into grasslands [4]. In North America, grasslands have dramatically declined; tallgrass, mixed-grass, and shortgrass prairie cover only 1%, 20%, and 30%, of their historical extent, respectively, with the remaining portions being highly fragmented [5,6].

Grasslands are fundamentally shaped by two key functional groups that have co-evolved for thousands of years, namely, large migratory mammalian herbivores and small to medium-sized burrowing herbivorous mammals [7,8]. Both functional groups of herbivores play key-stone and/or ecosystem engineering roles and have complementary and interactive effects on grassland ecosystem structure and function [9–12].

In North America, American bison (*Bison bison*), through their grazing and wallowing, create grazing lawns and increase grassland biodiversity, prevent encroachment of shrubs through trampling and consumption of woody vegetation, and increase nutrient availability through the deposition of dung and urine [13]. Grazing by bison impacts plant survival, stimulates plant nitrogen uptake and aboveground production, and alters grassland community structure and ecosystem processes [14,15].

Prairie dogs also increase habitat heterogeneity and biodiversity of grassland ecosystems by creating islands of unique habitat [12]. Like many other burrowing mammals, prairie dogs are highly social, and aggregate into large colonies where they transform the landscape through their burrowing and foraging activities [16,17]. They are prey of a wide variety of predators and their borrows provide refuge for numerous animals [18]. Prairie dog grazing increases forage quality by reducing leaf age and enhancing plant nitrogen uptake, attracting large herbivores to their colonies [19,20]. The center of the prairie dog colonies, where most borrow-mounds appear, is dominated by bare ground and a low mat of heavily-grazed forbs and a mix of perennial and annual grasses [21]. In contrast, the edges of the colonies, which experience less impact by prairie dogs, are characterized by fewer burrows, taller vegetation, and moderately grazed annual and perennial grasses [21]. Prairie dogs also maintain the presence of grasslands and prevent their succession into shrubland by clipping shrubs and consuming their seedlings [12,22].

Bison and prairie dogs have co-evolved for thousands of years and constitute a grazing association, whereby bison preferentially graze along the edges of prairie dog colonies because of the availability of high quality forage; they also tend to rest within the center of colonies [19,23]. Bison that graze within prairie dog colonies have been shown to gain more weight compared to those that feed in off-colony grasslands [24]. Likewise, bison benefit prairie dogs by increasing nutrient quality of vegetation through their grazing and deposition of dung and urine [19,23,25], and their grazing lowers vegetation height, improving the ability of prairie dogs to detect predators [26].

Black-tailed prairie dogs (*Cynomys ludovicianus*) historically ranged across 40 million hectares of North America's central grasslands. But, their populations have declined by more than 98% primarily as a result of habitat loss to agriculture, introduction of plague from Eurasia, and eradication campaigns designed to eliminate their purported competition with cattle for grazing resources [8,27,28]. In addition to the expenditure of millions of public tax dollars on eradication efforts to support private industry, the loss of prairie dogs has had a dramatic consequences on the ecological integrity of North America's grassland ecosystem. The decline in prairie dogs is largely responsible for the near extinction of the black-footed ferret (*Mustela nigripens*), declines in other prairie dog-dependent species, encroachment of mesquite (*Prosopis glandulosa*) and other woody shrubs dispersed by cattle, and reduction in the economic productivity of this ecosystem [27–30]. Despite research showing that management strategies utilizing large-scale, lethal-control are neither scientifically justified nor cost effective, these "control" programs are still employed today and remain funded by taxpayers [7,12,31,32].

Domestic cattle (*Bos taurus*) have largely supplanted native American bison which were near-extirminated during the 19th century [13,33]. Bison and cattle are ecologically similar, [13] and while overgrazing by cattle has caused widespread desertification because of poor

rangeland management [28,34], the activities of domestic cattle may partially substitute the functional role of the American bison [13,35,36]. In fact, cattle and prairie dogs seem to have a grazing association similar to that of bison and prairie dogs, with important interactive impacts on grasslands [8,27,37,38]. Cattle are frequent visitors to black-tailed prairie dog colonies [39,40], and in some areas where conservative grazing management schemes are employed, prairie dog populations have increased up to two-fold [8].

The Janos Biosphere Reserve (JBR), located in northwest Chihuahua, Mexico maintains one of the largest remnants of desert grassland in northwestern Mexico, and one of the largest remaining prairie dog colony complexes in North America [28,41]. Like most of the semi-arid grassland ecosystems in North America, the Janos grasslands have been transformed by the synergistic effects of chronic overgrazing due to poor cattle management, drought and climate change, and the expansion of industrial agriculture [28,41]. These changes in the Janos region have resulted in a 75% decline of the once 55,000 ha prairie dog complex, and widespread expansion of shrublands into native grasslands [28,41].

Despite the longstanding importance of effective and conservation-based management of grasslands, the ecological interactions between cattle and prairie dogs remains little studied [12]. Understanding and applying the ecological principles of the interactions between cattle and prairie dog is fundamental to informing sustainable grassland management policies and procedures. To understand this interaction and the impact on grassland health, we studied the ecological relationships between cattle and prairie dogs in the desert grasslands of the Janos Biosphere Reserve, Chihuahua, Mexico.

Our objective was to determine if cattle and prairie dogs form grazing associations similar to those described between prairie dogs and American bison [23,26]. We specifically addressed the following questions: i) Do cattle have habitat preferences for prairie dog colonies or other habitat types? ii) Do cattle show temporal variability in habitat selection, as bison do? iii) Do cattle selectively graze in particular areas of prairie dog colonies, such as colony edges? and iv) How can the results from this research be applied to conservation strategies for semi-arid grasslands?

Materials and Methods

Study site

We conducted our research within a 1,700 ha fenced area (30° 52' 58.13" N, 108° 27' 21.64" W) located in the "El Uno" Ecological Reserve within the Janos Biosphere Reserve, Chihuahua, northwestern Mexico [41]. Native annual grasses dominate the plant community, while native perennial grasses are sparse [8]. The mean annual precipitation in the region is 317 mm, and most of it occurs during the summer monsoon period. The mean annual temperature is 16.95°C [42].

Experimental design

We conducted two complementary experiments to understand the relationship between habitat selection by cattle and the presence of black-tailed prairie dog colonies: 1) a Large-scale cattle habitat preference experiment and 2) a Small-scale cattle grazing preference experiment (descriptions provided below). We repeated all the design elements of each experiment three times from 2006–2007 in order to capture cattle grazing behavior under different periods of plant productivity: 1) low forage availability during the summer dry season (June–July) in 2006; 2) high forage availability at the end of the growing season in the fall (September–October) in 2006; and 3) the grass dormancy season during the winter (December–January) in 2006/2007. Both experiments were conducted using the recommended conservative grazing conditions

(<40% use of available forage) [43], with the suggested stocking rate for this region being roughly 30–60 hectare by animal unit considering a 50% available forage consumption [44,45], because our goal, here, was to understand the ecological relationships between domestic cattle and black-tailed prairie dogs under conservative grazing.

Transportation and handling of domestic cattle in both experiments was according to the Norma Oficial Mexicana / Official Mexican Norm NOM-051-ZOO-1995 (Trato humanitario en la movilizacion de animales / Humanitarian treatment in animal mobilization) [46]. We followed low stress handling techniques performed by trained cattle technicians, in order to avoid stress and ensure humane treatment of all animals used in our study. No official permit was necessary to perform this experiment because pasture raised domestic cattle are not considered an experimental animal species under the Norma Oficial Mexicana NOM-062-ZOO-1999 (Especificaciones tecnicas para la produccion, cuidado y uso de los animales de laboratorio / Technical specifications for production, care and use of lab animals) [47]. All the facilities used in both experiments (trailer, paddocks, GPS collars and electric fences) were commercial equipment designed for cattle management. For the use of GPS collars we followed the American Society of Mastozoology recommendations [48]. Additionally, the animals were routinely observed and checked by a trained veterinarian. All the permissions and permits required for fieldwork and utilization of domestic cattle were requested and authorized by the cattle owners and the administration of The Nature Conservancy's "El Uno" Ecological Reserve.

Large-scale cattle habitat preference experiment

The first experiment assessed cattle habitat preference (vegetation types) by activity type (grazing, resting and walking) within a 1,700 ha pasture. We followed the movements of 36 cows (*Bos taurus*), randomly separated into three replicated groups of 12 individuals, to evaluate cattle habitat selection. Each cow was fitted with a Global Position System (GPS) collar equipped with movement sensors (Lotek, 2200LR) programmed to record spatial locations every 5-minutes. Cows were allowed to graze freely and move throughout the pasture for 6 consecutive days. Only the 12 cows fitted with the GPS collars were present within 1,700 ha pasture at the time, which represents 141 ha by animal unit. To record cattle activities, we used movement sensor data together and cattle movement patterns (see Peinetti *et al.* 2011 for details in the Peinetti *s*) [49].

We used a QuickBird satellite image with 0.6 m resolution object-oriented classification (see Laliberte *et al.* 2007) [50] to develop a vegetation map, enabling us to assess habitats with which cattle most associated. We identified six vegetation types: 1) Annual grassland [which covered 50% of the pasture and was dominated by six weeks three awn (*Aristida adscencionis*)]; 2) perennial gramma grassland [14% cover, dominated by perennial blue grama (*Bouteloua gracilis*.)]; 3) tobosa grassland [10% cover, dominated by tobosa, *Hilaria mutica*]; 4) vine mesquite grassland [8% cover, dominated by vine mesquite, *Panicum obtusum*]; 5) weedy annual forbs [5% cover; dominated by Russian thistle, *Salsola kali* & Palmer's amaranth (*Amaranthus palmeri*); and 6) prairie dog colonies [12% cover] (Fig. 1).

Data analysis. We performed a multivariate analysis of variance (MANOVA) with Repeated Measurements Analysis of Variance, to test the hypothesis of no difference in cattle habitat selection (location x vegetation) by activity and season, to test the null hypothesis of there being no variation in cattle habitat selection (records x vegetation) by activity and season. When the MANOVA tests were significant, we used general linear models (GLM) to identify the source of variation. There were no significant differences among replicates (i.e., 12 cow group) within seasons, so we performed complementary Chi-Square Goodness-of-Fit Test by season (all season locations x vegetation) to test the null hypothesis of random habitat use by

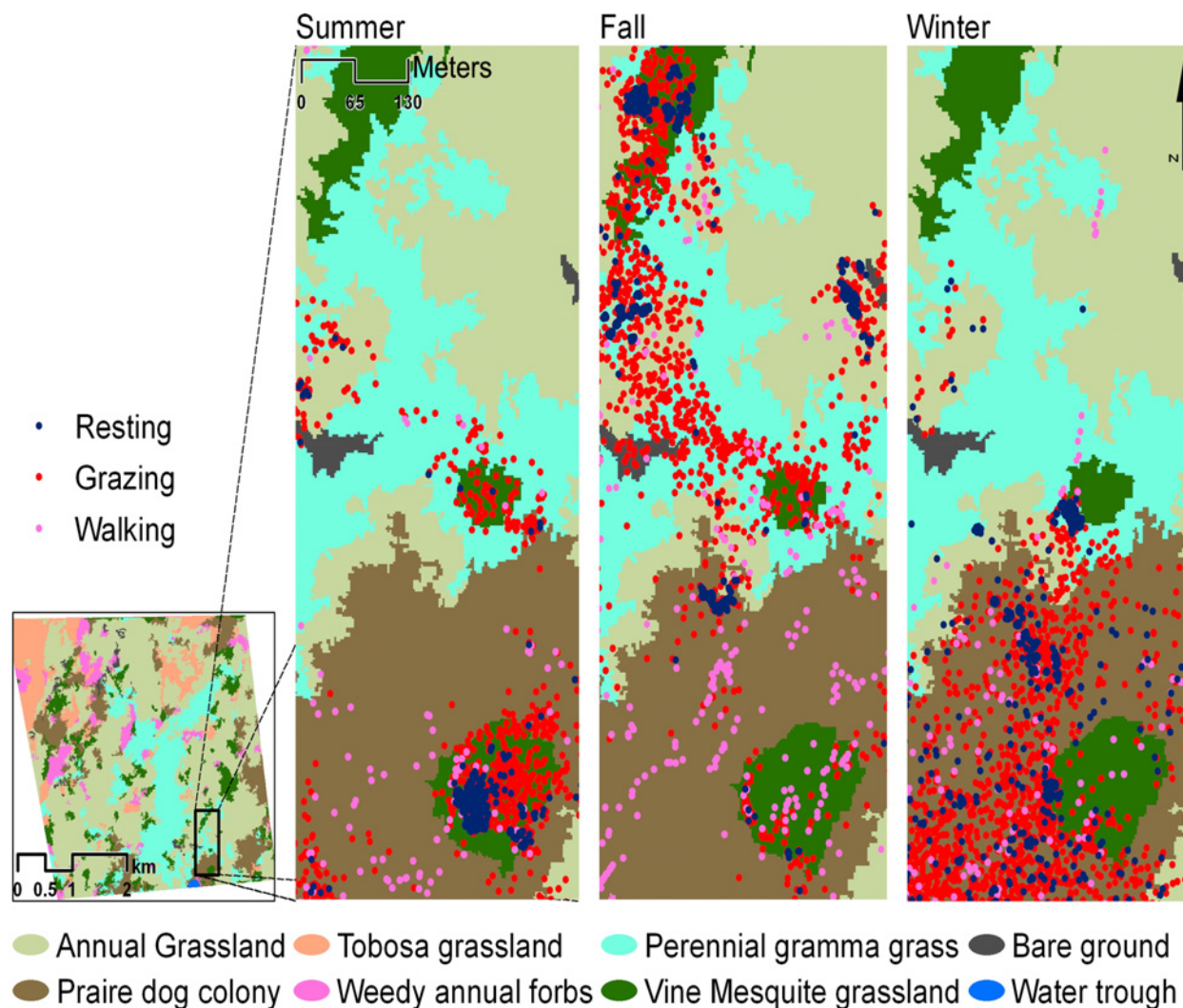


Fig 1. Spatial pattern of the three classes of cattle activity relative to the vegetation/ground cover types through seasons. Colored dots indicate cattle locations by activity across all weeks during each sample season.

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activity (activity x vegetation). To determine the type of vegetation cattle preferred by activity by season, within the pasture, we used Bonferroni confidence intervals, calculating the percent cattle used each habitat type. When the percentage of availability of any given vegetation type was below the confidence interval, we considered it to have been significantly selected ($P < 0.001$). When availability was above the confidence interval, that particular habitat was significantly avoided.

Small-scale cattle grazing preference experiment

We conducted a second experiment to determine if cattle preferentially forage on a particular section of prairie dog colonies (i.e., grazing zones): the colony center, along colony edges, or off colonies. To identify the grazing patterns, we established in three independent prairie dog colonies, three blocks containing three 60 m X 60 m experimental plots. A cattle-grade electric fence enclosed each plot and encompassed the three grazing zones. To determine if cattle grazing location preference changes with the proportion of colony occupancy of the landscape, we

varied the proportion of the grazing zones across the three plots on each colony: plot 1 consisted of 25% prairie dog colony and 75% off-colony grassland; plot 2 consisted of 50% prairie dog colony and 50% off-colony grassland; and plot 3 consisted of 75% prairie dog colony and 25% off-colony grassland. We calculated the prairie dog colony edge area for each plot by multiplying the average edge width by its length, using ArcMap 9.0 (ESRI). Four cows grazed each plot for 4 hours with a stocking rate of 65 ha by animal unit, once each season during the early morning grazing activity peak [51]. We recorded the type of cattle activity (grazing, resting and walking) observed for each cow within each plot every three minutes from a portable observation tower located 30 m from the edge of each plot.

Data analysis We performed a multivariate analysis of variance (MANOVA) with a Repeated Measurements Analysis approach to test the null hypothesis of cattle grazing zone selection by season. When MANOVA tests were significant, we performed a Chi-Square-Goodness-of-Fit to make comparisons of the cattle grazing zones (grazing x zone) by season. We also used Bonferroni confidence intervals to determine the preferred grazing zone; only grazing records were used in this analysis.

All data were assessed for normality, and if needed, normalized by log transformations using JMP version 8.

Results

Large-scale cattle habitat preference experiment

Cattle showed strong use preferences for prairie dog colonies, perennial gramma grassland, vine mesquite grassland and grassland dominated by annual weedy forbs (i.e., habitats used above their availability). In contrast, annual grassland and tobosa grassland were avoided (i.e., utilization below availability) (Fig. 1). Despite prairie dogs occupying only 12% of the landscape, cattle associated with colonies more than 24% of the total time; whereas, while annual grasslands covered 50% of the total area, cattle utilized them less than 20% of the time (Fig. 2 and Table 1).

Cattle habitat selection also differed seasonally (MANOVA: $P < 0.0001$; $F_{2,8} = 7.8e-5$). Activity locations varied across the three seasons (MANOVA $P < 0.035$; $F_{1,6} = 0.007$) and activities (i.e., grazing, resting, walking) (MANOVA: $P < 0.001$; $F_{4,27} = 0.03$ (Fig. 1). The chi-square values for cattle activity by season were: Grazing, summer $X^2 = 16,406.4$, $P = 0.05$; fall $X^2 = 8119.1$, $P = 0.05$; winter $X^2 = 8,282.67$, $P = 0.05$; Resting, summer $X^2 = 132,806$; $P = 0.05$, fall $X^2 = 36,234.4$, $P = 0.05$; winter $X^2 = 15,014.60$, $P = 0.05$; Walking, summer $X^2 = 32,806.1$, $P = 0.05$; fall $X^2 = 978.7$, $P = 0.05$; winter $X^2 = 1,724.6$, $P = 0.05$ (Fig. 2 and Table 1). Seasonal changes in location x vegetation by activity, were detected only for prairie dog colonies (GLM: $P = 0.02$, $F = 4.86$; $P = 0.02$, $F = 8.40$, respectively) and vine mesquite grassland (GLM: $P = 0.05$, $F = 3.44$; $P < 0.0001$, $F = 22.4$, respectively). Use of annual weedy forbs differed by activity but not by season (GLM: $P = 0.001$, $F = 10.32$).

Small-scale cattle grazing preference experiment

Cattle used prairie dog colonies for grazing and resting at rates above their availability during both the high forage availability season, in fall, and the grass dormancy season, in winter ($P < 0.001$), (Fig. 2 and Table 1).

There were no significant differences among the three plots across the three blocks (MANOVA $F_{1,2} = 0.79$, $P < 0.2$), meaning no variation between treatments and prairie dog colonies, but strong seasonal preferences for particular foraging zones were detected (MANOVA $F_{4,5} = 0.2035$, $P < 0.0001$). The chi-square values for cattle grazing locations by foraging zone were:

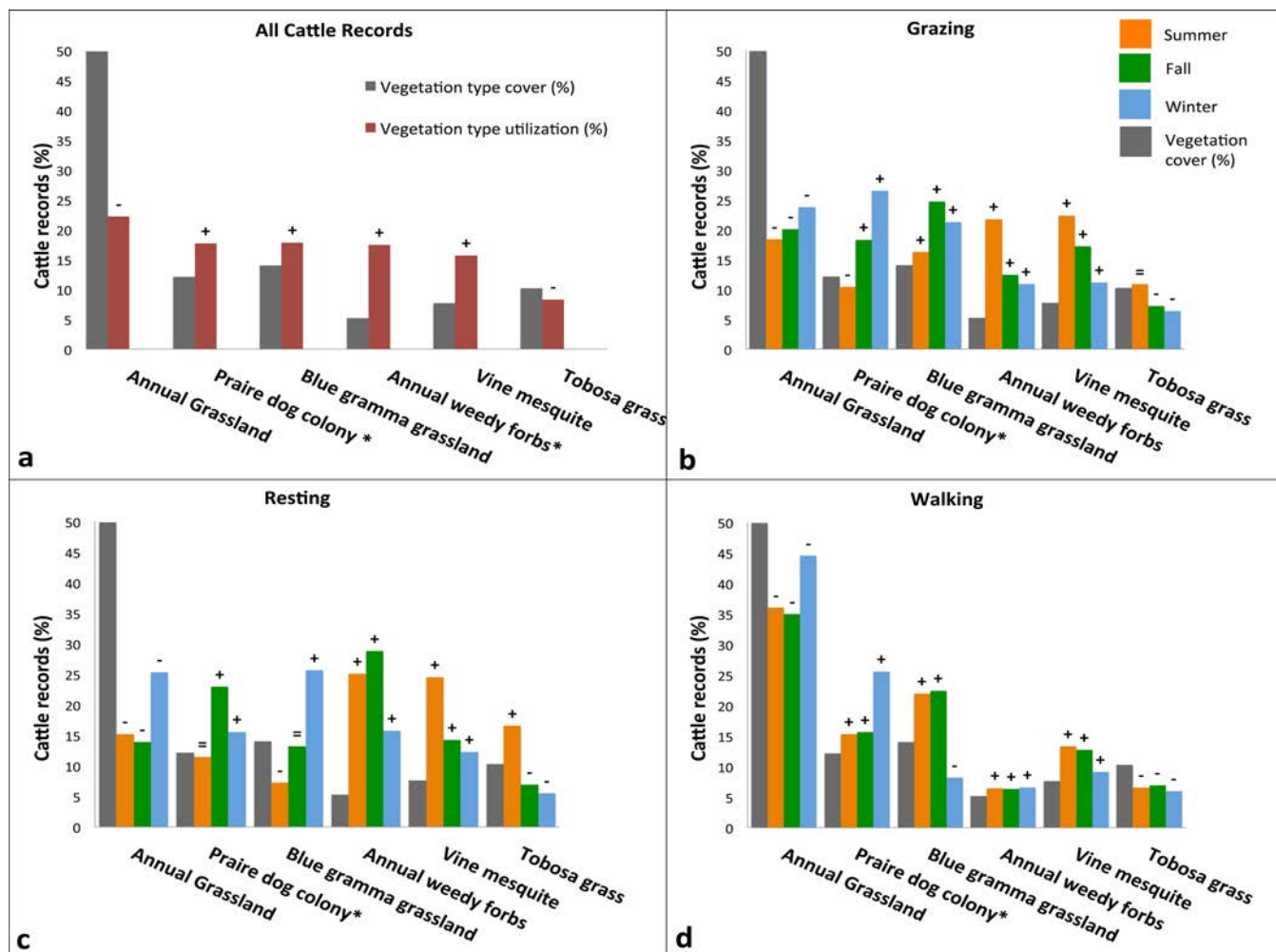


Fig 2. Large-scale experiment. Cattle record's percentage by vegetation type, activity, and season. a) Total time cattle utilized the different vegetation types v.s. vegetation type % cover; b) Grazing records by vegetation by season v.s. vegetation type cover %; c) Grazing records by vegetation x season v.s. vegetation type cover %. d) Grazing records by vegetation x season v.s. vegetation type cover %. Bonferroni confidence-interval results ($P < 0.001$) are given by the following signs: "+" indicates preference (utilization above availability); "=" indicates random (utilization equal to its availability); and "-" indicates avoidance (utilization below its availability); and "*" indicates vegetation types with significant differences in utilization across seasons.

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$\chi^2 = 619.2$, summer; $\chi^2 = 851.51$, fall; $\chi^2 = 2, 813.6$, winter, denoting a strong non-random utilization pattern.

Prairie dog colony edges were preferentially selected for grazing by cattle across all seasons and were the most utilized foraging zone during the winter season ($P < 0.001$, Fig. 3, Table 2). More than 50% of the grazing events occurred in only 7% of the total experimental area, being represented by the colony edge. Unlike the colony edge, cattle consistently avoided grazing within the prairie dog colony center across all seasons ($P < 0.001$) (Fig. 3, Table 2).

Discussion

We found that cattle preferred foraging on prairie dog colonies in Chihuahuan desert grasslands, especially during the winter grass dormancy season but also during the fall. Results from this large-scale habitat selection experiment also were consistent with our small-scale grazing preference experiment on cattle foraging behavior in relationship to prairie dog colonies.

Table 1. Large-scale experiment.

Large-scale cattle habitat preference experiment Bonferroni confidence-interval analysis						
Vegetation Type	Expected proportion	Confidence interval of occurrence ($P > 0.001$)	Season	Activity	Proportion observed	Utilization
Annual grassland	0.49	0.488 < P < 0.507	Summer	Grazing	0.18	-
				Resting	0.15	-
				Walking	0.35	-
			Fall	Grazing	0.19	-
				Resting	0.13	-
				Walking	0.34	-
			Winter	Grazing	0.23	-
				Resting	0.24	-
				Walking	0.44	-
Perennial gramma grassland	0.14	0.133 < P < 0.146	Summer	Grazing	0.16	+
				Resting	0.07	-
				Walking	0.21	+
			Fall	Grazing	0.24	+
				Resting	0.131	-
				Walking	0.22	+
			Winter	Grazing	0.21	+
				Resting	0.25	+
				Walking	0.08	-
Prairie dog colony	0.12	0.114 < P < 0.127	Summer	Grazing	0.10	-
				Resting	0.114	=
				Walking	0.15	+
			Fall	Grazing	0.18	+
				Resting	0.22	+
				Walking	0.15	+
			Winter	Grazing	0.26	+
				Resting	0.15	+
				Walking	0.25	+
Tobosa grassland	0.10	0.096 < P < 0.108	Summer	Grazing	0.108	=
				Resting	0.16	+
				Walking	0.06	-
			Fall	Grazing	0.07	-
				Resting	0.06	-
				Walking	0.06	-
			Winter	Grazing	0.06	-
				Resting	0.05	-
				Walking	0.05	-

(Continued)

Table 1. (Continued)

Large-scale cattle habitat preference experiment Bonferroni confidence-interval analysis						
Vegetation Type	Expected proportion	Confidence interval of occurrence ($P > 0.001$)	Season	Activity	Proportion observed	Utilization
Vine mesquite grassland	0.07	0.071 $<P < 0.081$	Summer	Grazing	0.22	+
				Resting	0.24	+
				Walking	0.13	+
			Fall	Grazing	0.16	+
				Resting	0.14	+
				Walking	0.12	+
			Winter	Grazing	0.11	+
				Resting	0.12	+
				Walking	0.90	+
Weedy annual forbs	0.05	0.047 $<P < 0.056$	Summer	Grazing	0.21	+
				Resting	0.25	+
				Walking	0.06	+
			Fall	Grazing	0.12	+
				Resting	0.28	
				Walking	0.06	+
			Winter	Grazing	0.10	+
				Resting	0.15	+
				Walking	0.66	+
Bare ground	0.008	0.007 $<P < 0.010$	Summer	Grazing	0.001	-
				Resting	0.0	-
				Walking	0.0	-
			Fall	Grazing	0.015	-
				Resting	0.009	=
				Walking	0.01	+
			Winter	Grazing	0.006	-
				Resting	0.01	+
				Walking	0.0	-

Cattle record's percentage by vegetation type, activity, and season. Bonferroni confidence-interval results ($P < 0.001$) are given by the following signs: "+" indicates preference (utilization above availability); "=" indicates random (utilization equal to its availability); and "-" indicates avoidance (utilization below its availability).

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During winter and fall seasons when cattle preferred prairie dog colonies for grazing, cattle spent most of their time grazing along the edges of colonies where forage quality is often higher than in off colony areas and where quantity is higher compared to colony centers [19,23,25]. In summer, when cattle did not prefer prairie dog colonies for grazing, cattle spent most of their foraging time off colonies, within the surrounding grassland, resembling the previously described American bison-prairie dog grazing association [7,12,18,19,23,25,27].

In our study, cattle grazed and rested on prairie dog colonies in the fall during the grass-growing season and especially in the winter during the grass dormancy season, suggesting that prairie dog colonies provide an important forage resource within the greater grassland landscape and during one of the harshest seasons for cattle grazing. These patterns probably resulted from prairie dog activities during the grass growing season that enhance forage quality, such as removal of standing dead biomass and clipping of vegetation that increases plant

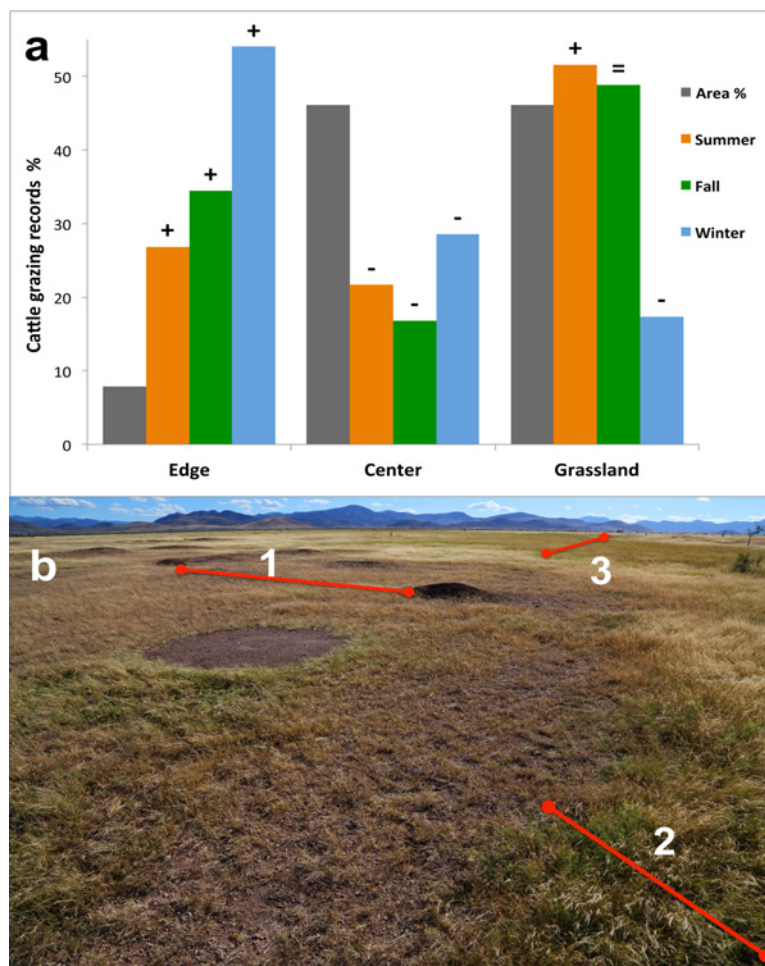


Fig 3. Small-scale experiment. Cattle grazing record's percentage by foraging zone and season v.s. foraging zone area cover %. (a) Bonferroni confidence-interval results ($P < 0.001$) are given by the following signs: "+" indicates preference (utilization above availability); "=" indicates random (utilization equal to its availability); and "-" indicates avoidance (utilization below its availability); (b) image of a typical prairie dog colony in the Janos grasslands, showing vegetation height and cover increasing away from the colony center (1) towards the colony edge (2) and the surrounding climax grasslands (3).

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nitrogen uptake, in addition to the lack of other more palatable forage options during the winter season [20,52].

Foraging behavior is strongly influenced by dietary preferences, and large herbivores spend more time grazing in plant communities that have higher quantities of preferred forage [53]. While cattle showed strong preferences for foraging on prairie dog colonies in our study, they also associated with other vegetation types. They spent considerable time in perennial gramma grassland, vine mesquite grassland and annual weedy forb habitat, but avoided tobosa grassland and annual grassland, the latter being the most abundant vegetation type within the Janos region. In North American grasslands, cattle prefer perennial grasses like blue gramma (*Bouteloua gracilis*) and vine mesquite (*Panicum obtusum*), which have their highest nutritional value during the summer and fall [49,54,55]. Annual grasses, such as the six weeks three awn have comparatively limited nutritional value; and other, more desert-adapted perennial grasses, such as tobosa grass, contains an abundant accumulated dead plant material which make them unpalatable [56].

Table 2. Small-scale experiment.

Small-scale cattle grazing preference experiment Bonferroni confidence-interval analysis					
Season	Foraging Zone	Expected Proportion	Proportion observed	Confidence interval of occurrence ($P > 0.001$)	Use
Summer $\chi^2 = 619.2$ $P < 0.005$	Margin	0.071	0.268	0.048 $< P < 0.094$	+
	Center	0.463	0.216	0.419 $< P < 0.509$	-
	Grassland	0.463	0.515	0.419 $< P < 0.509$	+
Fall $\chi^2 = 851.51$ $P < 0.005$	Margin	0.068	0.343	0.041 $< P < 0.095$	+
	Center	0.464	0.168	0.415 $< P < 0.518$	-
	Grassland	0.465	0.487	0.415 $< P < 0.518$	+
Winter $\chi^2 = 2813.6$ $P < 0.005$	Margin	0.095	0.540	0.072 $< P < 0.228$	+
	Center	0.452	0.285	0.413 $< P < 0.490$	-
	Grassland	0.452	0.173	0.413 $< P < 0.490$	-

Cattle grazing record's percentage by foraging zone and season v.s. foraging zone area cover %. Bonferroni confidence-interval results ($P < 0.001$) are given by the following signs: "+" indicates preference (utilization above availability); "=" indicates random (utilization equal to its availability); and "-" indicates avoidance (utilization below its availability).

doi:10.1371/journal.pone.0118602.t002

Cattle foraging behavior varies seasonally with plant phenological and nutritional changes [10]. Perennial grasses and weedy annual forbs begin to green-up at the end of the spring into the beginning of summer, and are at this time, preferred forage by cattle. Growth of perennial grasses accelerates following the summer rains through fall, developing new foliage and pushing off dead remnants from the preceding dormancy season, increasing their palatability [57]; whereas in summer weedy forbs flower, form sharp spines and accumulate anti-herbivore compounds, so cattle avoid them [58]. During winter, nutritional quality of perennial grasses declines, reducing their consumption by cattle, and consumption of seasonal forbs increases [59]. Our findings, consequently, demonstrate the importance of heterogeneity within semi-arid grasslands, which includes prairie dog colonies, for the provision of multiple forage alternatives temporally and spatially within semi-arid grassland landscapes [34,60]. The preferential foraging on prairie dog colonies by cattle highlights not only the role of prairie dogs in creating heterogeneous grassland landscapes, [8,27] but also their important contribution to supporting local communities that depend on cattle grazing for their livelihoods.

Our results not only support previous studies showing that cattle occur more commonly on prairie dog colonies in the Chihuahuan Desert grasslands [40], but also that cattle preferentially forage on them. However, these ecological relationships between cattle and prairie dogs probably vary across the geographic ranges and different species of prairie dogs, and with variation in precipitation and plant productivity [52]. For example, in the mixed-grass prairie, cattle spend significantly more time in pastures with prairie dog colonies compared to pastures without colonies [39]. In contrast, cattle do not appear to associate with prairie dog colonies in shortgrass prairies [38]. When comparing the weights of cattle that graze in areas with prairie dog colonies (at $< 30\%$ pasture occupancy) and areas without prairie dog colonies, no significant difference in cattle weight gains have been found, presumably because the reduction of available forage on colonies is compensated for by the improved vegetation quality [44,45]. Nevertheless, weight gains can decline in shortgrass prairie when colonies occupy more than 30% of the total area, and when prairie dog colonies occupy more than 60% of the total area, cattle weight gain is reduced further (14%) [61,62].

Our work suggest that prairie dogs and cattle can have a positive, mutualistic relationship, in North America's desert grasslands [8,37]. Cattle appear to benefit from modified vegetation

structure and composition and increased nutritional value on prairie dog colonies [12,52,61]. Similarly, prairie dogs are known to benefit from the presence of large grazers, like bison and cattle [12,19,23,25,27,37]. For example, black-tailed prairie dog density increased about 2-fold under conservative cattle grazing, on a companion study located adjacent to ours [8]. Cattle grazing positively affected prairie dog abundances, likely by improving their ability to see predators [8,12,27,39]. Similar results have been reported for Utah prairie dogs (*C. parvidens*), which prefer foraging in areas grazed moderately by cattle compared to non-grazed areas [63]. Additionally, others have observed that prairie dogs establish their colonies in areas that are intensively grazed by livestock [39]. Similar to the effects of American bison, cattle stimulate nitrogen uptake and lower leaf age through their grazing, and increase available nitrogen by depositing dung and urine [13,34]. So, like bison, cattle also may positively impact prairie dogs by increasing forage quality [23,38,63,64]. This ecological relationship is similar to the grazing association between prairie dogs and bison [19,23,25].

Management

This positive relationship between cattle and prairie dogs in the Chihuahuan Desert grasslands, challenges the long-standing view of prairie dogs as an undesirable pest species in rangelands [31]. The presence of prairie dogs can have a positive impact on cattle that is beneficial to the livestock industry, by prairie dog colonies providing favorable grazing habitat for cattle and reducing shrub invasion into grassland environments [22,28]. In turn, cattle can be used as a management tool to strategically graze areas where prairie dogs are needed to help promote biodiversity, enhance forage quality, and reduce shrub encroachment [34]. In sum, our work, along with that by Davidson, 2010, suggests that prairie dogs and cattle can have a mutualistic relationship. And, when their abundances are managed so that they interact synergistically together, they can enhance the productivity and biodiversity of grassland ecosystems [8], supporting local communities that depend on livestock grazing for their livelihoods and the livestock industry more generally.

A paradigm shift is needed on how rangelands are managed, from simply promoting maximization of livestock production and creating homogenous grassland landscapes dominated by only a few desirable forage species, to more integral management that benefits biodiversity, enhances habitat heterogeneity, and improves ecosystem services on which humans depend [34,60]. Given the widespread degradation of grasslands and loss to shrublands, the results of our work provide new insights into novel management strategies for grassland conservation and a potential win-win scenario for biodiversity and productive human activities. In addition to the possible direct benefits to cattle ranching and increasing grassland biodiversity, prairie dogs also increase groundwater recharge, forage availability, soil carbon storage, regulation of soil erosion, and regulation of soil productive potential [16]. Despite increasing awareness of the important functional role of prairie dogs, they are still considered a pest by range managers and still commonly subject to lethal control in both the US and Mexico [12]. Our research supports the argument that conservation and restoration of prairie dog populations should be key components of sustainable grassland management, and that conservation-guided cattle ranching can be a productive human enterprise, compatible with grassland biodiversity conservation objectives.

Supporting Information

S1 File. Norma Oficial Mexicana NOM-051-ZOO-1995, Trato humanitario en la movilización de animales.
(PDF)

S2 File. Norma Oficial Mexicana NOM-062-ZOO-1999, Especificaciones técnicas para la producción, cuidado y uso de los animales de laboratorio.
(PDF)

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Author Contributions

Conceived and designed the experiments: RSC ELF GC. Performed the experiments: RSC ELF EPG. Analyzed the data: RSC HLS HSA. Contributed reagents/materials/analysis tools: RSC AD HLS. Wrote the paper: RSC AD GC HLS HSA EPG.

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Strategic conservation for lesser prairie-chickens among landscapes of varying anthropogenic influence

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ABSTRACT

For millennia grasslands have provided a myriad of ecosystem services and have been coupled with human resource use. The loss of 46% of grasslands worldwide necessitates the need for conservation that is spatially, temporally, and socioeconomically strategic. In the Southern Great Plains of the United States, conversion of native grasslands to cropland, woody encroachment, and establishment of vertical anthropogenic features have made large intact grasslands rare for lesser prairie-chickens (*Tympanuchus pallidicinctus*). However, it remains unclear how the spatial distribution of grasslands and anthropogenic features constrain populations and influence conservation. We estimated the distribution of lesser prairie-chickens using data from individuals marked with GPS transmitters in Kansas and Colorado, USA, and empirically derived relationships with anthropogenic structure densities and grassland composition. Our model suggested decreased probability of use in 2-km radius (12.6 km²) landscapes that had greater than two vertical features, two oil wells, 8 km of county roads, and 0.15 km of major roads or transmission lines. Predicted probability of use was greatest in 5-km radius landscapes that were 77% grassland. Based on our model predictions, ~10% of the current expected lesser prairie-chicken distribution was available as habitat. We used our estimated species distribution to provide spatially explicit prescriptions for CRP enrollment and tree removal in locations most likely to benefit lesser prairie-chickens. Spatially incentivized CRP sign up has the potential to provide 4189 km² of additional habitat and strategic application of tree removal has the potential to restore 1154 km². Tree removal and CRP enrollment are conservation tools that can align with landowner goals and are much more likely to be effective on privately owned working lands.

1. Introduction

Conservation on working lands may require not only efforts to protect remaining tracts of high biodiversity but efforts to strategically apply management practices that simultaneously consider human well-

being and wildlife (Samson et al., 2004; Kareiva and Marvier, 2012). Since the start of the Progressive Era > 100 years ago, those that have strived to protect wildlife and wild areas have disagreed on whether to preserve by protecting and leaving areas alone, or by conserving wildlife friendly habitat through human imposed management (Fox,

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1981; Miller et al., 2011). More recently, this discussion has evolved to include ideas on land sparing versus land sharing and a “new conservation” that demonstrates human benefit to gain conservation success through public approval (Miller et al., 2011; Kareiva and Marvier, 2012; Kremen, 2015). Such considerations are relevant for prairie-grouse (*Tympanuchus* and *Centrocercus* spp.) management that occurs in areas that are either privately owned or leased for agricultural production (Ciuzio et al., 2013). To improve landowner participation, slogans such as “what’s good for the bird, is good for the herd” have been developed to disseminate wildlife-friendly land management practices to more widespread audiences (Wiklund, 2015). Outside of efforts to preserve large remaining tracts of grassland, the “new conservation” approach may be the best, and only, foreseeable option in the Great Plains of Kansas and Colorado, USA, where historical ecological drivers that once maintained habitat for numerous grassland dependent species have been greatly altered (Askins et al., 2007). Management that closely mimics site-specific historical ecological drivers is likely the best option to manage for biodiversity in grasslands; however, due to the extent of alterations and global change, more novel approaches to provide grassland on working lands may be beneficial. For example, free-ranging bison (*Bison bison*) have been replaced by cattle in fenced pastures, fire has largely been removed from the landscape, woody species are encroaching, the climate is changing, and increased food, fiber, and energy needs for growing human populations have greatly changed the Great Plains since pre-European settlement (Samson et al., 2004; Haukos and Boal, 2016).

It is estimated that grasslands have decreased 46% worldwide and only 4.5% of grasslands are protected (Hoekstra et al., 2005). In the Great Plains of North America, grasslands have decreased by an estimated 70% (Samson et al., 2004). This is especially problematic for grassland-dependent wildlife that need broad grassland availability to cope with weather driven variation in habitat availability (Wiens, 1974; Sala et al., 1998; Winter et al., 2005). Large grassland-dominated landscapes available for lesser prairie-chicken (*Tympanuchus pallidicinctus*) populations and other grassland birds have become rare due to conversion of native grasslands to cropland, establishment of anthropogenic features, and woody encroachment due to grassland management practices (Hagen et al., 2011; Rodgers, 2016; Lautenbach et al., 2017; Plumb et al., 2019).

Knowledge of how grassland composition (i.e., proportion of grassland in a landscape) and anthropogenic feature densities constrain the distribution of lesser prairie-chickens at multiple scales and among years of variable climate are needed. It remains unclear what constrains the distribution of lesser prairie-chickens and how available habitat is distributed in Kansas and Colorado, which together support > 80% of extant lesser prairie-chickens (McDonald et al., 2014). To fill knowledge gaps, a machine-learning approach can provide spatially explicit predictions of potential habitat of lesser prairie-chickens (Cutler et al., 2007). Once an empirically derived species distribution is estimated, the predicted distribution can be used to identify grassland strongholds to be protected and areas within those strongholds that can be spatially prioritized for conservation on working lands.

Two conservation actions that could increase habitat include tree removal in south-central Kansas and conversion of cropland to perennial grassland through the USDA Conservation Reserve Program (CRP) in northwest Kansas and eastern Colorado (Lautenbach et al., 2017; Sullins et al., 2018). For *Tympanuchus* spp., it is unlikely that a universal management practice will benefit populations similarly across their range, with a 40-cm annual precipitation gradient in our study area from Kansas to Colorado (McNew et al., 2013; PRISM, 2016). Therefore, we propose two distinct conservation practices that are spatially dependent, but potentially capable of large-scale application on working lands. Both conservation practices can be profitable for producers in the lesser prairie-chicken range of Kansas and Colorado where > 95% of the species-occupied range is privately owned (Becerra et al., 2016). However, tree removal and enrollment in CRP will only

benefit lesser prairie-chickens when surrounding landscapes can support sustainable populations. Conservation practices should be strategically applied where they are most likely to reap benefits within large grassland areas having limited anthropogenic structures (Winder et al., 2015; Sullins et al., 2018; Plumb et al., 2019).

Merely protecting a grassland as a wildlife-friendly grassland is not possible due to the dependence of the grassland itself, and its quality for wildlife, on ecological drivers that have been greatly altered (Askins et al., 2007). Alterations to ecological drivers (processes) that once maintained quality grasslands in this area have led to declines and distribution shifts in several grassland bird species (Peterjohn and Sauer, 1999). For example, there is evidence that prairie-grouse (*Tympanuchus* spp.), grasshopper sparrows (*Ammodramus savannarum*), and Henslow's sparrows (*A. henslowii*) exhibit declining trends in traditional portions of their range but have increased in areas where cropland has been converted to ungrazed grassland through the Conservation Reserve Program (CRP; Herkert, 1998; Johnsgard, 2001; Rodgers and Hoffman, 2005). The benefit of CRP for these species is a clear example, albeit by accident, of “new conservation” because the program incentivizes landowners to take land out of agricultural production. The financial benefit of CRP makes this a favorable tool for wildlife conservation.

Tree removal is another management practice that can benefit both cattle producer and prairie grouse by expanding grasslands that provide cover for prairie grouse and forage for cattle (Lautenbach et al., 2017; Severson et al., 2017). Deploying such management practices have promise of being well received and implemented by producers; however, because of various environmental and abiotic constraints, and our inability to preserve a pre-European settlement state at an appropriate scale, most conservation benefits are site dependent and therefore, must be spatially targeted (Samson et al., 2004; Ciuzio et al., 2013).

We provide an example of strategic conservation to target management practices on privately owned land that may benefit both producer and lesser prairie-chickens alike. Our first objective was to predict the distribution of lesser prairie-chicken habitat in Kansas and Colorado based on grassland composition, tree occurrence, and anthropogenic feature density constraints. We used a Random Forest model that incorporated locations from marked lesser prairie-chickens and available locations to create spatially-explicit predictions of use through the northern extent of the lesser prairie-chicken range. Our second objective was to use the predicted distribution to identify locations at which tree removal and enrollment of cropland into the CRP would have the greatest benefit to lesser prairie-chicken populations (Lautenbach et al., 2017; Sullins et al., 2018).

2. Study area

Our study area encompassed the northern portion of the extant lesser prairie-chicken distribution including portions of the Short-Grass Prairie/CRP mosaic (SGP), Mixed-Grass Prairie (MGP), and Sand Sagebrush Prairie Ecoregions (SSP; Fig. 1, McDonald et al., 2014). A longitudinal annual precipitation gradient spanned from east (~69 cm) to west (~37 cm) across the extent of Kansas into eastern Colorado with a concomitant transition from mixed- to short-grass prairie (PRISM, 2016). Pockets of sand sagebrush (*Artemisia filifolia*) prairie were interspersed on sandy soils, especially in the southwest portion of the study area. Mosaics of CRP and row-crop agriculture were associated in areas with arable soils. Most of the large remaining grasslands were restricted to areas of poor or rocky soils and areas with rough terrain that were unsuitable for cultivation (Spencer et al., 2017). Anthropogenic development was present in the form of oil wells, transmission lines, county roads, major roads, and other vertical features (e.g., cell towers, windfarms, grain elevators, etc.). Within the study area, data were collected at 6 study sites that varied in anthropogenic feature densities including 3 in Colorado (Prowers/Baca, Cheyenne, Comanche National Grasslands[NG]) and 3 in Kansas (Red Hills/Clark, Northwest,

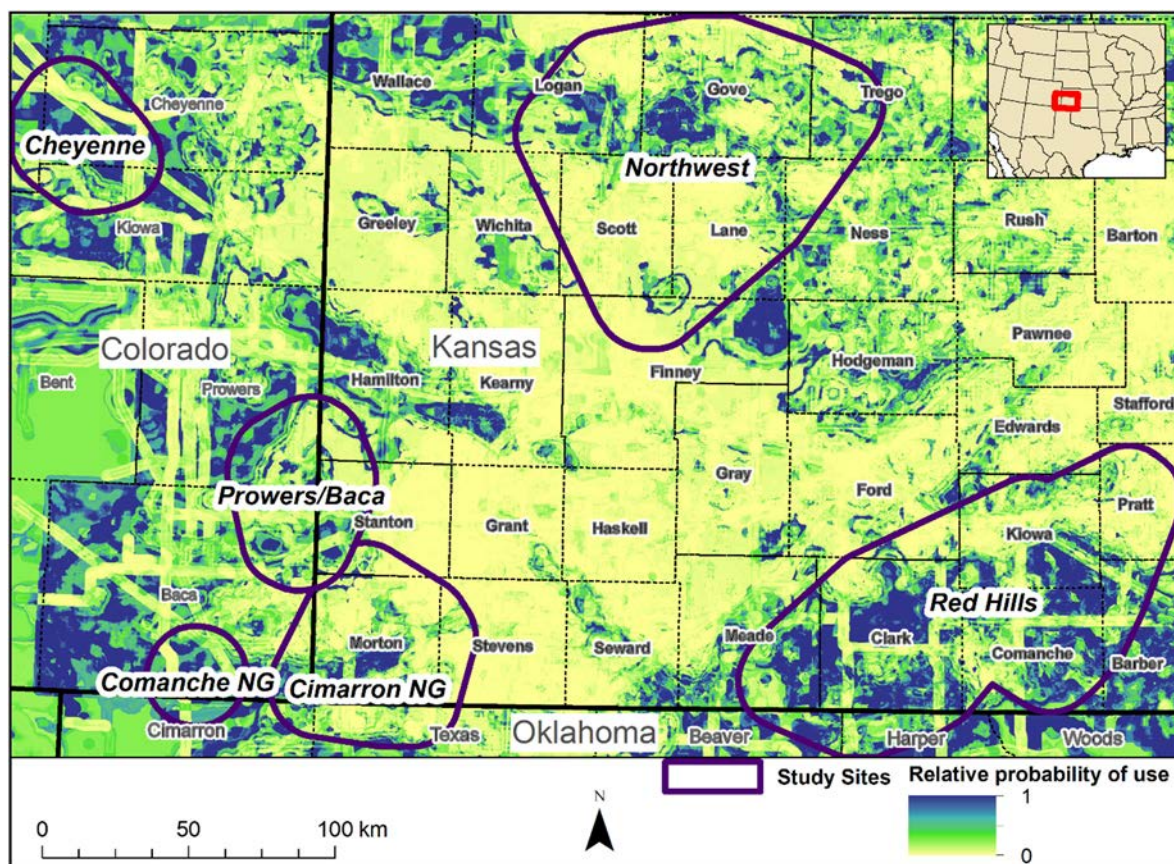


Fig. 1. Locations of the 6 study sites where lesser prairie-chickens were marked, captured, and monitored in Kansas and Colorado, USA, during 2013–2016 to estimate species distribution using a Random Forests model relative to presumed occupied range of lesser prairie-chickens. Study sites were established by creating minimum convex polygons from the subset of locations used by lesser prairie-chickens marked with GPS satellite transmitters then buffering the minimum convex polygons with the average net displacement during dispersal (16.18 km) following [Earl et al. \(2016; A\)](#). Values range from 0 (yellow) to 1 (dark blue) indicating the relative probability of use by lesser prairie chickens and predict the extent of habitat based on grassland composition within 5 km and anthropogenic feature densities within 2 km (B). The species distribution model encompasses 3 of 4 ecoregions used by the lesser prairie-chicken including the Short Grass Prairie/CRP mosaic (Northwest study site), Mixed Grass Prairie (Red Hills study site), and Sand Sagebrush Prairie Ecoregions (Cimarron NG, Comanche NG, Prowers/Baca, and Cheyenne study sites) as defined in [McDonald et al. \(2014\)](#). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Cimarron NG; [Fig. 1](#), Table S1, see supplemental material for further description of each study site). Temperatures ranged from -26 to 43 °C (extreme minimum and maximum temperature), with average daily minimum and maximum temperatures of 5 °C and 21 °C, respectively, during data collection (15 March 2013 to 15 March 2016; [NOAA, 2016](#)).

3. Methods

3.1. Capture and marking

We captured lesser prairie-chickens at all study sites on leks during spring (March to mid-May) and uniquely marked individuals with rump-mounted 22-g GPS (global positioning system) satellite PTT transmitters (SAT-PTT; PTT-100, Microwave Technology, Columbia, MD, USA, or North Star Science and Technology, King George, VA, USA; [Robinson et al., 2018](#)) or a 15-g very-high-frequency transmitter attached as a necklace with whip antennae down the middle of the back (VHF; A3960, Advanced Telemetry System, Isanti, MN, USA). We alternated attachment of GPS and VHF transmitters on every other bird captured. The GPS transmitters had a spatial error of ± 18 m, which was less than the $30\text{-m} \times 30\text{-m}$ (900 m^2) resolution pixels used in our analyses. We limited VHF location data to those with error polygons $< 1000\text{ m}^2$ ([Robinson et al., 2018](#)). Locations were recorded every

2 h during the day for GPS transmitters, with a 6-hour and 8-hour nocturnal gap during summer and winter, respectively. We attached VHF transmitters as a necklace with whip antennae down the middle of the back and estimated diurnal locations four times per week using triangulation and using Location of a Signal software to estimate error polygons (Ecological Software Solutions LLC, Hegymagas, Hungary).

3.2. Landcover covariates

We obtained landcover type classifications at a $30\text{-m} \times 30\text{-m}$ resolution from the 2011 National Landcover database (NLCD) and a shapefile identifying the distribution of Conservation Reserve Program (CRP) grasslands in 2014 provided under agreement with the U.S. Department of Agriculture, Farm Service Agency ([Homer et al., 2015](#)). We created continuous rasters of grassland and shrubland composition from the NLCD land cover classification using focal-point statistics in ArcGIS 10.2. We created surfaces using multiple windows that estimated grassland composition within $0.4\text{ km} - 5\text{ km}$ to represent potential scales of selection for lesser prairie-chickens. Throughout, we refer to the scale used as the length of the radius (e.g., 5-km scale). We examined multiple scales because of the uncertainty of the scale at which emergent and extrahierarchical properties of the landscape would best predict lesser prairie-chicken occupancy ([King, 1997](#)). We bounded scales assessed to be $\leq 5\text{ km}$ based on past lesser prairie-chicken

literature, which included demographic influences at the 3-km scale and selection of nest sites within 4.8 km of capture lek (Giesen, 1994, Ross et al., 2016a). We used the 0.4-km radius as a minimum scale because it is less than estimates for habitat requirements in Haukos and Zaveleta (2016).

3.3. Anthropogenic feature covariates

To estimate the distance to, and densities of, anthropogenic features, we acquired shapefile layers of oil wells, transmission lines, major roads, county roads, and cell phone towers (see Supplemental Materials for sources of anthropogenic feature data). In ArcGIS 10.2, we used the Euclidean distance tool to generate rasters depicting distance to feature and focal statistics tool to estimate summed densities of features within circular radii (0.5 km, 1 km, 2 km) of each pixel. The range of radii was selected to encompass known avoidance distances (~0.5–2 km) published in past literature (Pruett et al., 2009; Hagen et al., 2011; Plumb et al., 2019).

3.4. Species distribution modeling and validation

Predicted species distribution.— To model species distribution and potentially limit autocorrelation issues, we randomly selected two used locations weekly from each marked bird (Segurado et al., 2006). We then separated location data from GPS- and VHF-marked individuals to create a model training and independent validation data samples, respectively. Study sites were delineated using minimum convex polygons (MCP) around all marked bird locations. We then buffered the MCP by the average net displacement distance (16.18 km) to estimate the area available to all marked lesser prairie-chickens (Earl et al., 2016). Average net displacement distance provides an estimate of dispersal distance that is not based on circular movement but linear distance away from initial capture location, which we used to infer areas available to the lesser prairie-chickens at the population level (Earl et al., 2016). We randomly generated one pseudo absence location for each location used by lesser prairie-chickens throughout the estimated available area and to account for the lack of true absence data; the response variable was relative probability of use (Barbet-Massin et al., 2012).

Lesser prairie-chicken occurrence was predicted using a Random Forest method (package ‘randomForest’; Liaw and Wiener, 2002, R Development Core, 2017). Random Forest is a classification and regression tree method that uses bootstraps to handle over-fitting (Cutler et al., 2007). We first assessed multicollinearity of all variables at $\alpha = 0.05$ using a leave one out assessment. Then, the most influential scales of variables were identified using a model improvement ratio (MIR) based on predictions from a global model of all variables at all scales that also included distance to anthropogenic feature (Evans et al., 2011). Ranks were estimated using the mean decrease in out-of-bag error standardized from 0 to 1. The scale (grassland composition = 0.4–5-km radius circles, anthropogenic features = 0.5–2-km radius circles) achieving the greatest MIR was used in the final model for each variable. Predictions of presence or absence were generated based on majority votes across all trees using the final model. An occurrence threshold was estimated following Jimenez-Valverde and Lobo (2007) to identify the model output probability (0–1) where occurrence or non-occurrence were most discrete and to identify potential habitat.

Validation.— We validated the model using VHF location data that were not used to train the predictive model and collected concurrently with GPS locations. Models were validated based on accuracy, specificity, and sensitivity of the model in predicting presence or pseudoabsence of locations from the independent validation set. We also estimated an area under the receiver operating characteristic curve to evaluate the predictive power of the model (AUC; DeLong et al., 1988).

3.5. Spatial prioritization of tree removal

To identify priority areas where tree removal would most likely restore lesser prairie-chicken habitat within the MGP, we defined potential habitat from the Random Forest model using both grassland composition and anthropogenic features. We used the threshold that included the top 95% predicted values (values > 0.33) from VHF locations in the validation to incorporate a greater area for potential conservation than obtained following Jimenez-Valverde and Lobo (2007). We then derived a layer depicting tree densities from Falkowski et al. (2017), following methods of Lautenbach et al. (2017; see Supplemental Materials for tree canopy cover). Areas where predicted habitat overlapped with tree densities > 2 per ha were most likely to be restored as habitat through tree removal based on a habitat relationship in Lautenbach et al. (2017). Last, we identified predicted habitat areas affected by low (1–5%), medium (6–15%), and high (> 15%) canopy coverage identified in Falkowski et al. (2017).

3.6. Spatial prioritization of CRP enrollment

To identify areas where applying CRP would most likely benefit lesser prairie-chickens, we first predicted the distribution of habitat using the occurrence threshold estimated from the Random Forest model, based on avoidance of anthropogenic features (Jimenez-Valverde and Lobo, 2007). Previous research indicated that CRP in landscapes (4-km radius) with < 56 cm of annual average precipitation and > 30% grassland were most likely to be used by lesser prairie-chickens (Sullins et al., 2018). We multiplied binary layers detailing areas of predicted habitat, a layer indicating where landscapes were > 30% grassland, areas receiving < 56 cm of annual average precipitation, and areas that were currently in CRP to indicate priority areas for conservation as well as cropland as indicated from NLCD 2011 to indicate priority areas for enrollment (Homer et al., 2015). Priority areas for conservation included CRP grasslands that provided habitat for lesser prairie-chickens based on our model. Priority areas for enrollment were areas that were cropland but if enrolled as CRP would likely provide habitat.

We then estimated the composition of priority enrollment and conservation of CRP by tillage risk. To identify tillage risk, we used a layer developed by Smith et al. (2016) that predicts areas of high and low tillage risk based on soil, climate, and topography related variables. We identified areas of low (0.00–0.32), medium (0.33–0.66), and high (0.67–1.00) tillage risk for descriptive purposes.

4. Results

We randomly selected a subset of 9895 locations from 170 lesser prairie-chickens marked with GPS satellite transmitters monitored from 2013 to 2016 to build our species distribution model. We sampled two locations a week from an average of 29.16 (SD = 36.35; range = 2–136) weeks for each individual. The model included only locations from female lesser prairie-chickens from the Red Hills/Clark and Northwest study sites; however, small sample sizes from study sites in Colorado and Cimarron NG required the use of both male and female individuals for analyses.

Grassland composition at the 5-km scale had the greatest model variable importance (1.0) and was 38% more important than at the 4-km scale (Figs. S1 and S2). For all anthropogenic features (county roads, major roads, oil wells, transmission lines, and other vertical features) densities estimated at the 2-km scale had the greatest model variable importance with a mean importance of 0.28, which was 150% greater than densities estimated at the 1-km scale. We used grassland composition within 5 km and anthropogenic features within 2 km as covariates in the final model to predict available habitat.

Grassland composition was 79% greater in model importance compared to the next predictor in the final model. Peak relative

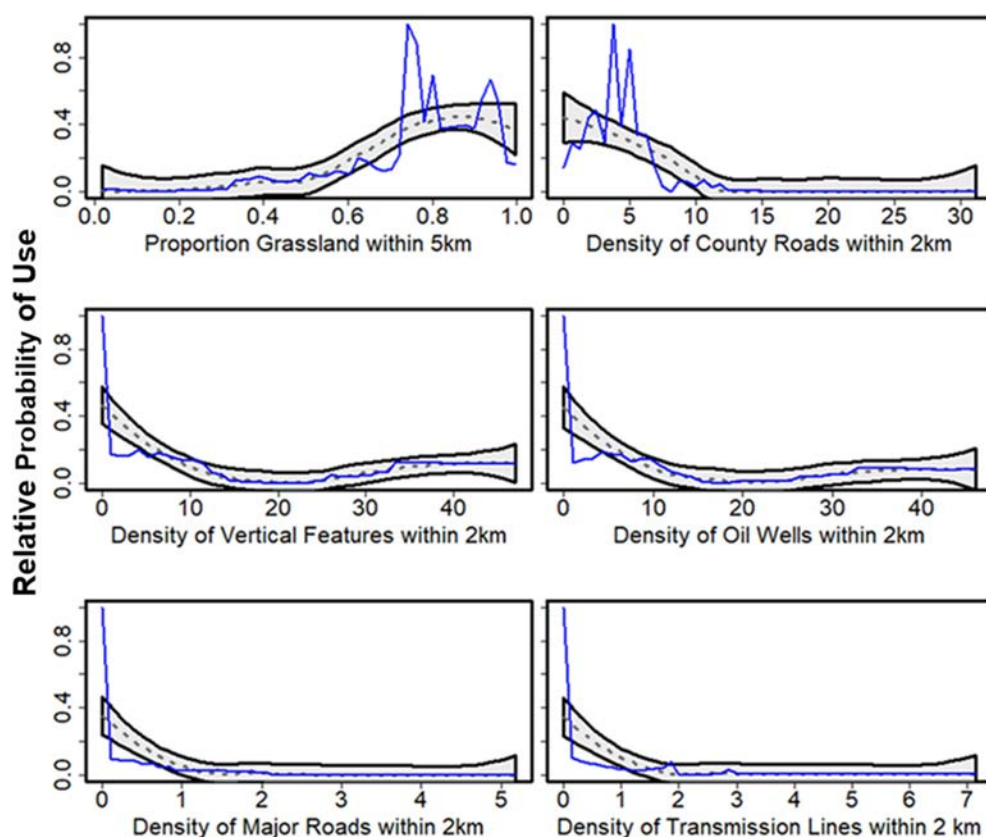


Fig. 2. Partial dependence plots for all grassland composition and anthropogenic feature densities used to predict the distribution of lesser prairie-chickens in Kansas and Colorado, USA, as depicted in Fig. 1 based on data from 2013 to 2016. A loess polynomial regression is plotted in as a dashed grey line with 95% prediction intervals highlighted in grey and the raw relative probability of use distribution is plotted as a blue line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1

Mean and standard deviation of grassland composition as a proportion of a 5-km radius scale and anthropogenic feature densities (2-km radius scale) estimated at lesser prairie-chicken locations ($n = 9895$) from 2013 to 2016, and random locations ($n = 9895$) distributed within dispersal range of Kansas and Colorado, USA, and throughout the entire extent analyzed for the species distribution model. The units for linear features (roads and transmission lines) are displayed as linear km densities within the 2 km (12.6 km^2) of each location while the vertical features (e.g., cell towers, large buildings, wind turbines, and oil wells) are represented by the densities of individual features. Estimates for the entire extent are based on the mean and variance of all pixel values estimated using a moving window analysis within the study area.

Variables	Used		Random		Entire extent	
	Mean	SD	Mean	SD	Mean	SD
Grassland composition	0.76	0.18	0.55	0.26	0.51	0.27
Anthropogenic features						
County roads ($\text{km}/12.6 \text{ km}^2$)	3.90	2.36	4.38	2.81	4.98	3.53
Major roads ($\text{km}/12.6 \text{ km}^2$)	0.09	0.39	0.31	0.70	0.34	0.73
Oil wells/ 12.6 km^2	2.42	3.89	2.95	5.04	3.49	6.67
Transmission lines ($\text{km}/12.6 \text{ km}^2$)	0.06	0.31	0.23	0.66	0.43	0.98
Vertical point features/ 12.6 km^2	2.43	3.91	3.16	5.28	3.82	7.41

probability of use occurred at $\sim 77\%$ grassland composition; similar to the 76% mean of used locations (Fig. 2, Table 1). Having lower model importance than grassland composition were densities of county roads, vertical point features, transmission lines, and major roads in decreasing order of model importance (Fig. S2). Overall, the relative probability of use decreased as cumulative densities of anthropogenic features increased (Fig. 2). However, the raw predicted probability of use increased from 0 to 5 km per 12.6 km^2 of county roads then declined sharply as densities increased beyond 5 km per 12.6 km^2 and was close to zero at densities $> 10 \text{ km}$ per 12.6 km^2 (Fig. 2). When county road densities surpassed a threshold of 8–10 km per 12.6 km^2 area, it

indicated an urban environment based on visual observations.

In addition to the county road threshold of $\sim 8 \text{ km}/12.6 \text{ km}^2$, all other anthropogenic features displayed patterns of sharp decreases in relative probability of use after surpassing a feature-specific density (Fig. 2). Based on the raw probability distribution, the occupancy threshold for vertical point feature densities occurred at ~ 2 vertical features per 12.6 km^2 (Fig. 2). A similar threshold was estimated for oil wells with areas having > 2 oil wells per 12.6 km^2 having 8 times lower relative probability of use. The threshold for major roads and transmission lines was achieved at 0.15 km per 12.6 km^2 ; relative probability of use decreased abruptly when surpassed.

Predicted species distribution.— The predicted relative probability of use output from the Random Forest model predicted a greater area of lesser prairie-chicken habitat in the MGP than in the SGP or SSP Ecoregions (Fig. 1; McDonald et al., 2014). An occurrence threshold for the model was estimated at a model output probability of 0.60 for the model incorporating both grassland composition and anthropogenic structures and 0.70 for the model including only anthropogenic structure densities based on maximizing the sum of model sensitivity and specificity (Jimenez-Valverde and Lobo, 2007).

The percentage of potential habitat (> 0.6 predicted occurrence threshold) within the northern extent of presumed range of the lesser prairie-chicken in Kansas and Colorado as delineated in McDonald et al. (2014) was 16% ($3099/14,790 \text{ km}^2$) in the MGP Ecoregion, 9% ($2613/27,899 \text{ km}^2$) in the SSP Ecoregion, and 8% ($3671/43,641 \text{ km}^2$) in the SGP Ecoregion. In the SGP Ecoregion of northwest Kansas, optimal habitat appears constrained to patches within 12 km of the Smoky Hill River in Gove and Logan counties; northeast Finney County; and northeast Wallace County. The model also predicted a substantial amount of habitat in the western most extent of the SGP in Kiowa and Cheyenne Counties of Colorado where a large expanse of undeveloped sand sagebrush prairie occurs within what is technically delineated as the SGP Ecoregion. Within the delineated SSP Ecoregion, predicted habitat is largely clumped in the western extent as well. In the MGP of

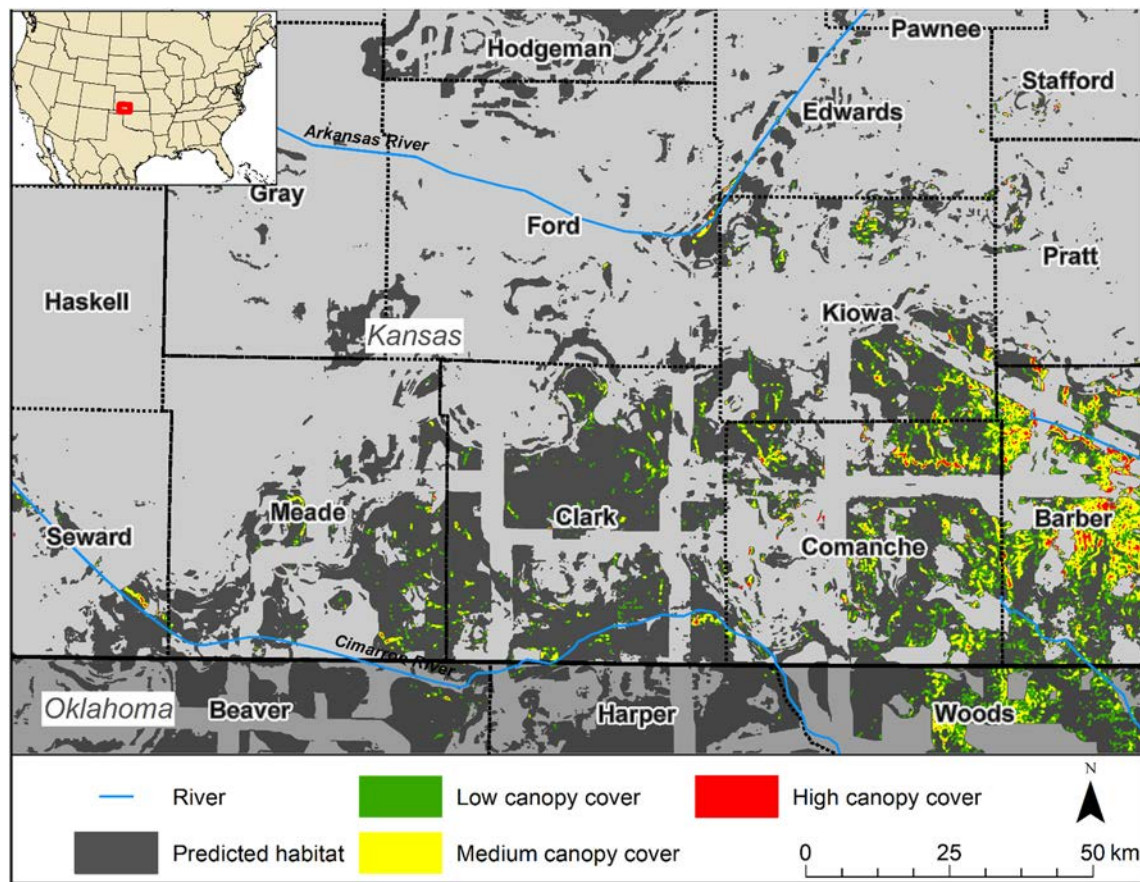


Fig. 3. Predicted areas of low (1–5%), medium (6–15%), high (> 15%) tree canopy cover where tree removal is most likely to restore lesser prairie-chicken habitat in Kansas and Colorado, USA, based on grassland composition within 5 km and anthropogenic feature densities (A). Areas having a high priority for tree removal were the top 66% of predicted values from the Random Forests model and where tree densities were > 2 trees/ha (Falkowski et al., 2017, Lautenbach et al., 2017, B).

Kansas and northern Oklahoma, habitat was more uniformly distributed (Fig. 1).

Validation.— We used subsampled VHF locations (2 locations per week from 113 individuals) to validate our predictions ($n = 4043$). Model performance was good with an estimated accuracy of 84%. The model correctly predicted 83% of VHF locations as habitat (sensitivity) and 83% of pseudoabsences as nonhabitat (specificity). The area under the receiver operating characteristics was 0.91 suggesting a fairly strong dichotomy between predicted habitat and nonhabitat (DeLong et al., 1988).

4.1. Spatial prioritization of tree removal

Based on our identification of areas with limited anthropogenic influence and adequate grassland availability, we estimated that 1154 km² of habitat for lesser prairie-chickens could be gained by tree removal and an alteration of land management practices to prevent further woody encroachment in the MGP of Kansas and northern Oklahoma (Fig. 3). Of the potential habitat, 12% is affected by low canopy cover (1–5%), 8% by medium canopy cover (6–15%), and 1% by high canopy cover (> 15%). Priority areas for tree removal were largely clustered to the eastern extent of the lesser prairie-chicken range.

4.2. Spatial prioritization of CRP enrollment

Our model suggests that 1570 km² of current CRP provides habitat for lesser prairie-chickens and should remain CRP if lesser prairie-chickens are a priority (Fig. 4). There were 4189 km² of cropland that

reside in areas where enrollment would benefit lesser prairie-chickens. However, based on our results, enrolling cropland into CRP would be most beneficial when increasing grassland composition within 5-km to approximately 80% in areas receiving < 56 cm of precipitation. Predicted effects of anthropogenic features resulted in a 7211 km² decrease in priority cropland for enrollment and 4312 km² decrease in priority areas to conserve CRP and highlights the importance of considering anthropogenic feature densities. Our model highlighted areas on the Lane, Ness, and Finney county lines in addition to areas near our study sites.

The proportion of area that was predicted as high, medium, and low risk for tillage varied among priority areas for enrollment and conservation. Priority areas for enrollment were 7%, 32%, and 61% of low, medium, and high risk to tillage respectively. Priority areas to conserve CRP were comprised of 25%, 48%, and 28% of low, medium, and high risk respectively.

5. Discussion

We provide empirical evidence that can be used to preserve remaining grassland strongholds of low anthropogenic feature densities as well as spatially target management practices that are likely to acquire voluntary participation on working lands. Our model indicates how the broad-scale availability of large grasslands unencumbered by anthropogenic features is limited within the study area and likely imposes strong constraints on the distribution of grassland-obligate wildlife; especially those requiring large spatial extents for populations to persist (e.g., lesser prairie-chicken). We estimated the presence of 9383 km² of available habitat (> 0.60 relative probability of use) for

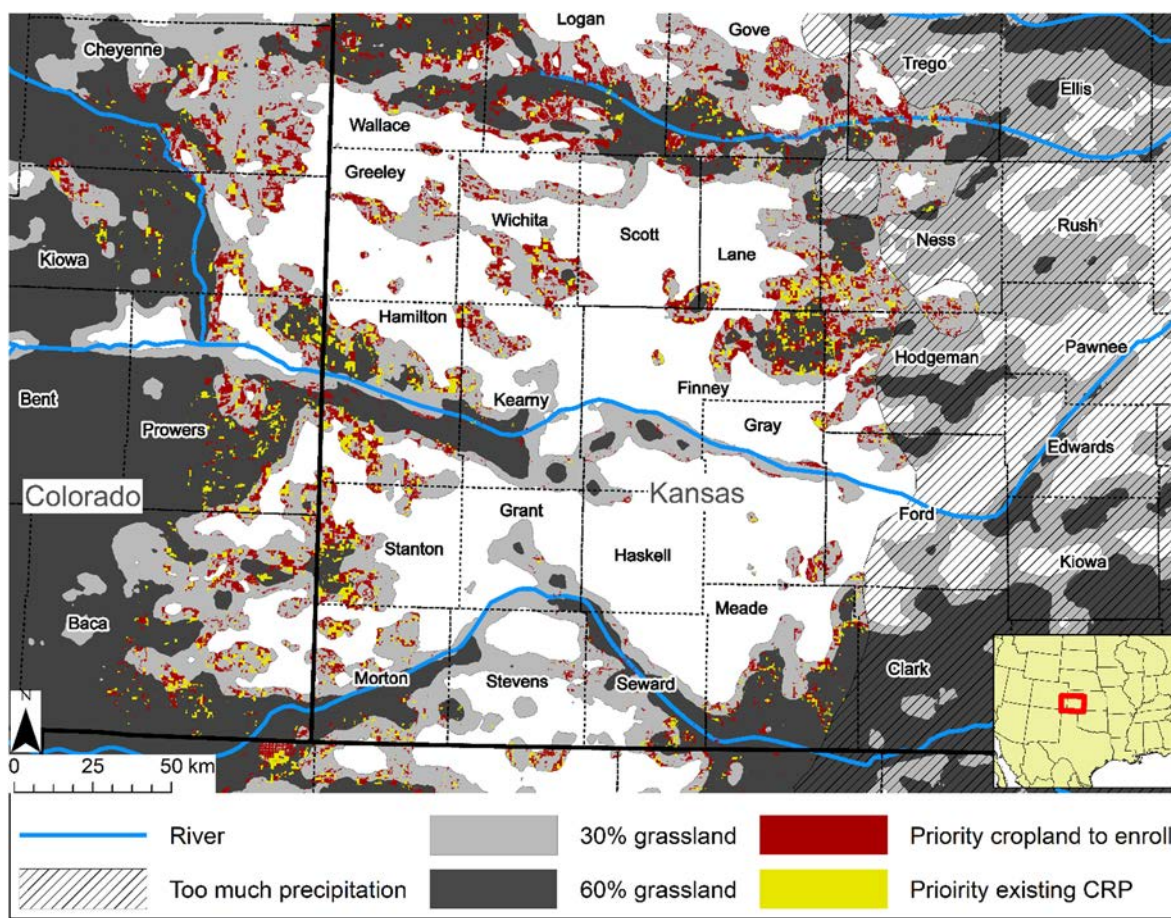


Fig. 4. Predicted priority areas where current CRP grasslands (yellow) and cropland that could be enrolled in CRP (red) were most likely to be used by lesser prairie-chickens in Kansas and Colorado, USA (A). Priority areas occur in locations having > 30% native working grassland (light grey) within 4 km and where the top 30% of values from a Random Forests model using only anthropogenic features occurred. Also, shown are areas that had > 60% native working grassland (dark grey) within 4 km (B). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

lesser prairie-chickens in the study area. There is potential to increase available habitat by 1154 and 4189 km² (57%) through strategic removal of trees and conversion of cropland to CRP grasslands. Area of predicted habitat was greatest in the SGP ecoregion, followed by the MGP and SSP ecoregions. However, the model likely overestimated the amount of available habitat in the far western extent of the distribution where short-grass prairie is largely contributing to the grassland composition of the model and may not provide habitat due to insufficient vegetation structure (Giesen, 1994). In contrast, the area in the far northwestern extent of the lesser prairie-chicken range is predominantly sand sagebrush prairie that is free of anthropogenic features and may become more important for lesser prairie-chickens given climate change projections (Grisham et al., 2016). Based on our predictions, it appears lesser prairie-chickens at current population abundance are constrained to areas having > 70% grassland within a 5-km radius (78.5 km²) and with minimal anthropogenic features (e.g., < 10 vertical features in 12.6 km²).

In the working landscapes of the Southern Great Plains, the need for strategic conservation is critical (Samson et al., 2004). Future expected increases in global food and energy needs may take a further toll on biodiversity in this region. There has been much discussion on whether approaches that would “spare” land parcels and allow for intensification of production elsewhere or whether landscapes should be “shared” to provide large areas that are marginal for both agriculture and biodiversity (Kremen, 2015). We did not explicitly test these ideas but the optimization of lesser prairie-chicken habitat at 77% grassland, the purported population increase following low intensity agriculture at the

turn of the century, and the underlying spatial variability in farming suitability suggest that a combination of “sparing” and “sharing” strategies may be best (Kremen, 2015; Rodgers, 2016). Diet analyses have also demonstrated the use of some crops and crop pests as foods (Sullins et al., 2018). Our results and past literature highlight the utility of large grassland areas adjacent to low intensity row crop agriculture for lesser prairie-chickens. Our model does not account for the influence of dispersal on population persistence. Successful conservation will likely need to consider how the cropland matrix, adjacent to, and within grassland dominated landscapes facilitates successful dispersal. Having a matrix that facilitates movement by grassland dependent wildlife from one optimal habitat patch to another is likely important (Simberloff, 1994; Kremen and Merenlender, 2018).

Grassland abundance in a landscape likely influences the occurrence of lesser prairie-chickens both directly, as extrahierarchical boundaries, and indirectly through emergent properties operating at finer scales (King, 1997). Occurrence of lesser prairie-chickens is a product of the finer scale availability of lekking, nesting, brooding, and nonbreeding habitats that are properly abundant and configured to allow the establishment of home ranges and populations at subsequently broader scales (Hagen et al., 2013; Winder et al., 2015; Robinson et al., 2018). In addition to the spatial heterogeneity needed to satisfy all life-stage needs, the vegetation structure requirement (e.g., 25–80 cm tall herbaceous cover) must also be realized among dry and wet years in a dynamic grassland ecosystem (Sala et al., 1988; Ross et al., 2016a; Ross et al., 2016b). Habitat must also be abundant enough, and properly configured when fragmented, for dispersal to facilitate demographic

and genetic rescue at even broader scales (Simberloff, 1994; Ross et al., 2016a). Our estimate of optimal grassland area (77% of 78.5 km² landscape) lies between the 49 km² and 202 km² estimates of habitat to support a single lek and overall population respectively (Haukos and Zaveleta, 2016). The estimate also falls within a range of scales at which established CRP grasslands and prescribed grazing influence lesser prairie-chicken occupancy (Hagen et al., 2016). Our predictions are based on the landscape rather than a single contiguous patch of grassland and suggest that landscapes that have limited vertical structures (e.g., oil wells, trees) and ≥ 60.5 km² of grassland within a 78.5 km² area would be optimal – assuming the grasslands are managed properly.

5.1. Effects of anthropogenic feature densities

The presence of vertical structures at high densities can make a landscape that would otherwise function as habitat unavailable to lesser prairie-chickens (Hagen et al., 2011; Plumb et al., 2019). Lesser prairie-chickens have evolved mechanisms to avoid vertical structures likely to minimize risk of predation from perching raptors (Reinert, 1984; Manzer and Hannon, 2005). Vertical structures avoided by lesser prairie-chickens include trees, transmission lines, oil wells, wind turbines, and cell phone towers (Pitman et al., 2005; Hagen et al., 2011; Lautenbach et al., 2017; Plumb et al., 2019). The avoidance of tall vertical features is not absolute and is largely contingent on the density of features at a landscape scale, life-stage of individual birds, and may be reduced if access to high-quality habitat outweighs the presence of vertical features (Lautenbach et al., 2017; Plumb et al., 2019). For example, lesser prairie-chickens avoid areas having > 2 trees/ha at the 16-ha scale when nesting and areas having > 8 trees/ha otherwise (Lautenbach et al., 2017). Such constitutive relationships and interactions among life stages likely drive the complex hierarchical system from which population occupancy emerges. Although there is considerable variation of the effect of anthropogenic features on lesser prairie-chickens based on life-stage and landscapes in which they occur, we provide evidence of thresholds where anthropogenic feature densities may act as overall constraints.

The lack of avoidance of county roads suggests that they do not affect lesser prairie-chicken occurrence at low densities (< 15 km per 12.6 km²). Locations of roads in upland areas may additionally be a result of overlapping desirable conditions for road placement and lesser prairie-chicken habitat. We expect this to partially be a function of county roads being largely gravel surfaced and often occurred in upland areas of relatively higher elevation that are more likely used by lesser prairie-chickens (Lautenbach, 2015). Additionally, traffic volume on certain roads may dictate avoidance more than presence of the road itself (Blickley et al., 2012).

Although our reported avoidance density thresholds are specific for lesser prairie-chickens, there are other grassland birds that avoid anthropogenic structures and exhibit area sensitivity (Ribic et al., 2009; Ludlow et al., 2015; Londe et al., 2019). The area sensitivity of several grassland songbirds likely make them more susceptible to the fragmentation effects of anthropogenic structures and infrastructure (Ribic et al., 2009). Some grassland birds may not be negatively affected by anthropogenic structures and more species-level information is needed (Ludlow et al., 2015). However, our model predictions identify areas where anthropogenic feature densities are minimal and due to the lesser prairie-chicken's strong sensitivity to anthropogenic features may provide an estimate based on a worst case scenario for many grassland birds.

5.2. Spatial prioritization of tree removal

To increase the amount of potential habitat for lesser prairie-chickens, we identified strategic areas where tree removal, primarily eastern red cedar (*Juniperus virginiana*), would have maximum benefits.

However, it is imperative that trees are not merely removed, then allowed to return (estimated encroachment: +2.3% forest cover/year; Briggs et al., 2002). We suggest that on-site tree removal follow Lautenbach et al. (2017) and implementation of a prescribed fire component following the mechanical removal of trees (Ortmann et al., 1998). Additionally, lower canopy cover areas could be prioritized first followed by medium and high percent canopy coverage areas to be cost effective. Based on cost estimates in Lautenbach et al. (2017), it would cost US\$32.6 million to remove trees in priority areas in Kansas and Colorado (more details in supplemental material). Tree removal in predicted priority areas would likely benefit cattle producers by increasing available forage and therefore may be more likely to be implemented (Ciuzio et al., 2013; Severson et al., 2017).

5.3. Spatial prioritization of CRP enrollment

The underlying ability of CRP to benefit both producer and grassland dependent wildlife is likely the reason for its conservation importance in areas > 95% privately owned (Johnson, 2005; Sullins et al., 2018). To build on the underlying conservation importance of CRP on working lands, current continuous CRP signup programs were developed that pay more per acre than traditional CRP signup (Stubbs, 2014). Increased payments are used to encourage further management within CRP tracts to benefit pollinators, waterfowl, and upland game birds by requiring interseeding with native forbs and desired native grasses (North American Bird Conservation Initiative, 2015).

Although CRP can benefit wildlife, the future of CRP remains uncertain and its ability to provide habitat for lesser prairie-chickens is contingent on renewal of the program with each new Farm Bill and the enrollment and reenrollment of CRP grasslands in contracts that typically span 10–15 years (Stubbs, 2014). Based on our model estimates of 1570 km² of current CRP providing habitat for lesser prairie-chickens, US\$11.7 million annually in rental rates will conserve these areas for lesser prairie-chickens in addition to providing several other ecological services (Johnson, 2005; more details in supplemental material). Financial support may be necessary to maintain conservation gains achieved through CRP, as voluntary participation can decline when financial incentives are removed (Mascia and Mills, 2018). Efforts to connect CRP, or other forms of grassland restoration, with existing community actions and social movements may be other options for increasing participation on private lands (Kremen and Merenlender, 2018).

6. Conclusion

For grassland birds in the Great Plains, conservation on working lands is the only feasible option to provide habitat at a relevantly broad scale. Implementation of conservation practices that simultaneously create wildlife habitat and improve human well-being will be the most likely to positively affect wildlife populations (Samson et al., 2004; Kareiva and Marvier, 2012). Broad scale (78.5 km²) grassland composition and anthropogenic feature densities appear to exert constraints on the distribution of lesser prairie-chickens and likely other grassland-obligate wildlife in our study area. The study area was > 95% privately owned and using tree removal and CRP at landscape scales may be the best management options to improve habitat availability for lesser prairie-chickens due to their likelihood of achieving voluntary participation (Lautenbach et al., 2017; Sullins et al., 2018). Comparing costs of tree removal to CRP enrollment suggest that CRP enrollment may be more cost efficient. However, lesser prairie-chickens use of habitat at a landscape scale make tree removal and CRP enrollment not directly comparable. Efforts to preserve remaining habitat matched with strategic management efforts that take into account human well-being have the greatest potential to conserve lesser prairie-chickens and other grassland-dependent wildlife on working lands.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2019.108213>.

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BLACK-FOOTED FERRET DRAFT RECOVERY PLAN



Second Revision

February 2013

Recovery Plan for the Black-footed Ferret (*Mustela nigripes*)

Second Revision

Original Recovery Plan Approved in 1978

First Revision Approved 1988

Region 6
U.S. Fish and Wildlife Service
Denver, Colorado

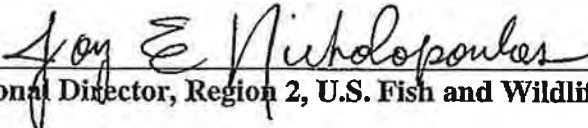
Approved: _____


Deputy Regional Director, Region 6, U.S. Fish and Wildlife Service

APR 3 2013

Date: _____

Concurred: _____


Acting Regional Director, Region 2, U.S. Fish and Wildlife Service

MAR 21 2013

Date: _____

DISCLAIMER

Recovery plans delineate such reasonable actions as may be necessary, based upon the best scientific and commercial data available, for the conservation and survival of listed species. Plans are published by the U.S. Fish and Wildlife Service (Service or USFWS), sometimes prepared with the assistance of recovery teams, contractors, State agencies, tribes and others. Recovery plans do not necessarily represent the views, official positions, or approval of any individuals or agencies involved in the plan formulation, other than the Service. They represent the official position of Service only after they have been signed by the Regional Director. Recovery plans are guidance and planning documents only; identification of an action to be implemented by any public or private party does not create a legal obligation beyond existing legal requirements. Nothing in this plan should be construed as a commitment or requirement that any Federal agency obligate or pay funds in any one fiscal year in excess of appropriations made by Congress for that fiscal year in contravention of the Anti-Deficiency Act, 31 U.S.C. 1341, or any other law or regulation. Approved recovery plans are subject to modification as dictated by new findings, changes in species' status, and the completion of recovery actions.

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Additional copies of the draft document can be obtained from:

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National Black-footed Ferret Conservation Center
P.O. Box 190
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Recovery plans can be downloaded from:

<http://www.fws.gov/endangered/recovery/index.html>

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EXECUTIVE SUMMARY

Current Species Status: The black-footed ferret (*Mustela nigripes*) was listed as endangered in 1967 pursuant to early endangered species legislation in the United States (U.S.) and was “grandfathered” into the Endangered Species Act of 1973 (ESA).

We estimate that the average minimum number of breeding adult ferrets in the wild is approximately 364 animals (Table 3), with a minimum of 270 of those animals at self-sustaining sites. Approximately 280 additional animals are managed in captive breeding facilities. At this time, the downlisting criteria may be 40 percent complete with regard to establishing 10 successful populations and approximately 18 percent complete with regard to the goal of 1,500 breeding adults at successful sites. Four reintroduction sites (Aubrey Valley, Arizona; Cheyenne River Reservation, South Dakota; Conata Basin, South Dakota; and Shirley Basin, Wyoming) are considered self-sustaining at present. The species remains vulnerable to several threats, including sylvatic plague and inadequate regulatory mechanisms.

Habitat Requirements and Limiting Factors: The black-footed ferret depends on prairie dogs for food and on their burrows for shelter. The historical range of the ferret coincided with the ranges of the black-tailed prairie dog (*C. ludovicianus*), Gunnison’s prairie dog (*C. gunnisoni*), and white-tailed prairie dog (*C. leucurus*). The ferret’s close association with prairie dogs was an important factor in the ferret’s decline. From the late 1800s to approximately the 1960s, prairie dog occupied habitat and prairie dog numbers were dramatically reduced by the effects of both temporal and permanent habitat loss caused by conversion of native grasslands to cropland, poisoning, and disease. The ferret population declined precipitously as a result.

Recovery Strategy: In preparing this revised recovery plan, we solicited extensive partner review from the Black-footed Ferret Recovery Implementation Team (BFFRIT). The BFFRIT was established by the Service in 1996. One of its guiding principles has been its focus on involvement by many partners across the historical range of the ferret, including tribes, States, Federal land management agencies, non-governmental organizations, Canada, and Mexico. Recovery will be achieved by establishing a number of ferret populations where appropriate habitat exists and by ameliorating threats impacting the species so as to allow the ferret’s persistence. Although ferret habitat has been dramatically reduced from historical times, a sufficient amount remains, if its quality and configuration is appropriately managed. This management, for the most part, is likely to be conducted by traditional State, tribal, and Federal fish and wildlife and land management agencies. Additionally, private parties, including landowners and conservation organizations, must continue to support ferret recovery. Many partners contributing to ferret recovery in many places will help minimize the risk of loss of wild populations.

Recovery Goal: The goal of this plan is to recover the black-footed ferret such that it no longer meets the ESA’s definition of endangered or threatened and can be removed from the Federal List of Endangered and Threatened Wildlife (i.e., delisted).

Recovery Objectives: The recovery of black-footed ferrets will depend upon: (1) the continued efforts of captive breeding facilities to provide animals of suitable quality and quantity for release into the wild; (2) the conservation of prairie dog habitat adequate to sustain ferrets in several populations distributed throughout their historical range; and (3) the management of sylvatic plague to minimize impacts to ferrets at reintroduction sites.

Recovery Criteria: This recovery plan revision provides reasonable biological and logistically achievable criteria that may be used to realize downlisting and delisting objectives. In particular, we believe that we can achieve recovery of the ferret through more proactive management of existing prairie dog habitat.

Downlisting Criteria:

- Conserve and manage a captive breeding population of black-footed ferrets with a minimum of 280 adults (105 males, 175 females) distributed among multiple facilities (at least 3).
- Establish free-ranging black-footed ferrets totaling at least 1,500 breeding adults, in 10 or more populations, in at least 6 of 12 States within the historical range of the species, with no fewer than 30 breeding adults in any population, and at least 3 populations within colonies of Gunnison's and white-tailed prairie dogs.
- Maintain these population objectives for at least three years prior to downlisting.
- Maintain approximately 247,000 acres (ac) (100,000 hectares (ha)) of prairie dog occupied habitat at reintroduction sites (specific actions are described in Part II of this plan) by planning and implementing actions to manage plague and conserve prairie dog populations.

Delisting Criteria: Delisting criteria are new since the 1988 Recovery Plan. Delisting may occur when the following recovery criteria are met.

- Conserve and manage a captive breeding population of black-footed ferrets with a minimum of 280 adults (105 males, 175 females) distributed among multiple facilities (at least 3).
- Establish free-ranging black-footed ferrets totaling at least 3,000 breeding adults, in 30 or more populations, with at least one population in each of at least 9 of 12 States within the historical range of the species, with no fewer than 30 breeding adults in any population, and at least 10 populations with 100 or more breeding adults, and at least 5 populations within colonies of Gunnison's or white-tailed prairie dogs.
- Maintain these population objectives for at least three years prior to delisting.
- Maintain approximately 494,000 ac (200,000 ha) of prairie dog occupied habitat at reintroduction sites by planning and implementing actions to manage plague and conserve prairie dog populations (specific actions are described in Part II of this plan).
- Complete and implement a post-delisting monitoring plan, in cooperation with the States and tribes, to ensure recovery goals are maintained.

After Delisting:

- Conserve and manage a reduced captive breeding population of black-footed ferrets in order to maintain knowledge, incorporate developing technologies, and address potential population extirpations.

Actions Needed: We believe the single, most feasible action that would benefit black-footed ferret recovery is to improve prairie dog conservation. If efforts were undertaken to more proactively manage existing prairie dog habitat for ferret recovery, all other threats to the species would be substantially less difficult to address. Several States within the historical range of the species do not manage prairie dogs in a manner that supports ferret recovery. Some of these States have disease-free areas that would be especially valuable to ferret recovery. We recommend that the following actions be undertaken. These actions are not listed in order of priority, but all tasks and subtasks are prioritized in Table 7.

1. Conserve and manage a captive ferret population of reasonable size and structure to support genetic management and reintroduction efforts.
2. Identify prairie dog habitats with the highest potential for supporting future free-ranging populations of ferrets.
3. Establish free-ranging populations of ferrets to meet downlisting and delisting goals.
4. Ensure sufficient habitat to support a wide distribution of self-sustaining ferret populations.
5. Reduce disease-related threats in wild populations of ferrets and associated species.
6. Support partner involvement and conduct adaptive management through cooperative interchange.

Date of Recovery: We believe that downlisting of the black-footed ferret could be accomplished in approximately 10 years if conservation actions continue at existing reintroduction sites and if additional reintroduction sites are established. Downlisting and delisting could occur more quickly if additional partners became involved in recovery efforts.

Estimated Cost of Recovery Actions (\$1,000s) (not adjusted for inflation): The following table summarizes the costs by decade of the various recovery actions that are described by individual task in Part II and prioritized in Part III of this revised recovery plan. Costs through 2020 address downlisting of the black-footed ferret. Subsequent costs address delisting the ferret.

Estimated Cost of Recovery Actions (\$1,000's) (not adjusted for inflation)

<i>Years</i>	<i>Action 1</i>	<i>Action 2</i>	<i>Action 3</i>	<i>Action 4</i>	<i>Action 5</i>	<i>Action 6</i>	<i>Total</i>
2010-2020	7,000	90	9,950	23,000	8,110	6,990	55,140
2021-2030	5,000	60	10,960	22,000	4,940	5,040	48,000
2031-2040	5,000	60	10,960	22,000	4,940	5,040	48,000
Total	17,000	210	31,870	67,000	17,990	17,070	151,140

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ACRONYMS

APHIS:	Animal and Plant Health Inspection Service
AZA:	Association of Zoos and Aquariums
BFFRIT:	Black-footed Ferret Recovery Implementation Team
BLM:	U.S. Bureau of Land Management
CBSG:	Conservation Breeding Specialist Group (SSC/IUCN)
CS:	Conservation Subcommittee under BFFRIT
EPA:	U.S. Environmental Protection Agency
ES:	Executive Subcommittee under BFFRIT
ESA:	Endangered Species Act of 1973
IS:	Incentives Subcommittee under BFFRIT
IUCN:	International Union for the Conservation of Nature
NEPA:	National Environmental Policy Act
NPS:	U.S. National Park Service
OIS:	Outreach and Information Subcommittee under BFFRIT
PDMS:	Prairie Dog Management Subcommittee under BFFRIT
SCTAG:	Small Carnivore Taxon Advisory Group of the AZA
Service:	U.S. Fish and Wildlife Service
SPVS:	Sylvatic Plague Vaccine Subcommittee
SSC:	Species Survival Commission of the World Conservation Union
SSP®:	Species Survival Plan
USFS:	U.S. Forest Service
USFWS:	U.S. Fish and Wildlife Service
USGS:	U.S. Geological Survey

GLOSSARY

Beringia:	a land bridge that joined Alaska and Siberia during the Pleistocene ice ages
endemic:	native to a particular region
enzootic:	a disease outbreak causing a low level of mortality, persistent over a long time period
epizootic:	a disease outbreak causing a high level of mortality, persistent over a short time period
fossorial:	adapted to digging and life underground
heterozygosity:	having different forms of genes present for a particular trait
homozygosity:	having similar forms of genes present for a particular trait
mustelid:	of the weasel family in the order Carnivora (carnivorous mammals)

PART I. BACKGROUND

INTRODUCTION

The black-footed ferret recovery program is one of the oldest endangered species recovery programs in the U.S. (Biggins et al. 1997). The first recovery plan was published in 1978 (Linder et al. 1978), when no wild ferrets were thought to exist. A second recovery plan was completed in 1988 (U.S. Fish and Wildlife Service 1988) when captive breeding efforts had begun, but no reintroduction efforts had yet been initiated. The objective of the 1988 plan was to ensure the immediate survival of the ferret by: (1) increasing the captive population to 200 breeding adults by 1991, (2) establishing a pre-breeding population of 1,500 free-ranging adults in 10 or more populations with no fewer than 30 breeding adults in any population by 2010, and (3) encouraging the widest possible distribution of reintroduced populations for risk management purposes. These three objectives were further divided into numerous actions, tasks, and subtasks. Most of the original tasks associated with objective 1 have been achieved. Some related tasks are no longer relevant, such as searching for additional wild populations (Hanebury and Biggins 2006). Since 1988, ongoing efforts have highlighted the need for a new recovery plan that addresses additional considerations under objectives 2 and 3. Tasks associated with objectives 2 and 3 will require added emphasis as the recovery program matures. In particular, these new considerations include: (1) the availability of a sufficient quantity and quality of prairie dog habitat to support recovery of the species, (2) the impacts of disease, especially sylvatic plague, on reintroduced populations and their habitat, and (3) the adequacy of proactive management efforts and existing regulatory mechanisms in addressing the preceding two considerations. The tasks in this recovery plan have been discussed extensively between the Service and BFFRIT partners.

Part I of this recovery plan includes the evolving biological species status information pertinent to recovering the black-footed ferret. Part II outlines a general strategy for long-term recovery of the ferret in the wild, presents criteria for downlisting and delisting the species, and describes specific actions and recovery tasks. Part III provides a

schedule for implementing recovery tasks. The recovery plan will continue to be revised as needed to reflect changes in information, strategies, and actions.

This recovery plan relies extensively on several black-footed ferret status reviews (CBSG 1992, Hutchins et al. 1996, CBSG 2004, Garelle et al. 2006, U.S. Fish and Wildlife Service 2008), Service evaluations of tasks identified in the 1988 Black-footed Ferret Recovery Plan, and extensive review and input by parties associated with the BFFRIT. In particular, the “Annotated Recovery Plan Outline for the Black-footed Ferret” (Ray 2006) thoroughly examined all prior recovery tasks and existing literature. This outline contributed significantly to this recovery plan and is frequently referenced.

SPECIES STATUS

The black-footed ferret was listed as endangered in 1967 (32 FR 4001; March 11, 1967) and again in 1970 (35 FR 8491; June 2, 1970) under early endangered species legislation and was “grandfathered” into the ESA in 1973. Critical habitat was not designated for the species; the species was listed prior to amendments that added critical habitat provisions. We assigned the ferret a recovery priority number of 2C on a scale of 1C-18, with 1C equaling the highest priority. This number indicates that the ferret faces a high degree of threat, with potential economic conflicts regarding the ferret’s obligatory dependence on prairie dogs, which are viewed as pests by some parties (U.S. Fish and Wildlife Service 2008). The high degree of threat is largely due to inadequate management and conservation of prairie dogs, and is described in detail in the section “Threats and Reasons for Listing.” The ranking also reflects the ferret’s taxonomic status as a full species. Table 1 further describes recovery prioritization. Notably, this species continues to have a high potential for recovery despite the management challenges noted.

Table 1. Recovery priorities

Degree of Threat	Recovery Potential	Taxonomy	Priority	Conflict
High	High	Monotypic Genus	1	1C
		Species	2	2C
		Subspecies/DPS	3	3C
	Low	Monotypic Genus	4	4C
		Species	5	5C
		Subspecies/DPS	6	6C
Moderate	High	Monotypic Genus	7	7C
		Species	8	8C
		Subspecies/DPS	9	9C
	Low	Monotypic Genus	10	10C
		Species	11	11C
		Subspecies/DPS	12	12C
Low	High	Monotypic Genus	13	13C
		Species	14	14C
		Subspecies/DPS	15	15C
	Low	Monotypic Genus	16	16C
		Species	17	17C
		Subspecies/DPS	18	18C

The above ranking system for determining Recovery Priority Numbers was established in 1983 (48 FR 43098; September 21, 1983 as corrected in 48 FR 51985; November 15, 1983).

TAXONOMY

The black-footed ferret is in the Order Carnivora, Family Mustelidae, Genus *Mustela*, and Subgenus *Putorius*. No subspecies are recognized (Hillman and Clark 1980, Anderson et al. 1986). The species is one of five members of the genus *Mustela* in North America that also includes the ermine (*M. erminea*), long-tailed weasel (*M. frenata*), least weasel (*M. nivalis*), and American mink (*M. vison*) (Wilson and Ruff 1999). The black-footed ferret is the only ferret species native to the Americas. Other ferret species in the subgenus are the Siberian polecat (*M. eversmanni*) and the European ferret (*M. putorius*) (Hillman and Clark 1980, Anderson et al. 1986), which has been domesticated and is sold as a pet. The black-footed ferret is most closely related to the Siberian polecat (Hillman and Clark 1980, Anderson et al. 1986). The earliest fossil record of the black-footed ferret is from approximately 100,000 years ago (Anderson et al. 1986). The species was first formally described in 1851 by J.J. Audubon and J. Bachman (Anderson et al. 1986, Clark 1986).

SPECIES DESCRIPTION

The black-footed ferret is a medium-sized mustelid, typically weighing 1.4–2.5 pounds (645–1125 grams) and measuring 19–24 inches (479–600 millimeters) in total length. Upper body parts are yellowish buff, occasionally whitish; feet and tail tip are black; and a black “mask” occurs across the eyes (Hillman and Clark 1980, Anderson et al. 1986).

LIFE HISTORY

Four populations of the black-footed ferret have been studied intensively including: (1) Mellette County, South Dakota (1964–1974), (2) Park County, near Meeteetse, Wyoming (1981–1986), (3) a reintroduced population at UL Bend National Wildlife Refuge, Montana (1994 to present), and (4) a reintroduced population in Conata Basin, South Dakota (1996-present). Much of the information pertaining to the species’ life history, survival, and behavior has been obtained from these four populations.

The ferret breeds at one year of age from mid-March through early April in the wild (Wilson and Ruff 1999). Gestation is about 42–45 days, and litter size averages approximately 3.5 individuals (Wilson and Ruff 1999). The ferret is solitary, except for breeding and the period when mother and young are together (Forrest et al. 1985). It is generally a nocturnal predator, appearing above ground at irregular intervals and for irregular durations (Clark et al. 1986). The ferret is an extreme specialist that depends on prairie dogs for food and shelter (Biggins 2006). Forrest et al. (1985) concluded that ferret densities at the last known wild population near Meeteetse, Wyoming, were linearly correlated with white-tailed prairie dog (*Cynomys leucurus*) colony size, with an average density of one adult ferret per 99–148 ac (40–60 ha) of occupied prairie dog habitat. Information on ferret life expectancy is sparse. However, mustelids typically have short mean life expectancies and 50 percent or greater juvenile mortality (Clark 1989). The mean life expectancy of free-ranging ferrets in the Meeteetse population was 0.9 years (Biggins et al. 2006).

HABITAT REQUIREMENTS

The black-footed ferret was historically found throughout the Great Plains, mountain basins, and semi-arid grasslands of North America wherever prairie dogs occurred (Hillman and Clark 1980, Figure 1). The species depends on prairie dogs (*Cynomys spp.*) for food and on prairie dog burrows for shelter (Biggins 2006). Field observations by Hillman (1968) indicate that ferrets feed entirely on prairie dogs. Diet samples support this, although other species of vertebrate prey have occasionally been reported (Oldemeyer et al. 1993, Miller et al. 1996).

DISTRIBUTION AND RANGE

The black-footed ferret is endemic to North America. The species entered North America from Siberia approximately 1–2 million years ago, spread across Beringia, and then advanced southward through ice-free corridors to the Great Plains by approximately 800,000 years ago (Wisely 2006). The species was probably common historically, contrary to early characterizations that addressed its natural history. However, its secretive habits (nocturnal and often underground) probably made it difficult to observe (Forrest et al. 1985, Anderson et al. 1986, Clark 1989).

The historical habitat of the black-footed ferret coincided with the ranges of the black-tailed prairie dog, Gunnison's prairie dog, and white-tailed prairie dog. These prairie dog species collectively occupied approximately 100 million ac (40.5 million ha) of intermountain and prairie grasslands extending from Canada into Mexico (Anderson et al. 1986, Biggins et al. 1997). The habitat occupied by prairie dogs existed within a range of an estimated 562 million ac (228 million ha) (Ernst 2008). There has been no documented occurrence of the ferret within the range of either the Utah prairie dog (*C. parvidens*) or the Mexican prairie dog (*C. mexicanus*), which have small, disjunct ranges (Lockhart et al. 2006). Ferrets from Arizona, Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, Utah, Wyoming, Alberta, and Saskatchewan have been collected as museum specimens since the late 1800s (Anderson et al. 1986). Ferrets also likely occurred in Mexico in recent times, as

evidenced by: (1) the fairly contiguous historical distribution of prairie dogs between Arizona, New Mexico, and Mexico, (2) the similarity of biological communities in these areas, (3) the presence of a museum specimen from a site just north of the Mexico and U.S. border, and (4) fossil records further south in Mexico (Lockhart 2001).

Ernst (2008) utilized a geographic information system database to identify the likely distribution of prairie dog habitat where the black-footed ferret probably occurred historically in the United States. She concluded that 85 percent of all ferrets may have occurred in black-tailed prairie dog habitat, 8 percent in Gunnison's prairie dog habitat, and 7 percent in white-tailed prairie dog habitat. Although potential biases are possible in this characterization of the historical distribution of ferrets, most ferrets probably occurred in black-tailed prairie dog habitat based on the more expansive extent of their distribution and the higher quality ferret habitat they represent in terms of prairie dog densities. Figure 1 depicts both the historical and current distribution of the species. Current ferret populations are all the result of reintroduction efforts.

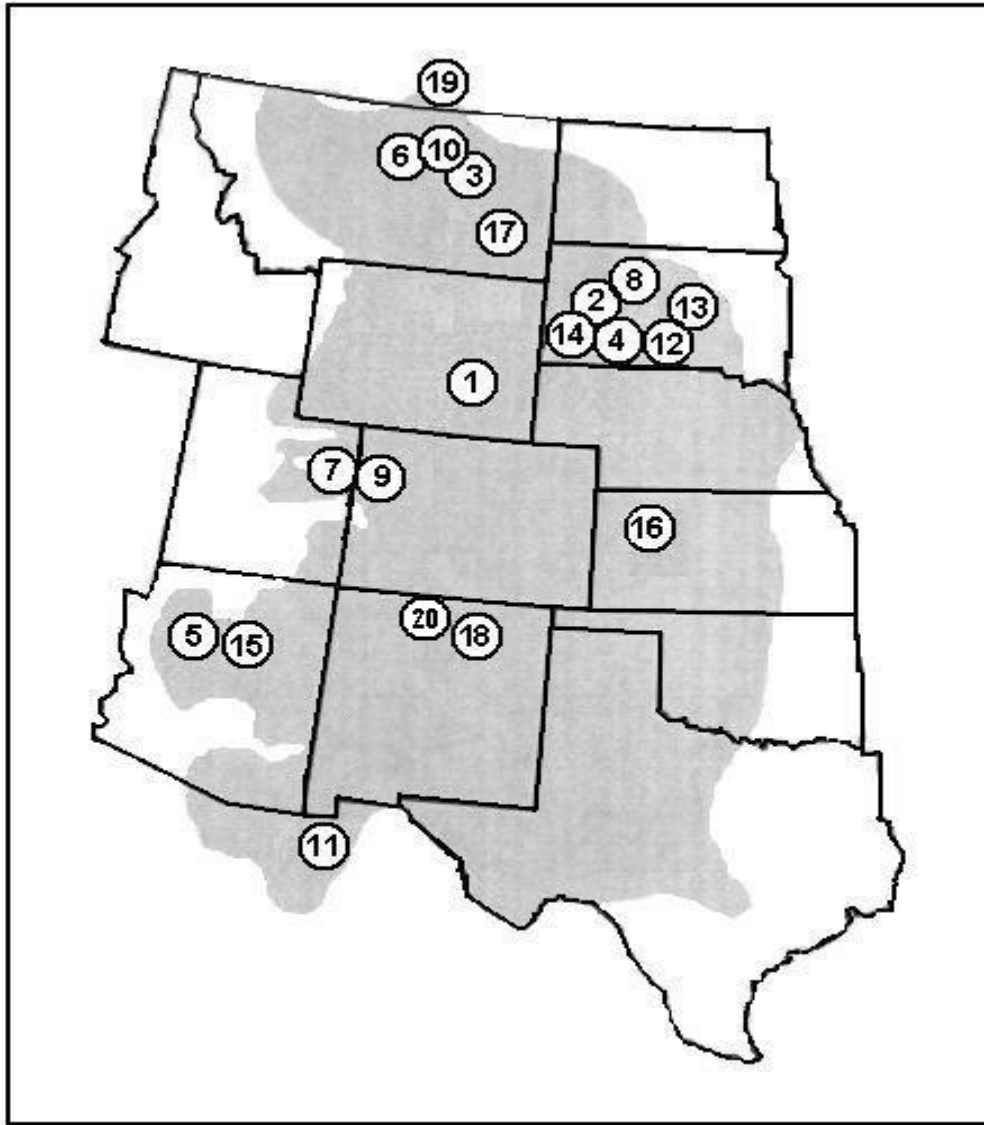


Figure 1. Probable historical range of the black-footed ferret (shaded) and current reintroduction sites. The locations of reintroduction sites are portrayed in their chronological order of implementation as follows: (1) Shirley Basin, WY (1991); (2) Badlands National Park, SD (1994); (3) UL Bend National Wildlife Refuge, MT (1994); (4) Conata Basin, SD (1996); (5) Aubrey Valley, AZ (1996); (6) Fort Belknap Indian Reservation, MT (1997); (7) Coyote Basin, UT (1999); (8) Cheyenne River Indian Reservation, SD (2000); (9) Wolf Creek, CO (2001); (10) BLM “40 Complex”, MT (2001); (11) Janos, Chihuahua, Mexico (2001); (12) Rosebud Indian Reservation, SD (2004); (13) Lower Brule Indian Reservation, SD (2006); (14) Wind Cave National Park, SD (2007); (15) Espee Ranch, AZ (2007); (16) Logan County, KS (2007); (17) Northern Cheyenne Indian Reservation, MT (2008); (18) Vermejo Ranch (black-tailed prairie dog habitat), NM (2008); (19) Grasslands National Park, Saskatchewan, Canada (2009); and (20) Vermejo Ranch (Gunnison’s prairie dog habitat), NM (2012).

POPULATION TRENDS

The black-footed ferret's close association with prairie dogs was an important factor in its decline. From the late 1800s to approximately 1960, both prairie dog occupied habitat and prairie dog numbers were reduced by the effects of: (1) habitat destruction from conversion of native prairie to cropland, (2) poisoning, and (3) disease. The ferret population declined precipitously as a result (Biggins 2006). These effects are described in more detail in the following section, "Threats and Reasons for Listing." The ferret was considered possibly extinct before a small population was located in Mellette County, South Dakota, in 1964 (Henderson et al. 1969). Breeding attempts with a few captured animals failed to produce surviving young. The last wild animals in the Mellette population were observed in the field in 1974 (Clark 1989). The last captive animal from the Mellette population died at Patuxent Wildlife Research Center in 1979 (U.S. Fish and Wildlife Service 1988) and again the ferret was presumed extinct. In 1981, a remnant population was discovered near Meeteetse, Wyoming (Clark et al. 1986, Lockhart et al. 2006). Disease outbreaks occurred at Meeteetse in the early 1980s. All surviving wild ferrets at Meeteetse were removed during 1985–1987. These ferrets were used to initiate a captive breeding program. Of the 18 remaining ferrets captured from Meeteetse, 7 produced a captive population lineage that is the foundation of present recovery efforts (Hutchins et al. 1996, Garrelle et al. 2006). Extant populations, both captive and reintroduced, descend from these "founder" animals.

No wild populations of black-footed ferrets have been found following the final capture of the last known Meeteetse ferret in 1987, despite extensive and intensive searches rangewide. It is very unlikely that any undiscovered wild populations remain (Hanebury and Biggins 2006, Lockhart et al. 2006).

There have been 20 specific black-footed ferret reintroduction projects, beginning in 1991 (Figure 1). These projects include: Shirley Basin, Wyoming, in 1991; Badlands National Park, South Dakota, in 1994; UL Bend National Wildlife Refuge, Montana, in 1994; Conata Basin, South Dakota, in 1996; Aubrey Valley, Arizona, in 1996; Fort Belknap Indian Reservation, Montana, in 1997; Coyote Basin, Utah, in 1999; Cheyenne

River Indian Reservation, South Dakota, in 2000; Wolf Creek, Colorado, in 2001; Bureau of Land Management 40 Complex, Montana, in 2001; Janos, Mexico, in 2001; Rosebud Indian Reservation, South Dakota, in 2004; Lower Brule Indian Reservation, South Dakota, in 2006; Wind Cave National Park, South Dakota, in 2007; Espee Ranch, Arizona, in 2007; Logan County, Kansas, in 2007; Northern Cheyenne Indian Reservation, Montana, in 2008; Vermejo Ranch (black-tailed prairie dog habitat), New Mexico, in 2008; Grasslands National Park, Saskatchewan, Canada, in 2009; and Vermejo Ranch (Gunnison's prairie dog habitat), New Mexico, in 2012.

Black-footed ferret reintroduction projects have experienced a range of success that we categorize in the following table. A site must meet the specified criteria in order to meet a particular classification. A site's classification may change over time. For example, both Badlands National Park, South Dakota, and Shirley Basin, Wyoming, were considered unsuccessful for several years, but are now considered as improving and successful, respectively.

Table 2. Black-footed ferret reintroduction efforts through 2012

Classification	Criteria	Site
Successful	• Self-sustaining • 30 or more breeding adults • Can support other sites with translocations • Multiple litters documented annually	• Aubrey Valley, AZ • Cheyenne River, SD • Conata Basin, SD • Shirley Basin, WY
Improving	• Increasing population • Litters documented annually	• Badlands NP, SD • Logan County, KS • Lower Brule, SD • Rosebud, SD • Wind Cave NP, SD
Marginal	• Performing minimally with no evidence of increasing populations • Few litters documented annually	• Coyote Basin, UT • Janos, Mexico • UL Bend NWR, MT • Wolf Creek, CO
Unsuccessful	• Populations declining or extirpated • No recent litters documented	• Espee Ranch, AZ • BLM 40 Complex, MT • Fort Belknap, MT

Recent	• Initiated within the past 5 years	• Grasslands NP, Canada • Northern Cheyenne, MT • Vermejo Ranch (btpd habitat), NM • Vermejo Ranch (gpd habitat), NM
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Black-footed ferret populations are difficult to enumerate due to their remote locations, difficult accessibility, nocturnal habits, and logistical problems and costs associated with the requisite field work. Accordingly, ferret populations at some reintroduction sites are not regularly or even accurately assessed. We view ferret population estimates at most sites as only approximate minimum numbers because of the aforementioned issues and because additional variables such as weather, intensity of search effort, and length of search effort may provide different perspectives. One striking example of the difficulty of enumerating ferret populations is Shirley Basin, Wyoming, where approximately 200 individuals were estimated to occur in the fall of both 2008 and 2010 on only one-seventh of the prairie dog habitat—the amount of habitat surveyed. This ferret population may or may not be larger than estimated, but does indicate the general difficulties of estimating ferret populations in the wild.

We have derived our best estimate of adult ferrets extant in the wild at this time as an average of the collective observations in 2008 and 2011. We recognize that ferret populations at some sites likely declined between 2009 and 2012, but conversely, populations at other sites likely increased during this same period. The following table summarizes recent information regarding the cumulative number of black-footed ferrets released and minimum numbers documented at the reintroduction sites. Note that the rounding to derive estimates of breeding populations results in estimates that are not exactly 50 percent of the fall populations. The most significant change in population in recent years is the decline in ferret numbers at Conata Basin due to sylvatic plague (see discussion in section on “Disease or predation”).

Table 3. Numbers of black-footed ferrets in the wild, 1991 - 2012

Site (year initiated)	Prairie dog spp.	Ferrets released	Minimum fall population ¹ 2008	Estimated breeding adults ² 2009	Minimum fall population 2011	Estimated breeding adults 2012	Average estimate of breeding adults
Shirley Basin, WY (1991)	Wtpd	301	196	98	203 (in 2010)	102 (in 2011)	100
UL Bend NWR, MT (1994)	Btpd	208	13	7	20	10	9
Badlands NP, SD (1994)	Btpd	175	20	10	33	17	14
Aubrey Valley, AZ (1996)	Gpd	206	66	33	75	38	35
Conata Basin, SD (1996)	Btpd	150	292	146	72	36	91
Ft. Belknap, MT (1997)	Btpd	167	0	0	0	0	0
Coyote Basin, UT (1999)	Wtpd	249	25	13	3	1	7
Cheyenne River, SD (2000)	Btpd	219	150	75	25 (partial survey)	>13	44
BLM 40complex, MT (2001)	Btpd	95	3	3	No data	No data	2
Wolf Creek, CO (2001)	Wtpd	209	16	8	No data	No data	4
Janos, Mexico (2001)	Btpd	282	13	7	No data	No data	4
Rosebud, SD (2003)	Btpd	99	30	15	No data	No data	8
Lower Brule, SD (2006)	Btpd	87	26	13	12	6	10
Wind Cave NP, SD (2007)	Btpd	49	26	13	46	23	18
Espee Ranch, AZ (2007)	Gpd	44	Recent release	No data	No data	No data	No data
Logan County, KS (2007)	Btpd	36	15	7	38	19	13
N. Cheyenne, MT (2008)	Btpd	8	Recent release	No data	No data	No data	No data
Vermejo Ranch, NM (2008)	Btpd	77	Recent release	No data	5	3	2
Grasslands NP, Canada (2009)	Btpd	45	Recent release	No data	12	6	3
Vermejo Ranch, NM (2012)	GPD	20	Recent release	No data	No data	No data	No data
Total		2726	891	448	544	274	364

¹ Minimum fall population counts are derived from spotlight surveys and trapping efforts except in Shirley Basin, WY, where a model was used to estimate fall population.

² Breeding adult figures are estimated to be one-half minimum fall population counts from the previous yr.

THREATS AND REASONS FOR LISTING

Black-footed ferret populations declined for three principal reasons. First, a major conversion of native range to cropland, particularly in the eastern portion of the species' range, began in the late 1800s. Second, poisoning of prairie dogs as a means of reducing competition with domestic livestock for forage began in the early 1900s. Third, the exotic disease sylvatic plague first impacted prairie dogs in the 1930s (Eskey and Hass 1940). Each of these resulted in a substantial loss of prairie dogs, which in turn led to an even greater decline in ferret populations due to the species' dependency on large expanses of habitat occupied by prairie dogs (Lockhart et al. 2006). Additionally, even a temporal loss of prairie dog habitat can create a population bottleneck for ferrets, despite the subsequent recovery of the prairie dog population.

Section 4 of the ESA (16 U.S.C. 1533) and implementing regulations (50 CFR, part 424) set forth procedures for adding species to, removing species from, or reclassifying species on the Federal Lists of Endangered and Threatened Wildlife and Plants. Under section 4(a)(1) of the ESA, a species may be determined to be endangered or threatened based on any of the following five factors: (A) the present or threatened destruction, modification, or curtailment of its habitat or range; (B) overutilization for commercial, recreational, scientific, or educational purposes; (C) disease or predation; (D) the inadequacy of existing regulatory mechanisms; or (E) other natural or manmade factors affecting its continued existence. We discuss each of these factors affecting the status of the black-footed ferret in more detail below.

Present or threatened destruction, modification or curtailment of habitat or range

The black-footed ferret's historical range (Figure 1) coincided with the ranges of the black-tailed, white-tailed, and Gunnison's prairie dogs. Historically, these prairie dog species occupied approximately 100 million ac (40.5 million ha) of intermountain and prairie grasslands rangewide (Anderson et al. 1986, Biggins et al. 1997). This occupied habitat existed within a range of approximately 562 million ac (228 million ha) (Ernst

2008) within the U.S. This is a minimum estimate of historical range because Ernst (2008) did not evaluate the ferret's range in Canada and Mexico. Occupied habitat likely shifted somewhat over time in response to drought, fire, and grazing by bison (*Bison bison*) and other animals, along with other factors.

In 1986, Anderson et al. (1986) estimated a 90 percent decrease in the amount of habitat occupied by all species of prairie dogs. Mac et al. (1998) estimated a 98 percent decline in numbers of prairie dogs throughout North America. Prairie dog occupied habitat reached a low point in the early 1960s when approximately 1.4 million ac (570,000 ha) were estimated to exist in the United States for black-tailed, white-tailed, and Gunnison's prairie dogs (Bureau of Sport Fisheries and Wildlife 1961). These low estimates likely continued for a decade thereafter, until Executive Order 11643 prohibited the use of certain toxicants that might cause secondary poisoning on Federal lands or through federally funded programs. The most recent Service estimates of prairie dog occupied habitat in the U.S. include 2,400,000 ac (972,000 ha) of black-tailed prairie dog occupied habitat (74 FR 63343; December 3, 2009), 841,000 ac (341,000 ha) of white-tailed prairie dog occupied habitat (69 FR 64889; November 9, 2004), and 340,000–500,000 ac (136,000–200,000 ha) of Gunnison's prairie dog occupied habitat (73 FR 6660; February 5, 2008) for a total of approximately 3,700,000 ac (1,500,000 ha) of occupied habitat. This is a decrease of approximately 96 percent from historically occupied habitat.

As prairie dog occupied habitat declined due to conversions from native prairie to cropland, poisoning, and disease during the late 19th century and the first half of the 20th century, black-footed ferret populations likewise declined (Fagerstone and Biggins 1986, Cully 1993, Biggins 2006, Lockhart et al. 2006). Prairie dog occupied habitat has increased approximately 250 percent since the 1961 estimate. However, by the 1960s, only two remnant ferret populations (in Mellette County, South Dakota, and Meeteetse, Wyoming) remained, and ferrets were unable to repopulate expanding prairie dog habitat.

Native Prairie Conversion: The conversion of native prairie to cropland is the primary, largely permanent, cause of habitat destruction within the historical range of the black-footed ferret. Approximately 112 million ac (45 million ha) of native prairie have been

converted to agricultural land within the ferret's historical range (Ernst et al. 2006). However, we estimate that approximately 400 million ac (163 million ha) of non-cultivated rangeland remain within the historical range of the ferret (U.S. Department of Agriculture 2005), and represent potential habitat for the prairie dog and ferret (Ernst et al. 2006). Rates of conversion from native prairie to cropland have slowed substantially in recent years, and we do not consider the present or threatened habitat loss due to cropland conversion as significant as historical levels of impact. Approximately 3.7 million ac (1.5 million ha) of prairie dog occupied habitat are currently available. It appears that sufficient potential habitat still occurs within the ferret's historical range to accommodate increases in occupied habitat when the 3.7 million ac (1.5 million ha) of currently occupied prairie dog habitat are contrasted with the 400 million ac (163 million ha) of current rangeland. Moreover, we project that less than 15 percent of currently occupied prairie dog habitat is necessary to recover the ferret, if this habitat is appropriately configured and managed (see Part II). We do not consider the present or threatened destruction of habitat or range due to conversion of native prairie to cropland a threat to ferret recovery at the present time. Cropland conversion no longer appreciably reduces survival or reproduction at the current level of cultivated land. In the absence of ESA protections, effects from cropland conversion at the current rate would not require regulation and would not be a threat.

Urbanization: Approximately 3.3 million ac (1.3 million ha) of historical black-footed ferret habitat have been lost to urbanization (Ernst 2008). However, it appears that sufficient potential habitat still occurs within the ferret's historical range to accommodate increases in occupied habitat when the 3.3 million ac (1.3 million ha) of urban lands are contrasted with the 400 million ac (163 million ha) of current rangeland. We describe the amount of prairie dog occupied habitat necessary to support a self-sustaining ferret population in more detail in Part II. We do not consider the present or threatened destruction of habitat or range due to urbanization a threat to ferret recovery at the present time. In the absence of ESA protections, effects from urbanization in their current state would not require regulation and would not be a threat.

Disease and Poisoning: We discuss the present or threatened modification of habitat or range due to sylvatic plague under factor C “Disease or predation” and the present or threatened curtailment of habitat or range due to poisoning of prairie dogs under factor E “Other natural manmade factors.”

Overutilization for Commercial, Scientific, and Educational Purposes: All black-footed ferrets are located either in captive breeding facilities or at managed reintroduction sites. No black-footed ferrets are being utilized for commercial purposes. ESA permits may be provided for specific scientific or educational activities, but other uses are illegal and subject to law enforcement actions.

The captive black-footed ferret population is guided by the Association of Zoos and Aquariums (AZA) Black-footed Ferret Species Survival Plan (SSP®) to conserve a breeding population of a minimum of 240 ± 35 animals of optimum sex and age ratio to maximize productivity and genetic diversity (Hutchins et al. 1996). Captive ferrets in excess of SSP® needs are allocated each year for reintroduction or for scientific and educational purposes. Animals used for scientific or educational purposes are often older animals that are past prime breeding age, although some kits have also been allocated for research purposes. For example, some ferrets have been used for research and development of a plague vaccine (Rocke et al. 2006). Some individuals are also used as display animals for educational purposes at zoos.

Free-ranging black-footed ferrets occur only at managed reintroduction sites. Wild-born kits from successful reintroduction sites are sometimes trapped and released on other reintroduction sites (Lockhart 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007, Larson 2008a). However, they remain part of the reintroduced population. Ferrets at some reintroduction sites are also trapped, given a plague vaccination, and promptly released. In very limited circumstances, studies that involve trapping and measuring various characteristics of ferrets in order to identify differences between captive and wild born ferrets have been authorized. No other collections of free-ranging ferrets for scientific or educational purposes are permitted.

We do not consider the overutilization for commercial, scientific, or educational purposes a threat to black-footed ferret recovery at the present time. It does not appreciably reduce survival or reproduction at present. In the absence of ESA protections, the SSP® would continue to appropriately allocate captive ferrets for purposes of captive breeding, reintroduction, scientific research, and education. State and Federal agencies do not allow take of free-ranging ferrets for purposes other than translocation or vaccination. In the absence of ESA protections, overutilization for commercial, scientific, or educational purposes would need to continue to be regulated.

Recreational Purposes: The interest in and the intensity of recreational prairie dog shooting has increased over the past decade at some black-footed ferret reintroduction sites. Depending on its intensity, shooting can impact local prairie dog populations, and the resulting loss in prey base likely affects black-footed ferret reintroduction sites (Pauli 2005, Reeve and Vosburgh 2006). Incidental take of ferrets by prairie dog shooters is also a potential, but as yet undocumented, source of ferret mortality. Recreational shooting of prairie dogs may contribute to the problem of lead accumulation in wildlife food chains that include prairie dogs (Pauli and Buskirk 2007). Killing large numbers of animals, not removing carcasses from the field, and using expanding bullets containing lead may present potentially dangerous amounts of lead to scavengers and predators of prairie dogs. However, no impacts from ingesting lead have been reported in ferrets.

Prairie dog shooting is presently managed at varying levels (seasonal to full closure) on all active black-footed ferret reintroduction areas by State wildlife agencies, Federal land management agencies, or tribes. Recreational shooting has not been intense enough to warrant suspension of recovery efforts at any site but was suspected of impacting ferrets at one site (Krueger 2008a). Recreational shooting of white-tailed prairie dogs at Wolf Creek, Colorado, appeared to restrict prairie dog densities and limit the carrying capacity or reproductive success for ferrets at this site (Krueger 2008b and Krueger 2008c). Recovery success at this site could likely be improved through the implementation of appropriate regulatory measures.

Prairie dog populations can recover from very low numbers following intensive shooting (Knowles 1988, Vosburgh 1996, Dullum et al. 2005, Pauli 2005, Cully and Johnson 2006). It appears that a typical scenario is either: (1) once populations have been reduced, shooters go elsewhere and populations recover; or (2) continued shooting maintains reduced population size at specific sites (Knowles 1988, Vosburgh 1996, Dullum et al. 2005, Pauli 2005, Cully and Johnson 2006). Some landowners maintain black-tailed prairie dog populations and derive income from charging people for recreational shooting. Monetary gain from shooting fees may motivate landowners to preserve prairie dog colonies for future shooting opportunities, which is preferable to eradicating them by poisoning (Vosburgh and Irby 1998, Reeve and Vosburgh 2006).

We do not consider overutilization of prairie dogs for recreational purposes a threat to black-footed ferret recovery at reintroduction sites at the present time, except in certain very limited circumstances. While recreational shooting of prairie dogs may occasionally limit the carrying capacity for ferrets, it does not appreciably reduce survival or reproduction at present. In the absence of ESA protections, recreational shooting would need to continue to be regulated at reintroduction sites by State and Federal agencies and tribes.

Disease or predation

Native canine distemper and nonnative sylvatic plague have seriously impacted both wild and captive populations of the black-footed ferret. Several other native diseases, including coccidiosis, cryptosporidiosis, and hemorrhagic syndrome also affect captive populations (Hutchins et al. 1996), but are not common in the wild.

Canine distemper: Canine distemper can significantly adversely impact the black-footed ferret. It was originally believed to have been the primary cause of the demise of the last wild population of ferrets at Meeteetse, Wyoming, in the mid-1980s (Clark 1989). At that time, it was believed that plague did not directly impact the species because many carnivore species, including other ferret species, were resistant (Cully 1993, Godbey et al.

2006). However, it is now believed that epidemics of both canine distemper and plague were likely responsible for the decline of the Meeteetse ferrets (Lockhart et al. 2006).

The canine distemper virus causes a systemic disease that is highly virulent to carnivore species, including the black-footed ferret. It is endemic in the United States and initially made reintroduction of ferrets more difficult (Wimsatt et al. 2006). Efforts in 1972 to breed ferrets from the Mellette County, South Dakota population were ultimately unsuccessful due to vaccine-induced canine distemper. Although safe in domestic ferrets, the vaccine induced fatal distemper in 4 of 6 vaccinated black-footed ferrets that were removed from the wild Mellette population for captive breeding purposes (Lockhart et al. 2006). Some ferrets in the Meeteetse population also succumbed to distemper in the mid-1980s (Clark 1989). More recently, an effective commercial distemper vaccine has become available and is widely employed in both captive and some wild ferret populations (Marinari and Kreeger 2006). Canine distemper vaccination can substantially reduce the threat of catastrophic population losses of ferrets. However, it is not practical to vaccinate all wild-born ferrets to protect them from periodic distemper events. Accordingly, wild populations may require monitoring and periodic augmentation.

We do not consider canine distemper a threat to black-footed ferret recovery at the present time. The distemper vaccine protects captive and newly released ferrets, and wild-born ferrets are monitored and managed to avoid long-term adverse impacts. Canine distemper does not appreciably reduce ferret survival or reproduction. In the absence of ESA protections, management for distemper would need to continue.

Sylvatic plague: Sylvatic plague infections are caused by the bacterium *Yersinia pestis*. Fleas acquire the bacterium from biting infected animals and can then transmit it to other animals in a similar manner. The disease can also be transmitted pneumonically (via the respiratory system) among infected animals or via the consumption of contaminated tissues (Godbey et al. 2006, Abbott and Rocke 2012). Recovery efforts for the black-footed ferret are hampered because both ferrets and prairie dogs are extremely susceptible to plague (Barnes 1993, Gage and Kosoy 2006). Plague can impact ferrets directly via

infection and subsequent mortality. It can also indirectly impact ferrets through the disease's effects on prairie dogs and the potential for dramatic declines in the ferret's primary prey base. The high densities and high rates of social contact of black-tailed and Gunnison's prairie dogs particularly enhance the spread of plague (Cully 1993).

The complex dynamics of sylvatic plague are not well understood. The potential significance of plague impacts on black-footed ferret populations underscores the value of establishing spatially separated reintroduction sites across the widest possible distribution of the species' historical range. Plague management tools and strategies are being developed (see following paragraphs and section on "Recovery Actions"). Releases in disease-free habitat should be prioritized whenever possible.

Sylvatic plague is a nonnative disease foreign to the evolutionary history of North American species. It did not exist on the North American continent prior to 1900, when it was inadvertently introduced into San Francisco (Gage and Kosoy 2006). It was first observed in prairie dogs in 1932 in Arizona (Cully 1993). Plague had been detected in prairie dogs in all States within the historical range of the black-footed ferret by 2005. The disease is currently present throughout the entire range of the white-tailed and Gunnison's prairie dogs and in at least the western two-thirds of the range of black-tailed prairie dogs (Barnes 1993, Lockhart et al. 2006). Figure 2 illustrates recent information regarding plague occurrence in the U.S. available from the U.S. Geological Survey (Abbott and Rocke 2012).



Figure 2. Western U.S. counties with plague-positive animal or flea samples (Abbott and Locke 2012)

Plague in prairie dogs has been documented at or within 25 miles (40 kilometers) of all black-footed ferret reintroduction sites except for Rosebud Indian Reservation in South Dakota, Logan County in Kansas, and Janos in northern Chihuahua, Mexico (Lockhart 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007). Recent discussions with personnel at Rosebud Indian Reservation have indicated the possibility of plague at this site. However, it has not yet been confirmed in prairie dogs at this site.

Conata Basin, South Dakota, has been regarded as the most successful black-footed ferret reintroduction site. Until very recently, it supported the largest self-sustaining ferret population documented since the listing of the species in 1967, and perhaps for decades

before. Conata Basin has provided a surplus of kits for translocation to other reintroduction sites since 2000 (Lockhart 2000, 2001, 2002, 2003, 2004, 2005, 2006, 2007, Larson 2008a). Plague was detected in prairie dogs approximately 25 miles (40 kilometers) south of Conata Basin in 2005. Approximately 3,500 pounds (1,600 kilograms) of the insecticide Deltamethrin (a powder formulation registered for flea control) were applied (dusted) on 7,000 ac (2,800 ha) of prairie dog burrows in known ferret habitat during the late summer and fall of 2005 in an effort to eliminate fleas. Despite continued dusting efforts, plague was identified at Conata Basin in May 2008.

Following detection of plague at Conata Basin, South Dakota, several Federal agencies undertook a dusting effort that targeted approximately 10,000 ac (4,000 ha) of prairie dog colonies on U.S. Forest Service (USFS) and National Park Service (NPS) lands (Griebel 2008a). Regardless, approximately 10,000 ac (4,000 ha) of untreated prairie dog colonies were impacted by plague (Griebel 2008b). Plague in Conata Basin continued into 2009 and removed approximately 5,000 additional acres (2,000 ha) of prairie dogs for a two-year reduction in occupied prairie dog acreage from 31,000 ac (12,600 ha) to 16,000 ac (6,500 ha) (Griebel 2009). Dusting at Conata Basin has continued annually to the present. Conata Basin and Badlands National Park ferret reintroduction sites have used techniques such as dusting and vaccination to actively manage ferret habitat in the midst of this plague outbreak and have maintained approximately 11,000 ac (4,455 ha) of ferret occupied prairie dog colonies (Griebel 2009). The precise extent of ferret mortality at Conata Basin is not known, but is presumed to be as much as 75 percent of the population, based upon recent surveys and the number of acres impacted at this site.

Sylvatic plague can be present in a prairie dog colony in either an enzootic (persistent, low level of mortality) or epizootic (high level of mortality over a shorter period of time) state. Most of the information we have regarding impacts from plague is from data collected during epizootic events. However, a recent study has expanded the understanding of enzootic plague and impacts to black-footed ferret recovery (Matchett et al. 2010). In that study, ferret survival significantly improved when plague vaccinations were given to ferrets or when Deltamethrin was applied to prairie dog burrows, even in the absence of a discernable die-off of prairie dogs. The researchers concluded that

increased ferret mortality associated with enzootic plague was hindering ferret recovery and fleas were a key component in transmission (Matchett et al. 2010).

In one instance, black-footed ferrets appear to have prospered despite the periodic presence of plague. In 1991, Shirley Basin, Wyoming, was the first site where ferrets were reintroduced. This site is occupied by white-tailed prairie dogs. Ferret releases at Shirley Basin were suspended in 1994 due to prairie dog population declines caused by plague. The small ferret population present at the site was expected to have been lost by the late 1990s. Only five ferrets were observed in 1997 (Grenier et al. 2007). However, 52 ferrets were observed in 2003. Thereafter, the Shirley Basin ferret population received additional augmentation and has grown rapidly (Lockhart et al. 2006, Grenier et al. 2007). White-tailed prairie dog complexes are less densely populated than typical complexes of black-tailed or Gunnison's prairie dogs. Apparently, scattered populations of prairie dogs avoided contracting plague and were able to sustain a small ferret population. However, ferrets and white-tailed prairie dogs at other reintroduction sites have not demonstrated similar resiliency, so Shirley Basin may be unique in this regard.

Rocke et al. (2006) are involved in research and development of vaccines to prevent plague in black-footed ferrets and prairie dogs. Ferrets immunized by a series of two subcutaneous injections had significantly higher antibody titers than un-immunized animals. Eleven of 16 vaccinated individuals survived when challenged with plague 6 months after immunization. All eight control animals died. The 11 survivors were again challenged by ingestion of a plague-infected mouse 2 months later and all survived. One vaccine under development may eventually be useful in protecting ferrets from habitat reduction due to plague, particularly if oral delivery to prairie dogs becomes feasible. Vaccine distributed via oral baits to protect prairie dogs has recently been shown to be effective in a laboratory setting (Rocke et al. 2008, Abbott and Rocke 2012). The use of a similar product in the field could protect habitat and prey base for ferrets, and provide long-term habitat stability. Most captive ferrets, including all of those provided for reintroduction, are currently vaccinated for plague. Many wild ferrets at Conata Basin are also vaccinated annually in an effort to minimize impacts from the ongoing plague epizootic. However, maximum protection is difficult to achieve in wild ferrets, which

must be trapped twice, two to four weeks apart, to receive an effective dose of the vaccine.

We consider sylvatic plague a medium magnitude, imminent threat to black-footed ferret recovery at the present time. Sylvatic plague affects the ferret both directly by causing mortality to ferrets and indirectly by causing mortality to prairie dogs. The recent encroachment of plague into South Dakota may pose a significant risk at reintroduction sites in that State. However, we believe that the threat from plague can be ameliorated by insecticidal dusting, ferret vaccine, prairie dog vaccine, and the maintenance of more reintroduction sites. Ferret recovery objectives could then be achieved despite periodic losses to plague. In the absence of ESA protections, management for plague would need to continue.

Predation: Natural levels of predation typically do not adversely impact overall population stability in healthy wildlife populations. However, if a population is vulnerable due to other factors, predation may become a contributing and ultimately limiting factor. Predation was a concern at early black-footed ferret reintroduction sites. Predation may have caused up to 95 percent of ferret mortality on some reintroduction sites without active plague before preconditioning became standard (Breck et al. 2006). Coyotes were a primary cause of predation-related death to ferrets at three reintroduction sites in Arizona, Montana, and South Dakota (Biggins et al. 2006). However, lethal control of coyotes may further impact ferret survival, possibly due to rapid rates of recolonization of coyotes after removal (Breck et al. 2006). Great-horned owls (*Bubo virginianus*) can also cause significant ferret mortality in some circumstances. Removal of predating great-horned owls benefited ferret survival in some instances (Breck et al. 2006).

Reintroductions into the wild of many captive-bred wildlife species are often less successful than reintroductions using wild-born individuals (Jule et al. 2008, Aaltonen et al. 2009, Maran et al. 2009). This lack of success is typically due to unsuccessful predator/competitor avoidance, starvation, and disease (Jule et al. 2008, Aaltonen et al. 2009, Maran et al. 2009). Behaviors critical to survival in the wild may be altered in

black-footed ferrets during generations in captivity. Trials showed increased boldness in ferrets through successive generations in captivity (Biggins 2000). This behavior could increase predation rates on released animals due to more time spent above ground. The author noted that quasi-natural rearing environments seemed to counteract some negative effects of captivity. Survival at several release sites from 1992–1995 was 10-fold higher for ferrets reared in outdoor pens than for ferrets raised in indoor cages (Biggins 2000). Increased preconditioning through outdoor pen rearing of captive-born ferrets in recent years has likely enriched learning of important natural behaviors. Outdoor pen rearing appears to have increased survival rates when those animals have been released in the wild (Biggins et al. 2011). Predation now has insignificant effects on ferrets at most sites, as evidenced by the reintroduction sites where ferret populations are apparently either stable or increasing, despite predators not being removed.

We do not consider predation a threat to black-footed ferret recovery at the present time because of the positive effects of preconditioning through outdoor pen rearing on survival of ferrets released into the wild. Predation no longer appreciably reduces ferret survival or reproduction. In the absence of ESA protections, recovered populations would be naturally sustained with wild-born kits, and predation would not be a threat.

Inadequacy of existing regulatory mechanisms

In analyzing whether the existing regulatory mechanisms are adequate, the Service reviews relevant Federal, State, and tribal laws, plans, regulations, memorandums of understanding, cooperative agreements, and other factors that influence conservation. Strongest weight is given to statutes and their implementing regulations, and management direction that stems from those laws and regulations. Other regulatory mechanisms (memorandums and agreements) are more voluntary in nature; in those cases we analyze the specific facts for that mechanism to determine the extent to which it can be relied on in the future. We consider all pertinent information, including the efforts and conservation practices of State and tribal governments. Existing regulatory mechanisms include all mechanisms that are pertinent to a comprehensive regime designed to conserve a wildlife population, whether or not they are enforceable.

Endangered Species Act: The ESA is the primary Federal law that provides protections for the black-footed ferret. It provides several tools to conserve the species. The establishment of multiple reintroduction sites throughout the species' range provides added resilience in the presence of threats such as sylvatic plague and poisoning that can periodically impact sites.

Section 4 of the ESA requires that, subsequent to listing, a review of the species be conducted to evaluate the status of the listed species. We completed the most recent 5-year review of the black-footed ferret in 2008. Section 4 also requires that we develop and implement recovery plans for the conservation and survival of listed species. This document is the second revision of a recovery plan for the ferret.

Section 6 of the ESA allows for cooperation between the Service and States in the management and funding of projects designed to enhance the conservation of federally listed species. Several States have received section 6 funding to either initiate black-footed ferret reintroductions or conduct monitoring at existing reintroduction sites. For example, in 2010, we funded section 6 proposals in Utah (\$40,000 to support ferret releases and monitoring efforts) and Wyoming (\$45,500 to support ferret recovery efforts).

Tribal wildlife grants (TWGs), administered by the Service, are used to provide technical and financial assistance to tribes for the development and implementation of programs that benefit fish and wildlife resources and their habitat, including species of Native American cultural or traditional importance and species that are not hunted or fished. A number of tribes have received TWG funding for black-footed ferret conservation. For example, in 2008-2009, we supported TWG projects for the Cheyenne River Sioux Tribe (\$133,890 in 2008 to begin a ferret recovery program and \$116,059 to survey for ferrets in 2009) and the Lower Brule Sioux Tribe (\$200,000 in 2008 to conduct research and management on ferrets and prairie dogs and \$24,450 in 2009 to protect ferrets from plague).

Section 7(a)(1) of the ESA requires Federal agencies utilize their authorities in furtherance of the purposes of ESA by carrying out programs for the conservation of listed species such as the black-footed ferret. Several Federal agencies, including the U.S. Bureau of Land Management (BLM), the USFS, and the NPS, have worked cooperatively with the Service to reintroduce ferrets onto lands they manage (more detailed information is provided in following paragraphs).

Section 7(a)(2) of the ESA requires Federal agencies to consult with the Service to ensure that any project funded, authorized, or carried out by such agency does not jeopardize the continuing existence of a listed species, or result in the destruction or adverse modification of designated critical habitat for the species. The black-footed ferret is exempt from critical habitat designation as it was listed prior to the critical habitat amendments to ESA. Numerous formal and informal section 7 consultations have been carried out in all States within the historical range of the ferret. The large number of informal consultations eventually led to the concept of block clearing large expanses of prairie dog occupied habitat to avoid redundant ferret surveys for each proposed project. All reintroduction sites in the United States require formal section 7 consultation. A formal section 7 was also conducted in 1994 with the U.S. Bureau of Indian Affairs regarding large-scale prairie dog control on Rosebud Sioux and Cheyenne River Sioux Reservations. A formal section 7 with the U.S. Environmental Protection Agency (EPA) regarding potential impacts to ferrets and other threatened and endangered species from the use of the pesticide chlorophacinone (trade name: Rozol) to poison prairie dogs was completed in 2012.

Section 9 of the ESA provides for direct protection of a federally-listed species by prohibiting “take” (i.e., to harass, harm, pursue, hunt, shoot, wound, kill, trap, capture, or collect, or to attempt to engage in any such conduct) by any person.

Section 10 of the ESA provides certain exceptions for otherwise prohibited actions. Most reintroduced black-footed ferrets have been released into nonessential experimental population areas as set forth in section 10(j). Under section 10(j), a listed species reintroduced outside of its current range, but within its historical range, may be

designated as “experimental.” This designation increases the Service’s flexibility and discretion in managing reintroduced endangered species and allows promulgation of regulation deemed appropriate for conservation of the reintroduced species. Additional management flexibility is possible if the experimental population is also designated “nonessential”. This tool has been successfully used to address concerns of other parties for reintroductions of California condors, gray wolves, whooping cranes, and many other species in addition to ferrets. Section 10(j) populations located in National Parks or National Wildlife Refuges are treated as threatened for the purposes of ESA section 7 consultations. Other section 10(j) populations are treated as a “proposed” species for the purposes of ESA section 7 consultations. Reintroduced ferrets in section 10(j) areas are protected by the specific regulations promulgated for the experimental population and section 9 of ESA.

Black-footed ferrets reintroduced into Canada and Mexico are regulated by their respective governments. Ferrets reintroduced at Espee Ranch, Logan County, Lower Brule Indian Reservation, Northern Cheyenne Indian Reservation, Vermejo, and Wind Cave National Park were authorized via scientific recovery permits issued by the Service under section 10(a)(1)(A) of ESA. Conditions stipulated under these permits and supporting ESA documents were developed to achieve State, tribal, and/or local support. Reintroduced ferrets in section 10(a)(1)(A) areas are protected by section 9 of ESA.

Timely establishment of wild ferret populations is critical in order to minimize deleterious effects resulting from too many generations of captive breeding. These effects include reduced reproductive fitness, physical abnormalities, behavioral abnormalities, and loss of natural selection. Many fewer black-footed ferret reintroductions would have been initiated during the past 20 years without the added flexibility of nonessential experimental designations. The Service is making progress toward achieving recovery goals. Progress toward downlisting and delisting will continue if active participation in reintroduction efforts by Federal, State, tribal, and local partners continues.

Without the protections and funding support provided by the ESA, progress toward black-footed ferret recovery would likely be much more limited than it is at present. However, once delisting criteria are achieved, we do not anticipate that the absence of ESA protections will reduce ferret survival or reproduction because the species will continue to be managed by other Federal, State, and tribal regulations.

National Environmental Policy Act (NEPA): NEPA requires all Federal agencies to participate in evaluations of Federal projects and their potential significant impacts to the human environment. Agencies must include a discussion of the environmental impacts of the various project alternatives, any adverse environmental effects which cannot be avoided, and any irreversible or irretrievable commitments of resources. Activities on non-Federal lands are also subject to NEPA if there is a Federal nexus. Cooperating agencies and the public can provide recommendations to the action agency for project modifications to avoid impacts or enhance conservation of the black-footed ferret or other wildlife species. NEPA provides an opportunity to negotiate conservation measures. However NEPA is a disclosure law, and does not require subsequent minimization or mitigation measures by the lead Federal agency. Evaluation of ferrets under NEPA would occur regardless of the species' listing status.

U.S. Bureau of Land Management: The BLM's mission is set forth in the Federal Land Policy and Management Act of 1976, which mandates that BLM manage public land resources for a variety of uses, such as energy development, livestock grazing, recreation, and timber harvesting, while protecting the natural, cultural, and historical resources on those lands. The BLM manages listed and sensitive species under guidance provided by their MS-6840 Manual - Special Status Species Management. The 6840 Manual directs BLM to proactively conserve special status and ESA-listed species and the ecosystems upon which they depend, ensure that all actions authorized or carried out by BLM are in compliance with the ESA, and cooperate with the planning and recovery of listed species. Four black-footed ferret reintroduction sites occur at least in part on BLM lands including: Shirley Basin in Wyoming, Coyote Basin in Utah, Wolf Creek in Colorado, and the BLM 40 Complex in Montana. Management of these reintroduction sites would likely continue regardless of the species' listing status.

U.S. Forest Service: Under the National Forest Management Act of 1976, as amended (16 U.S.C. §§ 1600-1614), the USFS shall strive to provide for a diversity of plant and animal communities when managing national forest lands. Conata Basin occurs on USFS land (Buffalo Gap National Grasslands) in South Dakota. Management of this reintroduction site would need to continue regardless of the species' listing status.

U.S. National Park Service: The NPS Organic Act (39 Stat. 535, 16 U.S.C. 1, as amended) states that NPS "shall promote and regulate the use of the Federal areas known as national parks, monuments, and reservations...to conserve the scenery and the natural and historic objects and the wildlife therein and to provide for the enjoyment of the same in such manner and by such means as will leave them unimpaired for the enjoyment of future generations." The black-footed ferret occurs in Badlands and Wind Cave National Parks in South Dakota, where they and their habitats are protected from large-scale loss or degradation due to NPS mandate. Management of these reintroduction sites would need to continue regardless of the species' listing status.

State Mechanisms: All States within the historical range of the black-footed ferret have produced State Comprehensive Wildlife Conservation Strategies. These strategies describe priorities for management of wildlife species, but do not result in any protection for the species. Three of the 12 States within the historical range of the species (Nebraska, New Mexico, and Oklahoma) do not identify the ferret as a management priority species. However, one of these States (New Mexico) supported a reintroduction effort in 2008. Management of these reintroduction sites would need to continue, regardless of the species' listing status.

Tribal Mechanisms: Black-footed ferrets have been reintroduced on five reservations since 1997 (Cheyenne River, Lower Brule, and Rosebud Sioux Tribes in South Dakota; Gros Ventre and Assiniboine Tribes in Fort Belknap, Montana; and Northern Cheyenne Sioux Tribe in Montana). In all instances all pertinent tribal fish and wildlife regulations have been followed by project managers. Any subsequent reintroductions on tribal lands

will adhere to this policy, and project proponents will be advised that all applicable tribal regulations must be followed during reintroduction activities.

Black-footed Ferret Recovery Implementation Team: The BFFRIT is a coalition of approximately 30 Federal and State agencies, tribes, and conservation organizations that was established in 1996. It is not regulatory in nature, but provides the Service with recommendations related to conservation and recovery of the black-footed ferret, with individual members often participants in ferret reintroductions. The BFFRIT consists of a policy and resource support body (the Executive Committee (EC)) and six technical subcommittees (the Conservation Subcommittee (CS), the Outreach and Information Subcommittee (OIS), the Incentives Subcommittee (IS), the Prairie Dog Management Subcommittee (PDMS), the Sylvatic Plague Vaccine Subcommittee (SPVS), and the SSP® Subcommittee). Functions of the EC include addressing broad-based policy issues, resource support, political problem-solving, review of overall organizational structural efficiency, and recommendations for Service decision-making purposes. The CS provides a forum for discussion and recommendations regarding field conservation issues. The OIS supports public relation and education efforts for the Black-footed Ferret Recovery Program. The IS supports the development of incentives that encourage private landowner participation in ferret recovery. The PDMS focuses on potential boundary control issues at recovery sites. The SPVS is investigating the development and application of vaccines to combat plague. The SSP® Subcommittee provides a forum for cooperation in the management of captive breeding programs.

The organization and activities of these committees have changed over time, and their effectiveness has varied. However, it is important to have a strong and effective BFFRIT to maintain overall coordination between program partners. Although BFFRIT is not directly involved in regulatory actions, many team members work with their respective agencies and constituencies on issues pertinent to ferret management and recovery. Without the BFFRIT, progress toward ferret recovery would likely be more limited than it is at present. Once delisting criteria are achieved, the BFFRIT would continue to maintain remaining captive breeding facilities and plan and conduct post-delisting monitoring.

Prairie Dog Management: Few protective regulations are in place for the prairie dog (which the black-footed ferret depends upon for food and shelter) in comparison to the ferret. The most recent reviews by the Service for the black-tailed prairie dog (74 FR 63343; December 3, 2009), white-tailed prairie dog (69 FR 64889; November 9, 2004), and Gunnison's prairie dog (73 FR 6660; February 5, 2008) all concluded that inadequate regulatory mechanisms were not likely to cause any of these species to become threatened or endangered within the foreseeable future. Prairie dogs appear able to persist in smaller, more fragmented populations than were common historically. However, most prairie dog populations may no longer be large and stable enough (due to plague, poisoning, and the lack of proactive management) to support recovery of the ferret, and the lack of regulatory mechanisms to support large prairie dog populations is a threat. More protective regulations for prairie dogs, particularly those related to poisoning (discussed below under Factor E) and maintenance of large prairie dog complexes, could improve opportunities for ferret recovery at sites with marginal potential at present. Ferret recovery is biologically possible; however, the restoration of adequate prairie dog habitats will take more time, patience, and commitment by Federal, State, tribal, and private land managers than has occurred to date.

Proactive management of prairie dogs, with regard to maintenance of sufficient quantity and quality of prairie dog habitat to support black-footed ferret recovery, is critical. Support is needed from Federal and State agencies and tribal governments for prairie dog conservation and management. For example, new recovery projects could be undertaken on National Grasslands in Colorado, Kansas, Nebraska, New Mexico, Oklahoma, Texas, and Wyoming. Tribal lands represent some of the best remaining potential habitat for ferrets due to the complexities involved with recovering ferrets on other land ownerships. In addition, many tribal lands offer larger, less-developed habitat for ferrets and are subjected to less frequent or intense prairie dog control efforts than lands managed by other entities. Development of additional cooperative tribal, State, and Federal partnerships for ferret recovery is needed. The development of partnerships, reintroduction projects, and prairie dog conservation on private lands is also essential for future ferret recovery. Prairie dog control programs may be necessary at the boundary of

ferret recovery areas in order to maintain local support. A prototype of such an effort has been initiated in Logan County, Kansas; similar efforts may be essential at other sites as well. Prairie dog management requires careful monitoring to maintain a balance between recovery needs and landowner needs.

Black-tailed, white-tailed, and Gunnison's prairie dogs are not threatened by inadequate regulatory mechanisms because they can continue to persist in smaller, more fragmented populations if they do not succumb to plague. However, we consider the lack of regulatory mechanisms that conserve stable, relatively large prairie dog populations a high magnitude, imminent threat to black-footed ferret recovery at the present time. It may be the single, most limiting factor regarding successful recovery of the ferret. Without large, stable prairie dog complexes, ferret recovery in the wild cannot be achieved. The lack of regulatory mechanisms for prairie dogs would persist regardless of the listing status for the ferret. However, we believe that this threat can be ameliorated through the development and implementation of adequate conservation measures by affected tribal, State, and Federal agencies. For example, a conservation plan for the black-tailed prairie dog has been developed and is supported by most States within the range of the prairie dog. It established objectives with regard to the size and number of prairie dog complexes that should be maintained by each State. However, at this point, only three States (Colorado, South Dakota, and Wyoming) have met those objectives. These objectives need to be supported and achieved by most States.

The successful establishment of black-footed ferret recovery sites that result in the eventual downlisting and delisting of the species will require coordinated management of prairie dogs including: (1) the successful control of flea vectors that transmit plague, including development of appropriate vaccines; (2) increased partner participation through regulatory assurances; (3) boundary control of prairie dogs as needed, and (4) grazing management assistance when necessary. In the absence of ESA protections, appropriate management of prairie dogs will need to remain in effect.

Memorandum of Understanding: A Memorandum of Understanding was recently signed by the Service, the Natural Resources Conservation Service (NRCS), USGS,

Animal and Plant Health Inspection Service (APHIS) Wildlife Services, and the Western Association of Fish and Wildlife Agencies (WAFWA). Its purpose is to facilitate cooperative conservation efforts among the parties in concert with willing landowners so as to maintain ranch land in prairie habitats, and to maintain the livestock operations that they support, while providing for the conservation and recovery of several wildlife species associated with prairie dogs, especially the ferret. While participation in this MOU is voluntary, it indicates the intention of several federal and state agencies to continue to contribute to ferret recovery.

Other natural or manmade factors

Other natural or manmade factors affecting recovery of the black-footed ferret include: poisoning of its principal prey (prairie dogs), climate change, and genetic fitness of the ferret.

Poisoning: Poisoning of prairie dogs is regarded as a major factor in the historical decline of prairie dogs and black-footed ferrets (Forrest et al. 1985, Cully 1993, Forrest and Luchsinger 2005). Similar to many of the other factors limiting ferret recovery, poisoning can affect the ferret directly, through inadvertent secondary poisoning of the ferret caused by consumption of poisoned prairie dogs, or indirectly, through the loss of the prairie dog prey base. The historical estimate of prairie dog occupied habitat was approximately 100 million ac (40 million ha). Concerns regarding competition for available forage between livestock and prairie dogs led to the development of extensive government sponsored prairie dog poisoning programs early in the 20th century. Organized prairie dog control gained momentum from 1916–1920, when prairie dogs were poisoned on tens of millions of acres of western rangeland (Bell 1921). By the 1960s, prairie dog occupied habitat reached a low of approximately 1.4 million ac (570,000 ha) in the United States (Bureau of Sport Fisheries and Wildlife 1961, Berryman and Johnson 1973). However, our most recent estimate of prairie dog occupied habitat is approximately 3.7 million ac (1.5 million ha) (74 FR 63343, December 3, 2009; 69 FR 64889, November 9, 2004; 73 FR 6660, February 5, 2008), an increase of 250 percent from its low point.

From the late 1800s to the early 1940s, strychnine was the primary substance used to poison prairie dogs (Bell 1921). Between World War II and 1972, Compound 1080 was the preferred poison for prairie dog control. In 1972, Executive Order 11643 prohibited the use of certain toxicants that might cause secondary poisoning on Federal lands or in federally funded programs. This order was revoked by Executive Order 12342 in 1982. However, poisoning prairie dogs with strychnine and Compound 1080 did not resume. Zinc phosphide became the preferred poison for prairie dog control by 1976, and its use continues to the present (Hanson 1993, Forrest and Luchsinger 2005). In recent years, manufacturers have promoted the use of the anticoagulant rodenticides chlorophacinone (Rozol) and diphacinone (Kaput) for control of prairie dogs (Bruening 2007, Lee and Hygnstrom 2007). These chemicals pose a much greater risk than zinc phosphide of secondary poisoning to non-target wildlife that prey upon prairie dogs, such as the black-footed ferret (Erickson and Urban 2004).

Poisoning on or adjacent to black-footed ferret recovery sites is of particular concern. The legal use of Rozol has occurred at one reintroduction site (Logan County, Kansas), and its illegal use occurred at another reintroduction site (Rosebud Indian Reservation, South Dakota). It is not known if any ferret mortalities occurred as a direct result of these two incidences. The ability to verify impacts to non-target species such as the ferret is quite limited due to the fossorial nature of ferrets, vegetative cover, possible consumption of poisoned ferrets by other predators, and delayed action of the rodenticide. Only a very small percentage of animals that die from secondary poisoning are ever located. However, the loss of prairie dog occupied habitat that resulted from these poisoning incidences reduced the quality and quantity of habitat available to support ferrets. In May, 2009, the EPA authorized the use of Rozol throughout the range of the black-tailed prairie dog via a Federal Insecticide, Fungicide, and Rodenticide Act Section 3 registration. We have recommended that the EPA withdraw its registration for Rozol and not issue a registration for Kaput (Gober 2006, Slack 2006, Arroyo 2009). The Western Association of Fish and Wildlife Agencies similarly requested that EPA reconsider use of anticoagulants for prairie dog control (Koch 2008). We have also funded two research projects to further investigate the secondary impacts from the use of anticoagulants for

control of prairie dog—one project is a laboratory study by the National Wildlife Research Center studying the retention time of Rozol in prairie dogs exposed to the poison; the other project is a study by the U.S. Geological Survey characterizing non-target hazards following poisoning of prairie dogs in the field. However, Rozol use to control prairie dogs is now legal in most of the western United States.

With the decline in prairie dogs, there was a concurrent decline in black-footed ferrets. Poisoning, if thorough enough, may result in permanent loss of prairie dogs, such as occurred in the extirpation of black-tailed prairie dogs in Arizona, though they were later reintroduced (Hoffmeister 1986, Arizona Game and Fish Department 1988). This loss can preclude ferret recovery opportunities. More typically, prairie dog numbers are reduced temporarily, but long enough for ferrets to disappear.

Prairie dog poisoning occurs on private, State, tribal, and Federal lands rangewide, but with more limited and localized efforts than occurred in past decades. The total acreage of prairie dog occupied habitat being poisoned annually has decreased dramatically since the 1960s. However, the amount of prairie dog occupied habitat available for poisoning has also been reduced, from approximately 100 million ac (40 million ha) historically to 3.7 million ac (1.5 million ha) at present. Consequently, the percentage of prairie dog occupied habitat being poisoned on an annual basis remains relatively high. For example, the South Dakota Bait Station, which is only one of several sources for zinc phosphide, has sold enough of this poison since 2004 (over 1 million pounds (400,000 kilograms)) to potentially poison all prairie dog occupied habitat in the United States (Kempema 2007, Larson 2008b). This scenario does not address the possibility of individuals stockpiling poison, re-applying poison at the same site, or applying poison at greater than the recommended rates. Poisoning of prairie dogs remains a concern with regard to impacts to black-footed ferrets.

Prairie dog control to address boundary encroachment issues from expanding prairie dog acreage at the Conata Basin black-footed ferret reintroduction site in South Dakota began in 2004 and peaked in 2006, with a 94 percent reduction in toxicant use by 2009 (Griebel 2010). The USFS, in response to local concerns about the impacts of drought and prairie

dogs, suggested a need to poison prairie dogs in interior portions of the ferret reintroduction area at Conata Basin in order to reduce alleged prairie dog damage to native grasslands and balance multiple use needs (U.S. Forest Service 2008). Proposed poisoning in the interior of the site could significantly reduce the viability of this ferret recovery site, reduce the number of wild-born kits available for translocation to other recovery sites, and slow progress towards the achievement of downlisting and delisting goals. The decision whether to allow expanded toxicant use on prairie dog colonies in the interior portion of Conata Basin has been deferred due to a recent plague epizootic.

We consider the poisoning of prairie dogs with zinc phosphide at black-footed ferret recovery sites a medium magnitude, imminent threat to ferret recovery at the present time due to the loss of habitat. We consider the poisoning of prairie dogs at ferret recovery sites with anticoagulants a high magnitude, imminent threat to ferret recovery at the present time due to the loss of habitat and the potential for secondary poisoning of the ferret. We consider large-scale poisoning of prairie dogs that curtails potential ferret habitat for future recovery sites a low magnitude, imminent threat to ferret recovery. The threat due to poisoning could be ameliorated by adequate regulatory mechanisms that provide management objectives for a sufficient amount of prairie dog habitat to achieve ferret recovery and limit the type of poison used at ferret recovery sites so as to preclude secondary impacts. In the absence of ESA protections, management of prairie dog poisoning would need to continue.

Climate change: Climate change could potentially impact the black-footed ferret. According to the Intergovernmental Panel on Climate Change (IPCC 2007), “Warming of the climate system is unequivocal, as is now evident from observations of increases in global average air and ocean temperatures, widespread melting of snow and ice, and rising global average sea level.” Average Northern Hemisphere temperatures during the second half of the 20th century were very likely higher than during any other 50-year period in the last 500 years and likely the highest in at least the past 1,300 years (IPCC 2007). It is very likely that over the past 50 years cold days, cold nights, and frosts have become less frequent over most land areas, and hot days and hot nights have become more frequent (IPCC 2007). It is likely that heat waves have become more frequent over

most land areas, and the frequency of heavy precipitation events has increased over most areas (IPCC 2007).

Changes in the global climate system during the 21st century are very likely to be larger than those observed during the 20th century (IPCC 2007). For the next two decades, a warming of about 0.2 degrees Celsius (°C) (0.4 degrees Fahrenheit (°F)) per decade is projected (IPCC 2007). Afterward, temperature projections increasingly depend on specific emission scenarios (IPCC 2007). Various emissions scenarios suggest that by the end of the 21st century, average global temperatures are expected to increase 0.6–4.0 °C (1.1–7.2 °F), with the greatest warming expected over land (IPCC 2007).

The IPCC (2007) report outlines several scenarios that are virtually certain or very likely to occur in the 21st century including: (1) over most land, there will be warmer and fewer cold days and nights, and warmer and more frequent hot days and nights, (2) areas affected by drought will increase, and (3) the frequency of warm spells/heat waves over most land areas will likely increase. The IPCC concludes that the resiliency of many ecosystems is likely to be exceeded this century by an unprecedented combination of climate change, associated disturbances (e.g., flooding, drought, wildfire, and insects), and other global drivers. With medium confidence, IPCC predicts that approximately 20–30 percent of plant and animal species assessed so far are likely to be at an increased risk of extinction if increases in global average temperature exceed 1.5–2.5 °C (3–5 °F).

The black-footed ferret, along with its habitat, likely will be affected in some manner by climate change. A shift in the species' geographic range may occur due to an increase in temperature and drought. Though drought could reduce vegetation and therefore prairie dog abundance in some locations, the net effect these changes will have on the distribution and abundance of ferret habitat is unclear. However, climate change would likely not pose as great a risk to ferrets and their habitat as it would to species in more restricted polar, coastal, or montane ecosystems.

A strong relationship between plague outbreaks and climatic variables has been established (Parmenter et al. 1999, Ensore et al. 2002, Stapp et al. 2004, Ray and

Collinge 2005, Stenseth et al. 2006, Snall et al. 2008). The key climatic variables appear to be maximum daily summer temperature (plague is enhanced by cooler summer temperatures) and late winter precipitation (plague is enhanced by increased precipitation).

Modeling efforts indicate that shifts in plague distribution may be a result of shifts of pathogen, vector, or host distribution following climate change (Nakazawa et al. 2007). The authors also suggest that the distribution of plague may expand north and east. The recent expansion of plague into South Dakota supports this theory. However, variables associated with climate change and increased plague activity conflict. Plague is enhanced by cooler summer temperatures and by increased precipitation. With climate change, summer temperatures are anticipated to be warmer rangewide and precipitation is anticipated to decrease throughout much of the ferret's historical range. Consequently, the extent to which plague may shift due to climate change versus expand or contract is supposition. The species is adaptable to a wide array of climes, as evidenced by a geographic range that includes 12 States, Canada, and Mexico. Unlike vulnerable species in polar, coastal, and montane ecosystems, we believe that the ferret could accommodate to a possible shift in climate change or to a possible shift in plague distribution.

We do not consider climate change a threat to black-footed ferret recovery at the present time. Although the ferret will likely be affected by climate change, and drought could reduce vegetation, prairie dogs, and consequently ferrets, it is not apparent that a net loss in occupied habitat or a significant impact to the status of the species will result. There is no indication that climate change has reduced ferret survival or reproduction.

Genetic fitness: Genetic fitness of the black-footed ferret has been a concern in the captive breeding program due to the extreme bottleneck that the species experienced (Groves and Clark 1986, U.S. Fish and Wildlife Service 1988, CBSG 1992, Hutchins et al. 1996, CBSG 2004, Garelle et al. 2006, Howard et al. 2006, Wisely 2006). The current captive breeding program began with the lineage of seven founder animals from the last wild population at Meeteetse, Wyoming (Hutchins et al. 1996, Wisely 2006). The magnitude of loss of genetic diversity was exacerbated by the especially isolated nature

of this last population. Meeteetse is located on the periphery of the historical ferret range and was likely a refugium during the last glacial period that subsequently remained isolated (Wisely 2006).

Two types of genetic effects can impact a population's survival: (1) inbreeding depression, caused by increased genetic homozygosity (uniformity) and the subsequent expression of deleterious genes; and (2) genetic drift, the random loss of genetic diversity in small populations (Clark 1989). In some species, genetic diversity of less than 90 percent of that in founder populations has been associated with compromised reproduction due to lower birth weights, smaller litter size, and greater neonatal mortality. Genetic diversity in the current black-footed ferret population is estimated to be 87 percent of that in the founder population (Garelle et al. 2006). Some periodic abnormalities observed in captive ferrets (reduced sperm viability, renal aplasia, and kinked tails) may be a result of inbreeding (Hutchins et al. 1996, Howard et al. 2006). A primary goal of the SSP® is to optimize genetic management of the captive population by maintaining 80 percent of the genetic diversity present in the founder population for the next 25 years (Marinari and Kreeger 2006).

The genetic uniformity of the black-footed ferret is unprecedented and rivaled by perhaps only one other carnivore, the African cheetah (*Acinonyx jubatus*) (Wisely 2006). However, carnivores typically have less genetic variability than other mammalian taxa (Kilpatrick et al. 1986). Felines are more susceptible to inbreeding than most taxa (Wisely 2006), and yet the cheetah continues to survive in the wild. The use of artificial insemination in ferret captive breeding programs has been effective and has helped preserve genetic diversity from an underrepresented male lineage (Howard et al. 2006). Approximately 7,500 ferret kits have been produced at captive breeding facilities (Marinari 2011). Ferret populations appear to flourish despite reduced genetic diversity where ample plague-free habitat exists (Wisely 2006). The species will likely persist with continued careful management of remaining genetic resources (Wisely 2006).

Successful reproduction has been documented in black-footed ferrets at almost all reintroduction sites. In 1999, a study detected no difference in genetic diversity between

captive-reared releases and their wild descendants at UL Bend, Montana and Conata Basin, South Dakota reintroduction sites (Wisely 2006). Nevertheless, the translocation of wild-born ferrets that have been exposed to natural selection processes that do not occur in a captive breeding program may aid with overall recovery and is being utilized in the establishment of new reintroduction sites. Ferret recovery has consistently emphasized releasing captive-bred animals to the wild as quickly as possible, as well as encouraging the translocation of wild-born ferrets to initiate new recovery sites.

Smaller populations are more susceptible to extinction from various causes (Shaffer 1981). In order to address the risks from loss of genetic diversity, and other possible threats such as disease, poisoning, and natural catastrophes, the downlisting and delisting criteria require a minimum number of black-footed ferrets at reintroduction sites, as well as multiple sites distributed throughout the historical range of the species. Captive ferret populations are also widely distributed at multiple facilities in order to protect against unforeseen events. These criteria are discussed in more detail in the following section on “Recovery.”

We do not consider genetic fitness a threat to black-footed ferret recovery at the present time, inasmuch as successful reproduction has occurred in the wild at all reintroduction sites. Although the ferret experienced a severe bottleneck in the 1980s, the species will likely persist with continued management of remaining genetic resources. In the absence of ESA protections, efforts to maximize genetic diversity would continue through captive breeding policies developed by the SSP® Subcommittee.

The following table summarizes factors affecting the black-footed ferret and the magnitude and immediacy of any threats.

Table 4. Black-footed ferret threat matrix

Listing Factor	Stressor	Magnitude	Immediacy
Present or threatened destruction, modification or curtailment of habitat or range	Present or threatened destruction of habitat or range via conversion of rangeland to cropland or urbanization	Not a threat	Not a threat
Overutilization for commercial, recreational, scientific, or educational purposes	Commercial use of ferrets	Not a threat	Not a threat
	Scientific, educational, and recreational shooting of prairie dogs	Not a threat with continued management	Not a threat with continued management
Disease or predation	Canine distemper	Not a threat with continued management	Not a threat with continued management
	Sylvatic plague (both direct impact to ferrets and indirect impact of modification of habitat through loss of prairie dogs)	Medium, additional management needed	Imminent
	Predation	Not a threat	Not a threat
Inadequacy of existing regulatory mechanisms	Prairie dog management sufficient for ferrets	High, additional management needed	Imminent
	Other regulatory mechanisms	Not a threat with continued management	Not a threat with continued management
Other natural or manmade factors	Poisoning of prairie dogs at ferret sites (with zinc phosphide)	Medium, additional management needed	Imminent
	Poisoning of prairie dogs at ferret sites (with anticoagulants)	High, additional management needed	Imminent
	Present or threatened curtailment of potential	Low, additional management	Imminent

	habitat or range due to conflicts with large-scale poisoning	needed	
	Climate Change	Not a threat	Not a threat
	Genetic fitness	Not a threat, with continued management	Not a threat, with continued management

PART II. RECOVERY

This section presents a strategy to recover the black-footed ferret, including actions and specific tasks that must be undertaken.

RECOVERY GOAL

The goal of the actions proposed in this recovery plan is to recover the black-footed ferret to the point where the species can be reclassified to a threatened status (downlisted) and ultimately removed from the lists of Threatened and Endangered Species (delisted). Downlisting could be achieved by 2020 if aggressive reintroduction efforts continue and conservation measures produce positive responses at most reintroduction sites. We believe that delisting could be realized by 2040 if the tasks specified in the following section are accomplished. Moreover, we believe that delisting could occur by 2022, if current and additional recovery actions were accelerated to facilitate six new reintroduction sites per year annually for the next 10 years.

RECOVERY CRITERIA

The ESA establishes policies and procedures for identifying, listing, and protecting species of wildlife and plants that are endangered or threatened with extinction. The ESA defines an “endangered species” as “any species which is in danger of extinction throughout all or a significant portion of its range.” A “threatened species” is defined as

“any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range.”

The goal of this plan is to recover the black-footed ferret such that it no longer meets the ESA definition of threatened and can be removed from the Federal List of Endangered and Threatened Wildlife (i.e., delisted). Changes in status require consideration of the same five categories of threats specified in section 4(a)(1) of the ESA. These factors are:

Factor A – the present or threatened destruction, modification, or curtailment of its habitat or range;

Factor B – overutilization for commercial, recreational, scientific, or educational purposes;

Factor C – disease or predation;

Factor D – the inadequacy of existing regulatory mechanisms; and

Factor E – other natural or manmade factors affecting its continued existence.

As required by section 4(f) of the ESA, this recovery plan includes objective, measurable criteria that, when met, will allow the species or populations to be removed from the Federal List of Threatened and Endangered Species. Section 4(f) of the ESA also requires that recovery plans include site-specific management actions thought necessary to achieve these criteria as well as provide time and cost estimates.

It is important to note that recovery plans are not regulatory documents and are instead intended to provide guidance to the Service, States, tribes and other partners on methods of minimizing threats to listed species and on criteria that may be used to determine when recovery is achieved. There are many paths to accomplishing recovery of a species and recovery may be achieved without all criteria being fully met. For example, one or more criteria may be exceeded while other criteria may not be accomplished. In that instance, the Service may judge that the threats have been minimized sufficiently, and the species is robust enough to reclassify from endangered to threatened or to delist. In other cases, recovery opportunities may be recognized that were not known at the time the recovery plan was finalized. These opportunities may be used instead of methods identified in the

recovery plan. Likewise, information on the species may be learned that was not known at the time the recovery plan was finalized. The new information may change the extent that criteria need to be met for recognizing recovery of the species. Recovery of a species is a dynamic process requiring adaptive management that may, or may not, fully follow the guidance provided in a recovery plan.

Downlisting Criteria: To reclassify the black-footed ferret from endangered to threatened status, the following criteria, originally established in the 1988 Recovery Plan, and expanded (as noted in italics) must be met:

- Conserve and manage a captive breeding population of black-footed ferrets with a minimum of 280 adults (*105 males, 175 females*) distributed among at least three facilities.
- Establish free-ranging black-footed ferrets totaling at least 1,500 breeding adults, in 10 or more populations, *in at least 6 of 12 States within the historical range of the species*, with no fewer than 30 breeding adults in any population.
- *Maintain these population objectives for at least three years prior to downlisting.*
- *Maintain approximately 247,000 ac (100,000 ha) of prairie dog occupied habitat at reintroduction sites by planning and implementing actions to manage plague and conserve prairie dog populations.*

Delisting Criteria: Delisting may occur when the following recovery criteria are met:

- Conserve and manage a captive breeding population of black-footed ferrets with a minimum of 280 adults (105 males, 175 females) distributed among at least three facilities.
- Establish free-ranging black-footed ferrets totaling at least 3,000 breeding adults, in 30 or more populations, with at least one population in each of at least 9 of 12 States within the historical range of the species, with no fewer than 30 breeding adults in any population, and at least 10 populations with 100 or more breeding adults.
- Maintain these population objectives for at least three years prior to delisting.

- Maintain approximately 494,000 ac (200,000 ha) of prairie dog occupied habitat at reintroduction sites by planning and implementing actions to manage plague and conserve prairie dogs.
- Complete and implement a post-delisting monitoring plan, in cooperation with the States and tribes, to ensure recovery goals are maintained.

After Delisting:

- Conserve and manage a reduced captive breeding population of black-footed ferrets in order to maintain knowledge, incorporate developing technologies, and address potential population extinctions.

The following table describes which threats are addressed by each of the downlisting and delisting criteria and briefly summarizes how those threats will be ameliorated.

Table 5. Downlisting and delisting criteria and threats addressed

Criteria	Downlisting or Delisting	Threat Addressed	Explanation
Conserve and manage a captive breeding population among at least 3 facilities	Both	Factor C (Plague)	Multiple facilities minimize risk of plague outbreak affecting captive ferrets, provide ferrets for disease research, and provide ferrets for augmentation at plague impacted sites.
		Factor D (Prairie dog management)	Captive population provides ferrets for release as prairie dog management improves existing reintroduction sites and creates new sites.
		Factor E (Poisoning of prairie dogs)	Captive population provides ferrets for release as poisoning becomes better regulated.
		Factor B (Use for scientific or educational purposes)	Captive population provides excess ferrets under SSP® protocol.
		Factor C (Distemper)	SSP® protocol includes vaccination of captive ferrets.
		Factor E (Genetic fitness)	SSP® protocol addresses maximizing genetic diversity in captive populations.
Establish free-ranging ferrets of $\geq 1,500$ adults, in ≥ 10 populations, in ≥ 6 States, with ≥ 30 breeding adults in any population	Downlisting	Factor C (Plague)	This number and distribution of ferrets would minimize likelihood of an epizootic affecting multiple populations simultaneously.
		Factor D (Prairie dog management)	This number and distribution of ferrets would maximize flexibility of various management options.
		Factor E (Poisoning prairie dogs)	This number and distribution of ferrets would minimize risk of affecting multiple populations simultaneously.

		Factor B (Recreational shooting of prairie dogs)	This number and distribution of ferrets would minimize risk of affecting multiple populations regulated by different States, tribes, and Federal agencies.
		Factor D (Other regulatory mechanisms)	This number and distribution of ferrets would increase flexibility of States, tribes, and Federal agencies using their authorities to manage ferrets on their lands.
		Factor E (Genetic fitness)	Multiple sites of adequate size distributed across the range will help maintain genetic diversity.
Maintain these population objectives for ≥ 3 years	Both	Factor C (Plague)	This will provide evidence of population stability in the presence of plague.
		Factor D (Prairie dog management)	This will provide evidence of population stability under current management.
		Factor E (Poisoning prairie dogs)	This will provide evidence of population stability in the presence of any poisoning.
		Factor B (Recreational shooting of prairie dogs)	This will provide evidence of continued active management by States, tribes, and Federal agencies.
		Factor D (Other regulatory mechanisms)	This will provide evidence of continued active management by States, tribes, and Federal agencies.
Maintain approximately 247,000 ac (100,000 ha) of prairie dog occupied habitat	Downlisting	Factor C (Plague)	Multiple sites of adequate size distributed across the range will minimize likelihood of an epizootic affecting multiple populations simultaneously and add management flexibility.

at reintroduction sites by planning and implementing actions to manage plague and conserve prairie dog populations.		Factor D (Prairie dog management)	Multiple sites of adequate size distributed across the range will provide adequate habitat for current and future reintroduction sites.
Establish free-ranging ferrets of $\geq 3,000$ adults, in ≥ 30 populations, in ≥ 9 States, with ≥ 30 breeding adults in any population, and ≥ 10 populations with ≥ 100 breeding adults	Delisting	Factor E (Poisoning prairie dogs)	Multiple sites of adequate size distributed across the range will add management flexibility by providing adequate habitat for current and future reintroduction sites.
		Factor E (Genetic fitness)	Multiple sites of adequate size distributed across the range will help maintain genetic diversity.
		Factor C (Plague)	This number and distribution of ferrets would minimize likelihood of an epizootic affecting multiple populations simultaneously.
		Factor D (Prairie dog management)	This number and distribution of ferrets would maximize flexibility of various management options.
		Factor E (Poisoning prairie dogs)	This number and distribution of ferrets would minimize risk of affecting multiple populations simultaneously.
		Factor B (Recreational shooting of prairie dogs)	This number and distribution of ferrets would minimize risk of affecting multiple populations regulated by different States, tribes, and Federal agencies.
		Factor D (Other regulatory mechanisms)	This number and distribution of ferrets would increase flexibility of States, tribes, and Federal agencies using their authorities to manage ferrets on their lands.
		Factor E (Genetic fitness)	Multiple sites of adequate size distributed across the range will help maintain genetic diversity.

Maintain approximately 494,000 ac (200,000 ha) of prairie dog occupied habitat at reintroduction sites by planning and implementing actions to manage plague and conserve prairie dogs.	Delisting	Factor C (Plague) Factor D (Prairie dog management) Factor E (Poisoning prairie dogs) Factor E (Genetic fitness)	Multiple sites of adequate size distributed across the range will minimize likelihood of an epizootic affecting multiple populations simultaneously and add management flexibility. Multiple sites of adequate size distributed across the range will provide adequate habitat for current and future reintroduction sites. Multiple sites of adequate size distributed across the range will add management flexibility by providing adequate habitat for current and future reintroduction sites. Multiple sites of adequate size distributed across the range will help maintain genetic diversity.
Complete and implement a post-delisting monitoring plan, in cooperation with the States and tribes, to ensure recovery goals are maintained	Delisting	All threats	A robust monitoring plan (including a regulatory framework) developed by the Service and State, tribal, and Federal partners will ensure recovery is maintained after the species is delisted.
Conserve and manage a reduced captive breeding population of black-footed ferrets in order to maintain knowledge, incorporate	Post-delisting	Factor C (Plague)	A post-delisting captive population will allow: (1) opportunity for continued research into better disease management and (2) ability to more quickly augment wild populations if needed following an epizootic or other unforeseen stochastic event.

developing technologies, and address potential population extinctions		Factor E (Genetic fitness)	Captive population will allow opportunity for continued research into maintaining genetic diversity.
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Justification for the Downlisting and Delisting Goals

Captive Breeding Population: Captive black-footed ferret breeding populations are currently housed at the U.S. Fish and Wildlife Service National Black-footed Ferret Conservation Center near Wellington, Colorado; the Cheyenne Mountain Zoological Park in Colorado Springs, Colorado; the Louisville Zoological Garden in Louisville, Kentucky; the Smithsonian Biology Conservation Institute in Front Royal, Virginia; the Phoenix Zoo in Phoenix, Arizona; and the Toronto Zoo in Toronto, Ontario (Marinari and Kreeger 2006). The Henry Doorly Zoo in Omaha, Nebraska previously participated in captive breeding efforts. In addition to the principal captive populations, intermittent field breeding facilities have been managed by the Arizona Fish and Game Department in Seligman, Arizona, by the Turner Endangered Species Fund in Cimarron, New Mexico (Garelle et al. 2006), and by the Bowdoin National Wildlife Refuge in Malta, Montana. More than 50 percent of all captive ferrets are housed at the National Black-footed Ferret Conservation Center (Marinari and Kreeger 2006).

The 1988 Black-footed Ferret Recovery Plan set a goal of 200 breeding adults in captive populations by 1991 to ensure adequate genetic fitness of captive ferret populations and provide surplus animals for release. In 1996, the Small Carnivore Taxon Advisory Group (SCTAG) of the AZA recommended modification of this goal to at least 240 ± 35 breeding adults of optimum sex ratio (90 male:150 female), with surplus animals provided for reintroduction purposes (Hutchins et al. 1996). In 2004, the SSP® recommended that consideration be given to further increasing the size of the captive population in order to promote retention of gene diversity and increase production potential (CBSG 2004). Thereafter, SCTAG recommended a total target captive population of 350 individuals (Garelle et al. 2006). However, the target population of

350 includes non-reproductive display animals and the possibility of future increases in the number of breeding facilities.

The captive population has expanded to approximately 280 animals at present. We consider this number of animals necessary to ensure maintenance of the 240 animals previously specified. We believe that the emphasis of our recovery strategy should be on expanding black-footed ferret recovery in the wild. Therefore, further expansion of the captive population is not appropriate because it would result in fewer animals being released into the wild. The potential limited advantages of expanding the captive program are also offset by the added financial costs to the program. As previously explained, the more time that ferrets spend in captivity, the more that wild behaviors are lost, and the more difficult reintroduction becomes. Additionally, as wild populations continue to expand, the translocation of wild-born kits to developing reintroduction areas will become increasingly important. Survivorship of wild-born kits is much greater than that of reintroduced animals of captive origin. Therefore, the importance of maintaining a large captive population will diminish somewhat as the availability of wild kits increases. Consequently, we adopt a goal of a minimum of 280 captive breeding adults for the purpose of this recovery plan.

The black-footed ferret was considered possibly extinct twice in recent years. Therefore, we do not intend to immediately disband the captive breeding program following delisting. There will not be a need for as many captive ferrets after the species is delisted. However, a reduced number of animals should be maintained at some facilities to enhance opportunities for continued research, particularly related to plague and genetic fitness. Additionally, captive animals could be used to augment wild populations in the event of a plague epizootic or other unforeseen stochastic event.

Free-ranging Population: The goal of the 1988 Recovery Plan was to establish 1,500 breeding adult black-footed ferrets in the wild in 10 or more populations, with a minimum of 30 adults in each population. An additional qualitative goal was to space these populations as widely as possible across the historical range of the species. This distribution would provide for multiple recovery opportunities (and partners) and serve as

a risk management strategy to guard against adverse impacts and potential periodic population losses.

The goal of 1,500 breeding adult ferrets was derived based upon a general agreement among geneticists that populations require an effective size of approximately 500 breeding adults to retain genetic heterozygosity sufficient for evolution in an idealized or carefully controlled population (U.S. Fish and Wildlife Service 1988). The 1988 Recovery Plan further noted that in wild populations, which experience less control, the actual number of breeding adults ranges from 20-50 percent of all potential breeders. Consequently, we assume that approximately one-third of all potential breeders will actually breed in a given year due to adverse individual and population impacts. Therefore, a goal of 1,500 breeding adults was derived. This will ensure that at least 500 adult ferrets will actually breed in a given year. Due to habitat fragmentation, inter-population transfers of individuals will likely be necessary in perpetuity.

These downlisting goals are readopted for this revision of the species' recovery plan but are further refined. Specifically, jurisdictional entities by State are encouraged to provide contributions to recovery goals in proportion to the amount of historical ferret habitat (i.e., prairie dog colonies) that once occurred on these lands (see subsequent discussion of "Recovery Guidelines by State").

Reintroductions in Mexico and Canada are also important in reestablishing black-footed ferret populations across the species' historical range proportional to the distribution and abundance of historical prairie dog habitat. However, recovery opportunities outside of the United States are restricted due to limited potential habitat that is at the extreme periphery of the ferret's historical range. Based upon the most recent estimates of prairie dog habitat (74 FR 63343, December 3, 2009; 69 FR 64889, November 9, 2004; and 73 FR 6660, February 5, 2008), approximately 41,000 ac (16,600 ha), or one percent of the total prairie dog occupied habitat rangewide, occurs in Canada and Mexico. Additionally these lands are not managed under U.S. regulatory mechanisms; consequently, it is more difficult to engage agencies with regard to regulatory mechanisms. Therefore, we do not consider them in the numeric downlisting and delisting criteria for wild populations.

However, we do consider them with regard to maximizing recovery throughout the historical range of the ferret.

We believe that the 1,500 breeding adult black-footed ferrets downlisting criteria and 3,000 breeding adults delisting criteria are achievable with proactive management actions, including completion of the tasks proposed in the section, “Recovery Actions.” These goals appear to be consistent with methodologies explored by both Gedir et al. (2004) and Ray (2006). These methodologies used guidelines established by the International Union for the Conservation of Nature to identify recovery needs for various species. For both of these methodologies, the degree of management effort needed was inversely proportional to the population size required to ensure conservation. In other words, lower, less stringent recovery goals are possible if more conservation assurances are provided. We believe the recovery criteria for the ferret strike a balance between the difficulties of establishing more large populations in the wild and the greater management needs associated with maintaining fewer and/or smaller wild populations.

The scientific community has debated whether a single large or several small reserves are more appropriate for conserving biodiversity in a fragmented habitat. Initially, a single large reserve was considered preferable; however, more recently, ecologists have concluded that either management approach can be appropriate (Soule and Simberloff 1986). The authors note that several small reserves can contain as many individuals as a single large one. Reserves should be large enough to sustain a population, and there should be many of them in order to minimize the probability of extinction due to any of threats facing the species (Soule and Simberloff 1986). Recovery criteria for the black-footed ferret address these concerns by requiring a minimum number of 30 breeding adults at each of many widely distributed sites. These scattered reintroduction sites will be managed as a metapopulation through immigration and emigration at a few adjacent sites as well as through translocation of wild-born ferrets at more widely separated sites.

Black-footed ferret reintroduction efforts started in 1991 and will continue in the future. There have been ferret reintroduction efforts at 20 different sites over the past 22 years. For the purpose of evaluating reintroduction efforts collectively, the relative success of

these sites was categorized in Table 2 as successful, improving, marginal, unsuccessful, or recent (too new to adequately assess). It is important to recognize that this basic categorization is current as of the date of this recovery plan, but can change quickly. Two reintroduction sites that were thought to be doing poorly in the past have shown substantial growth in recent years. The ferret population of Shirley Basin, Wyoming was regarded as unsuccessful a few years ago, but is considered large and successful today. Similarly, Badlands National Park, South Dakota has improved markedly in the past 2–3 years. Conversely, some successful sites could falter if disease or other factors affect habitat quality. Additionally, some currently unsuccessful sites may show promise in the future with progressing innovation, such as disease vaccines.

The availability of suitable reintroduction sites is a key limiting factor on the rate and success of black-footed ferret recovery. Estimates of large potential reintroduction areas available for ferret recovery efforts range from 3–5 (Lockhart et al. 2006, Luce 2006). However, Luce (2008) suggests that there are possibly 181 sites throughout the historical range of the ferret with intermediate potential (available in the next 3–10 years) for ferret reintroduction. These intermediate sites would require increased management to enhance occupied prairie dog habitat before ferrets could be reintroduced.

The precise total number of breeding adult black-footed ferrets currently extant in the wild is unknown because of monitoring limitations. However, we estimate that a minimum of 274 breeding adult ferrets occurred in the wild in 2012 (Table 3). Accordingly, it appears that downlisting efforts may be 40 percent complete with regard to establishing 10 successful populations and approximately 18 percent complete with regard to the goal of 1,500 breeding adults (see Tables 2 and 3). Approximately 1,230 additional breeding adults are needed at existing or new sites to meet the downlisting goals. It has taken 20 years of reintroduction efforts to reach this point in ferret recovery. Accordingly, we are modifying the year of achieving downlisting goals estimated in the 1988 Recovery Plan from 2010 to 2020. Additionally, we estimate meeting delisting goals by 2040. These estimates assume continued progress similar to what has been achieved in recent years. More aggressive recovery efforts could result in delisting by 2022.

To inform our recovery criteria, we determined the amount of prairie dog occupied habitat needed to achieve recovery of the black-footed ferret. Approximately 75 ac (30 ha) of black-tailed prairie dog occupied habitat or approximately 100–150 ac (40–60 ha) of white-tailed or Gunnison’s prairie dog occupied habitat are required to support one female black-footed ferret (Biggins et al. 2006). Male ferrets have overlapping ranges with female ferrets and do not require additional prairie dog habitat beyond that considered for the females (Biggins et al. 2006). The male:female sex ratio in wild ferrets at Meeteetse was approximately 1:2 (Forrest et al. 1988). At Conata Basin, South Dakota, at least 146 adults (including 97 females) were estimated to occur on 21,000 ac (8,500 ha) in 2009. This approximates the previously reported sex ratio. However, this equates to 1 female per 216 ac (88 ha), which is nearly 3 times the acreage anticipated by Biggins et al. (2006). There are many possible explanations for this higher than anticipated acreage including undercounting ferrets, climatic factors, poisoning, and disease. In recognition of these variables, we suggest that a more conservative estimate of black-tailed prairie dog habitat required to support ferrets should be 225 ac (90 ha) per female ferret based upon the Conata Basin data, or 3 times the 75 ac (30 ha) estimated by Biggins et al. (2006). Using an average of 125 ac (50 ha) of white-tailed and Gunnison’s prairie dog habitat required to support one female black-footed ferret (Biggins et al. 2006), a similar three-fold adjustment would result in an estimate of 375 ac (150 ha) needed to support a female ferret in white-tailed or Gunnison’s prairie dog habitat.

A population of 1,500 wild adult black-footed ferrets could be assumed to contain approximately 1,000 females. Eighty-five percent of ferrets are anticipated to occur in black-tailed prairie dog habitat (850 females). Therefore, downlisting may require approximately 191,000 ac (77,000 ha) of black-tailed occupied prairie dog habitat (850 female ferrets x 225 ac/90 ha per female ferret) and 56,000 ac (23,000 ha) of white-tailed and Gunnison’s habitat (150 female ferrets x 375 ac/150 ha per female ferret). This represents a minimum of 247,000 ac (100,000 ha) of prairie dog occupied habitat to achieve downlisting of the ferret. A similar calculation would result in a minimum of 494,000 ac (200,000 ha) of prairie dog occupied habitat to achieve delisting of the ferret. We recognize that these acreage figures may change if further monitoring determines that

ferrets require less habitat than our conservative approach estimates. To provide some perspective on the size of the area necessary for recovery, delisting could be supported by careful management of approximately 15 percent of existing prairie dog occupied habitat, which is 0.5 percent of lands within the ferret’s historically occupied habitat, or 0.08 percent of lands within the ferret’s historical range. The intent of this discussion is to point out that recovery of ferrets will not require that more lands be occupied by prairie dogs than at present, but it will require better management of existing prairie dog occupied habitat.

The following figure illustrates the past rate of recovery and the average future rate needed to achieve downlisting and delisting goals in the suggested timeframe. It should be noted that in a real world situation black-footed ferret and prairie dog populations will fluctuate from year to year due to sylvatic plague and other factors.

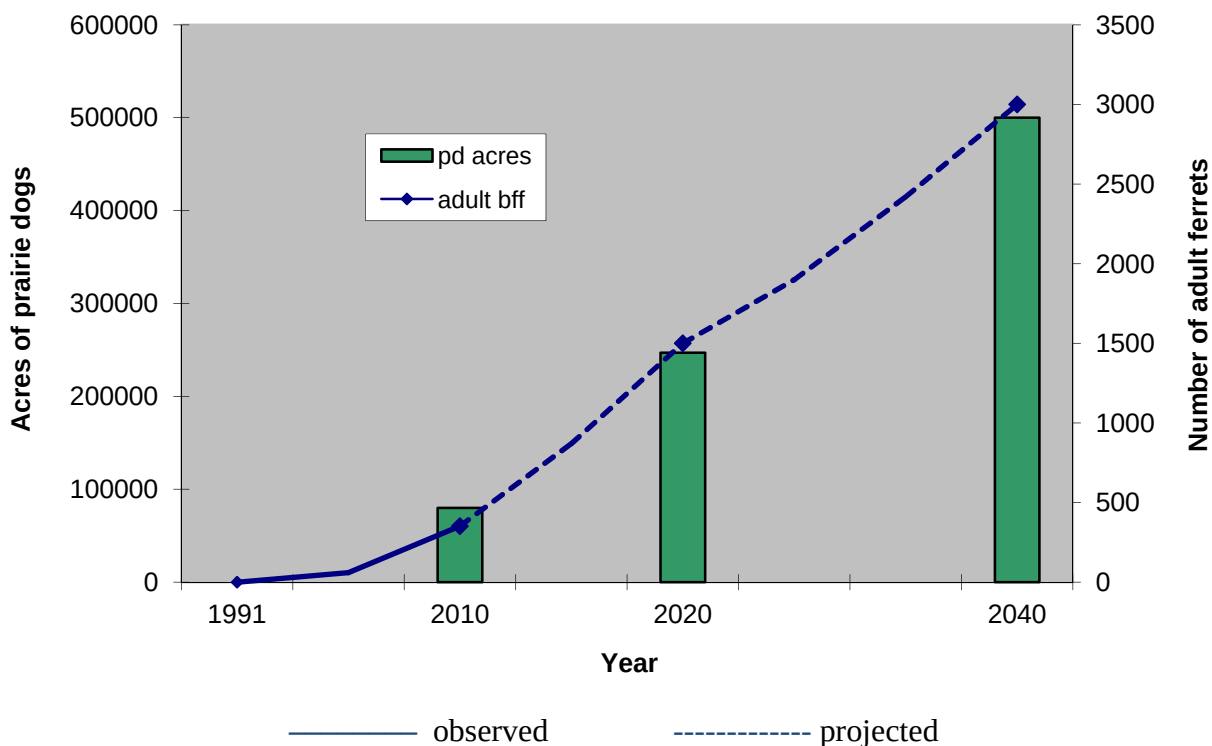


Figure 3. Number of adult black-footed ferret and corresponding acres of prairie dog occupied habitat at successful recovery sites in 2010 and projected requirements for downlisting (2020) and delisting (2040)

Meeting our downlisting goal of 1,500 breeding adult black-footed ferrets by 2020 will require significant population expansion at existing sites where habitat is unfilled and/or reintroduction into new sites. Realistically, the addition of approximately 1,300 breeding adult ferrets in populations with 30 or more breeding adults over the next 10 years would require large population increases at most existing sites in Arizona, western Colorado, Kansas, Montana, New Mexico, South Dakota, Utah, and Wyoming. Ferret populations at several existing sites have been established in habitat modified by disease and/or where there is likely to be ongoing political opposition to substantial prairie dog population increases. New sites will need to be initiated in States and portions of States not yet participating in reintroduction efforts (Nebraska, North Dakota, Oklahoma, Texas, and eastern Colorado). Downlisting by 2020 would require six additional successful sites in the next 10 years. Delisting by 2040 would require 20 additional successful sites or one new successful site achieved annually. We believe that this level of population expansion is possible, if aggressive management is pursued via prairie dog occupied habitat conservation and disease management. Failing these efforts, downlisting and delisting goals should be readdressed after 2020. However, even more aggressive recovery efforts could result in delisting much sooner.

Participation by all States within the historical range of the black-footed ferret is important to maximize the redundancy, representation, and resilience of the ferret and result in equitable recovery goals for all States. There are many uncertainties inherent in recovery projections. Therefore, we recommend that each of the 12 States within the historical range of the black-footed ferret consider initiating and maintaining some combination of the following types of reintroduction efforts, to provide the numbers of ferrets suggested to meet recovery guidelines:

- One or more large size ferret reintroduction sites with the potential for more than 100 adult breeding ferrets,
- One or more medium size ferret reintroduction sites with the potential for 50–100 adult breeding ferrets, and
- One or more small size ferret reintroduction sites with the potential for 30–50 adult breeding ferrets.

Furthermore, we recommend that at least two black-footed ferret reintroduction sites be initiated per year from 2021–2040 to successfully establish at least 20 additional sites for attaining the delisting goal of 30 successful populations. These efforts will require the continued success or expansion of existing reintroduction sites. Moreover, all initiated sites that prove successful must be maintained. If more partners and resources are provided for recovery, we recommend the establishment of six new reintroduction sites for each of the next 10 years, which could result in delisting the species by 2022.

The following table is adapted from Ernst (2008). It proposes recovery guidelines by State for the number of adult breeding black-footed ferrets required to meet rangewide recovery goals and the estimated amount of prairie dog habitat that would be needed to support that number of animals. Note that rounding of numbers results in downlisting and delisting goals slightly higher than 1500 and 3000 breeding adults respectively, as well as slightly higher acreage goals. Data from Canada and Mexico are not included. It should also be noted that breeding adults would not be counted toward a downlisting or delisting goal unless they are in a population of at least 30 breeding adults.

Table 6. Black-footed ferret recovery guidelines by State

State	Breeding adults established to date	Adults/acres to downlist	Adults/acres to delist
Arizona	35	74 adults/17,000 ac	148 adults/34,000 ac
Colorado	4	149 adults/29,000 ac	288 adults/58,000 ac
Kansas	13	123 adults/18,500 ac	246 adults/37,000 ac
Montana	11	147 adults/22,000 ac	294 adults/44,000 ac
Nebraska	0	134 adults/20,000 ac	268 adults/44,000 ac
New Mexico	2	220 adults/39,000 ac	440 adults/78,000 ac
North Dakota	0	38 adults/6,000 ac	76 adults/12,000 ac
Oklahoma	0	70 adults/10,500 ac	140 adults/21,000 ac
South Dakota	185	102 adults/15,000 ac	204 adults/30,000 ac
Texas	0	254 adults/38,000 ac	508 adults/76,000 ac
Utah	7	25adults/6,000 ac	50 adults/12,000 ac
Wyoming	100	171 adults/35,000 ac	341 adults/70,000 ac
Total	357	1,507 adults/256,000 ac	3,004 adults/512,000 ac

These guidelines are provided to assist planning needs and encourage broader recovery support across the black-footed ferret's historical range. The Service and BFFRIT regard such expanded participation as the most useful approach to overall species recovery and eventual State and tribal management of the ferret after delisting. These guidelines are a means of improving risk management and ensuring more uniform equity of recovery responsibilities across State boundaries. Species recovery has more likelihood of timely achievement if the currently non-participating or minimally-participating States engage in ferret reintroductions and recovery. However, recovery goals should not be subject to individual State efforts. The species may be downlisted and delisted if population and habitat objectives identified above are met by some other configuration than the one outlined above.

Management of Sylvatic Plague and Prairie Dogs: As previously noted, plague can impact the black-footed ferret directly via infection and subsequent mortality, and indirectly through the disease's effects on prairie dogs and the potential for dramatic declines in the ferret's prey base. Current management techniques include dusting prairie dog burrows with flea control powder and vaccinating ferrets prior to release. At Conata Basin in South Dakota, wild ferrets are also being trapped and vaccinated in the field as protection against the ongoing epizootic. Research is currently investigating the potential of supporting ferrets by providing vaccine to protect wild prairie dogs via oral bait. This has the potential to limit periodic plague cycles more effectively and economically than direct vaccination of ferrets. Specific tasks are described under "Recovery Actions." We believe that the threat from plague can be ameliorated by dusting, vaccines, and the maintenance of more reintroduction sites.

In addition to management of prairie dogs for better control of sylvatic plague, actions are needed to conserve prairie dogs in complexes of sufficient size and stability to support reintroduction of black-footed ferrets. We believe that in some cases control at the periphery of reintroduction sites may be appropriate to facilitate cooperation of adjacent landowners. However, the type of poison applied to control prairie dogs and the extent of its use can impact the ability of a prairie dog complex to sustain ferrets. As

previously noted, anticoagulant poisons can result in secondary impacts to any wildlife that consumes a poisoned prairie dog. In 2012, the Service completed formal consultation with the EPA to evaluate potential impacts to threatened and endangered species, including the black-footed ferret, from the use of the anticoagulant Rozol to poison prairie dogs. The final biological opinion prohibits application of Rozol within current and future ferret recovery sites.

RECOVERY STRATEGY

Key Facts and Assumptions

Recovery under the ESA is the process by which listed species and their ecosystems are restored and their future is safeguarded to the point that protections under the ESA are no longer needed. The primary biological constraint for the endangered black-footed ferret is its nearly complete dependency on prairie dogs, for both food and shelter. Consequently, if we safeguard prairie dogs, we will greatly facilitate ferret recovery.

Overarching Strategy

In preparing this revised recovery plan, we solicited extensive partner review from the BFFRIT. One of its guiding principles has been a focus on extensive and intensive involvement by many partners, including tribes, States, Federal land management agencies, and non-governmental organizations across the historical range of the black-footed ferret. Recovery will be achieved by establishing a number of ferret populations where appropriate habitat exists and by ameliorating threats impacting the species so as to allow the ferret's persistence. Although ferret habitat has been dramatically reduced from historical times, a sufficient amount of habitat persists, if its quality and configuration are appropriately managed. This management, for the most part, is likely to be conducted by traditional State, tribal, and Federal fish and wildlife and land management agencies. Additionally, private parties, including landowners and conservation organizations, must continue to support ferret recovery. Many partners

contributing to ferret recovery in many places will help minimize the risk of loss of all wild populations simultaneously from stochastic events such as disease.

Primary Objectives

There are two primary objectives for achieving recovery of the black-footed ferret, which to some extent overlap: (1) improve management of prairie dogs and (2) protect against sylvatic plague.

Other Considerations

The most expedient means of improving management of prairie dogs and protecting against sylvatic plague will require the continued active efforts of the BFFRIT.

Cooperation between the many affected Federal, State, tribal, and private parties is essential to the eventual recovery of the black-footed ferret.

RECOVERY ACTIONS

Since the 1988 Recovery Plan, there have been several major reviews of black-footed ferret recovery efforts including reviews by the Conservation Breeding Specialist Group (CBSG) of the Species Survival Commission of the World Conservation Union (CBSG 1992), Hutchins et al. (1996), CBSG (2004), Ray (2006), and U.S. Fish and Wildlife Service (2008). There have been other reviews somewhat narrower in scope that also addressed recovery including COSEWIC (2000), Esch et al. (2005), and Garelle et al. (2006). The conclusions and recommendations of this recovery plan are generally consistent with the findings of these reviews. Ray (2006) addressed major reviews through 2006 in her descriptions of recovery actions and tasks. We relied on her evaluations to address conclusions from other review efforts. However, in some cases the Service has adopted positions which consider all viewpoints, but do not specifically endorse the precise conclusions of any particular evaluation.

The recovery goals should ameliorate threats to the black-footed ferret (see Table 5) if successful recovery is to be achieved. The following actions address these threats.

1. Conserve and manage a captive ferret population of reasonable size and structure to support genetic management and reintroduction efforts.
2. Identify prairie dog habitats with the highest potential for supporting future free-ranging populations of ferrets.
3. Establish free-ranging populations of ferrets to meet downlisting and delisting criteria.
4. Ensure sufficient habitat to support a wide distribution of self-sustaining ferret populations.
5. Reduce disease-related threats in wild populations of ferrets and associated species.
6. Support partner involvement and conduct adaptive management through cooperative interchange.

The specific listing factors addressed by each action are described in the text below. The actions and accompanying tasks outlined in this strategy represent a general consensus derived from several years of meetings, reviews, and comments by members of BBFRIT. The conclusions from these ongoing efforts are summarized below.

Action 1. Conserve and manage a captive ferret population of reasonable size and structure to support genetic management and reintroduction efforts. Demographic and genetic management of the captive population is carried out under the guidance of the AZA Black-footed Ferret SSP® and includes maintaining a core breeding population of 280 animals of optimum sex ratio (105 males:175 females) and age (1-3 years) for a stable captive population, with a high level of genetic diversity, and a sustainable source of ferrets for reintroduction. Six captive breeding facilities produce approximately 250 juvenile ferrets annually. Currently, approximately 80 juveniles (30 male:50 female) are retained annually in SSP® facilities for future captive breeding purposes. The remaining juveniles are considered excess to the SSP®, and are allocated annually for reintroduction, or occasionally for research.

This action and its associated tasks will promote management of a sufficient number of animals with maximum genetic diversity to maintain a captive breeding population that will provide animals for reintroduction into suitable habitat throughout the historical range of the black-footed ferret. This action addresses all of the factors considered a threat to the species by providing ferrets for reintroduction into habitat where it was previously extirpated due to the destruction, modification, or curtailment of habitat, disease, inadequate regulatory mechanisms for prairie dogs, or poisoning of prairie dogs.

1.1. Maintain a SSP® Husbandry Manual that provides up-to-date protocols for the care, propagation, preconditioning, and transportation of captive ferrets.

A SSP® Husbandry Manual will be used at all captive breeding facilities participating in the black-footed ferret SSP®. Some variability in protocols is appropriate among facilities due to specific facility circumstances. Protocol adjustments are regularly discussed during conference calls and summarized during annual meetings. The protocols are dynamic and provide for development of adaptive husbandry procedures.

1.2. Ensure adequate facilities for breeding ferrets in captivity pursuant to Husbandry Manual guidelines. Approximately 55 percent of all captive black-footed ferrets are located at the Service's National Black-footed Ferret Conservation Center near Wellington, Colorado. The remaining captive breeding populations are housed at the Smithsonian Biology Conservation Institute in Front Royal, Virginia; Louisville Zoological Garden in Louisville, Kentucky; Cheyenne Mountain Zoological Park in Colorado Springs, Colorado; Phoenix Zoo in Phoenix, Arizona; and the Toronto Zoo in Toronto, Ontario.

1.3. Provide a description of research needs related to genetic and demographic management of captive populations. Research needs are discussed and prioritized at annual meetings of the BFFRIT and its subcommittees.

1.4 Minimize the potential for disease outbreaks and other potential catastrophes in captive ferret populations. Disease continues to pose a threat to ferret recovery. Protocols are in place at all breeding facilities to limit the prevalence of diseases such as coccidiosis and cryptosporidiosis that can sometimes impact captive populations. Canine distemper has also notably impacted ferret populations in the past. However, a commercial distemper vaccine has become available and is now widely employed in both captive and wild ferret population management. Sylvatic plague is considered a major threat to ferret recovery due to its devastating effects on both ferrets and their obligate prey (prairie dogs). Therefore, efforts to improve plague prevention and management such as vaccination of captive ferrets and research into field vaccination are ongoing.

1.4.1. Maintain multiple captive populations located in at least three separate geographic locations to avoid catastrophic loss at a single facility. As noted in Action 1.2, there are six SSP® breeding facilities.

1.4.2. Follow protocols for disease prevention described in the Husbandry Manual. All breeding facilities shall employ disease prevention protocols as specified in the SSP® Husbandry Manual.

1.4.3. Develop disease outbreak contingency plans. Guidelines for quick action in the event of a disease outbreak in a facility (evacuation, isolation, veterinary care, convalescence, disposal of tissues, and disease containment) are considered in the SSP® Husbandry Manual.

1.4.4. Maintain a list of disease research contacts. A list of plague researchers has been compiled with contact information. This list will be regularly updated. Contact lists for other diseases and concerns should also be updated regularly by the BFFRIT.

1.4.5. Support appropriate disease research. Plague vaccines are available or under development by the National Wildlife Health Lab for both reintroduced ferrets and prairie dogs. Plague vaccines are routinely used for some captive ferret populations. Potential outbreaks of other infectious diseases should be considered as appropriate to determine effects on ferret recovery.

1.5. Implement breeding strategies to maintain genetic diversity in the captive population while providing suitable genetic and demographic stock for reintroduction programs. Management goals for captive breeding have progressed from largely demographic (i.e., initial population expansion) to the optimal management of genetic, demographic, and institutional resources. The current core population bred annually under the SSP® should maintain 80 percent of the genetic diversity present in the founders of the captive population for at least 25 years. This genetic management strategy balances the need to maintain genetic diversity with the demographic demands of producing animals for reintroduction.

1.5.1. Conduct regular reviews of breeding strategies. Breeding protocols will be updated as necessary. Breeding vigor may be lower in captivity than in free-ranging ferret populations. Research to obtain information for improving breeding success is supported, such as consideration of costs and benefits of including wild ferrets in the captive breeding program, evaluation of sperm viability in captive vs. wild populations, and consideration of possible links between chronic stress and reproductive functioning in captive ferrets.

1.5.2. Conduct and evaluate efforts to improve reproductive output to support genetic management and reintroduction efforts. Increase the number of animals available for release from pen facilities through husbandry and management practices that promote reproduction and kit survival. These practices should consider improved breeding strategies

and enhanced artificial means of conserving the genetic contribution of individuals who do not reproduce by natural means.

1.5.3. Continue management efforts to balance the genetic representation of founders in the captive population. The genetic contribution of the 7 founders could be substantially reduced or lost if they are inadequately represented in future generations or are represented through only one sex. The genetic contribution of the 7 founders remains disproportionate. Efforts by the captive breeding program to balance representation of all founders will continue and periodically be evaluated. These efforts include minimizing genetic relatedness among mates, transferring ferrets between SSP® facilities to maintain heterozygosity, and continuing development of techniques for cryopreservation of ferret semen for use in artificial insemination.

1.5.4. Evaluate the reproductive fitness, genetics, and demography of the captive population. Reproductive fitness is evaluated annually and compared under different breeding scenarios. The SSP® includes adaptive genetic and demographic management strategies to maintain the reproductive fitness and productivity of the captive population. Records will be kept on all captive ferrets, as described in the Husbandry Manual.

1.5.5. Provide optimal stock for reintroduction purposes. The most genetically valuable ferrets will be retained for captive breeding. Animals intended for reintroduction should receive adequate preconditioning.

1.6. Establish policies for the use and handling of dead, non-reproductive, or otherwise excess ferrets. Use current Service guidelines to dispose of ferrets that are considered surplus to the SSP®. Surplus animals not suitable for reintroduction should be used for research or live educational exhibit. All carcasses should be made available for scientific research or educational display. Ferret tissue samples should also be made available for scientific research.

Action 2. Identify prairie dog habitats with the highest potential for supporting future free-ranging populations of ferrets. No remnant wild black-footed ferrets have been found outside of reintroduction areas since the extinction of the Meeteetse, Wyoming population in 1987. Searches of potential habitats are no longer considered a high priority given the extensive searches completed with negative results, the substantial resources required to continue such efforts, and the degraded and fluctuating status of remaining prairie dog habitat in North America. Therefore, targeted searches for remnant wild ferret populations have been discontinued. Consequently, some tasks related to searches that were described in earlier recovery plans have been discontinued. However, search methodologies originally designed to locate wild ferrets continue to be critical for selecting future reintroduction sites (described below) and monitoring reintroduced populations (described under task 3.6).

This action and its associated tasks address the threat from inadequate existing regulatory mechanisms by encouraging participation from State, tribal, and Federal governments.

2.1. Use recent prairie dog surveys to identify and prioritize habitats with potential as future ferret reintroduction sites. State wildlife agencies within the range of prairie dogs have agreed to complete prairie dog surveys at 3–5 year intervals. Results from these surveys can be useful in the identification of potential ferret reintroduction sites.

2.2. If a remnant ferret population is located, develop a plan to integrate any population into the recovery program. The likelihood of finding wild ferrets outside of reintroduction areas diminishes with time. However, if this occurred, the Service would immediately consult with members of the BFFRIT and take actions appropriate to the situation. Once discovered, new populations should be integrated into the monitoring and captive breeding programs to the extent possible.

Action 3. Establish free-ranging populations of ferrets to meet downlisting and delisting criteria. There have been 20 black-footed ferret reintroduction projects (see Figure 1, Tables 2 and 3). One of the downlisting objectives from the Recovery Plan is to establish a pre-breeding population of 1,500 free-ranging adults in 10 or more populations with no fewer than 30 breeding adults in any population by 2020. Current ferret reintroduction efforts are approximately 40 percent successful with regard to the number of established populations. A minimum of approximately 270 breeding adults occur in these four populations, which is 18 percent of the 1,500 free-ranging adult population goal. The geographic distribution of attempted ferret reintroduction effort is fairly well distributed across the species' historical range (with the notable exception of much of the eastern one-third of the range). The four successful sites are in Arizona, Wyoming, and South Dakota (contains two successful sites).

This action and its associated tasks will identify the sites best suited to maximizing black-footed ferret recovery, allocate animals for reintroduction accordingly, and require follow-up monitoring to facilitate adaptive management. This action addresses all of the factors considered a threat to the species by reintroducing ferrets into habitat where it was previously extirpated due to the destruction, modification, or curtailment of habitat, disease, inadequate regulatory mechanisms for prairie dogs, or poisoning of prairie dogs.

3.1. Maintain a list of research needs related to reintroduction and population monitoring. The most important research questions that remain, and their priorities, will be considered by the Service and technical subcommittees of the BFFRIT.

3.2. Maintain a standardized ranking procedure for allocating ferrets to candidate reintroduction sites. The Service uses a standardized ranking procedure for allocating ferrets to reintroduction sites. Reintroduction sites are ranked according to many site-specific criteria including project background and justification, involved agencies/parties, habitat conditions, ferret population information, predator management, disease monitoring and management,

contingency plans, potential for preconditioning of released ferrets, veterinary and husbandry support, and research contributions. Site-specific values for each criterion are entered into an allocation matrix that allows sites to be ranked based on overall contribution to ferret recovery efforts. Reintroduction proposals and the Service's rankings of the proposals are reviewed by BFFRIT members. The Service determines ferret allocations by mid-summer and incorporates site visit information to resolve any outstanding concerns regarding specific reintroduction projects.

- 3.3. Develop and approve new reintroduction sites.** The limited number of ferrets available for release each year requires that they be efficiently allocated. The number of new sites will be carefully considered.

3.3.1. Work with site managers, landowners, and stakeholders to develop long-term site management assurances for potential new reintroduction sites. Management agreements are established for each reintroduction area. Land ownership patterns differ between sites. Agreements should stipulate the responsibilities of all parties for long-term commitments to ferret management. Management of candidate sites is necessary before recovery activities can proceed. The management of reintroduced populations is primarily the responsibility of the agency or tribe originally involved in establishment of the population.

3.3.2. Collect information for site screening and baseline data purposes. Habitat data are collected prior to evaluation of each reintroduction site. Data collection typically continues annually or on an intermittent basis over early project years and should include prairie dog occupied habitat and density, plague history, presence of canine distemper, and predator occurrence.

3.3.3. Include site-specific prairie dog management plans in evaluation of new recovery sites. Prairie dog colonies at existing and proposed

reintroduction sites should be characterized, managed at appropriate levels, monitored and managed for plague, and managed for grazing as appropriate.

3.3.4. Conduct site-specific monitoring of ferret populations and environmental variables. Post-release monitoring should identify causes and degree of mortality, characterize dispersal, and refine recovery strategies. Although the level of monitoring employed during initial reintroduction efforts may not be sustained on a permanent basis, some systematic monitoring of demographic, genetic, and environmental variables should continue throughout the duration of each recovery effort. Information from monitoring efforts is shared with the Black-footed Ferret Recovery Coordinator and members of the CS.

3.3.5. Standardize annual site monitoring and reporting to the extent practical. Standardization of survey methods increases opportunities for comparisons between sites and years. Standards are needed to: (1) define general requirements for future reintroduction sites, (2) provide consistent feedback from participants, and (3) refine methods (e.g., radio-telemetry, dog searches, aerial survey, and snow-tracking).

3.4. Complete site and ferret preparations for releases. Specific guidance appears below.

3.4.1. Comply with obligations of the ESA, NEPA, and other laws. State and Federal statutes, tribal statutes and resolutions, and other legal requirements will be evaluated and completed prior to implementing reintroduction projects.

3.4.2. Assess site conditions prior to ferret releases. Plague screening will be conducted prior to release. Allocation requests and site visits will be used to determine specific release locations.

3.4.3. Schedule and prepare ferrets for releases. Each ferret released will have a record of studbook identification number, transponder tag numbers, birth date, facility of origin, preconditioning treatment, and recommended schedule of release. To the extent possible, ferrets should be released in numbers and sex ratios that will optimize long-term survival and reproduction.

3.5. Release ferrets into approved reintroduction sites as capacity and production permit. Specific guidance appears below.

3.5.1. Release sufficient numbers of ferrets to meet downlisting criteria of establishing 1,500 free-ranging adults distributed among at least 10 populations, with no less than 30 breeding adults in each population. Based on the best information available, it appears that four reintroduction sites (Aubrey Valley, Cheyenne River Indian Reservation, Conata Basin, and Shirley Basin) currently meet these criteria. Reintroduction efforts will continue at other existing sites as appropriate and at new sites with downlisting criteria in mind.

3.5.2. Continue releases to meet the delisting criteria. The delisting criteria include the establishment of a pre-breeding census population of 3,000 free-ranging breeding adult ferrets in 30 or more populations with no fewer than 30 breeding adults in any population. Reintroduction efforts will continue following downlisting, with the goal of delisting the ferret.

3.5.3. Represent all founders as equally as possible in each released population. All founders are currently represented among animals released at reintroduction sites. However, founder genes may be lost from wild populations due to chance, selection, and natural breeding patterns. Genetic monitoring of reintroduced populations should be considered to

determine the rates at which diversity is lost, and to guide genetic management strategies.

3.5.4. Support the use of wild-born ferrets for reintroduction at other sites.

All ferret reintroduction programs are authorized under the principle that if a population becomes established, contributions of excess ferrets will be used to manage other recovery sites. As reintroduced ferret populations grow, the translocation of wild-born ferret kits to new reintroduction sites is expected to become increasingly important as a tool for ferret recovery. Disease-prevention protocols for translocation of wild-born stock will be updated as needed based on protocols for transfer of captive-born stock.

3.6. Implement management and monitoring prescriptions for each reintroduction site. The Service and the BFFRIT support long-term monitoring of all ferret reintroduction sites to evaluate success and provide information of value to other reintroduction sites.

3.6.1. Monitor ferrets. Local recovery partners will maintain a high level of monitoring for five years following the last release (see task 3.3.4.). This should include analysis of annual reproduction and survival. Other parameters such as short-term survival, a pre-breeding census, recruitment, and home range size can be evaluated as resources permit. Thereafter, demographic and genetic surveys should be completed periodically to track population status.

3.6.2. Monitor and evaluate changes in prairie dog density and distribution. Monitoring habitat conditions is an ongoing requirement of reintroduction programs and is critical to the success of reintroduction efforts. Aspects of habitat conditions other than plague also should be considered.

3.6.3. Monitor disease dynamics. Readily available carcasses will be collected and submitted to the National Black-footed Ferret Conservation Center for

detailed necropsy when monitoring at reintroduction sites reveals deceased ferrets. Necropsy reports also should be held at this facility for subsequent data analysis and use by program participants.

3.6.4. Monitor and evaluate changes in the site environment. Environmental change associated with reintroduction may give valuable clues to recovery success and will be considered.

3.7. Use release and monitoring opportunities to improve ferret management.

Preconditioning prior to release substantially increases ferret survival and is now a standard protocol. Efforts to breed ferrets in naturalistic pen environments have been undertaken in Arizona, Colorado, Montana, and New Mexico, but none are currently in operation. Several different release procedures have been employed, such as encircling release sites with temporary anti-predator (electric) fencing, which may increase ferret survival during the critical period immediately following release. At present, all releases are “hard releases” wherein ferrets are simply released into suitable habitat without protection from predators. Annual management plans should be developed by all reintroduction sites to determine whether additional ferrets are to be released. Allocation requests should be submitted as appropriate.

3.7.1. Continue the use of ferret preconditioning techniques. Research has demonstrated that preconditioning is beneficial to post-release survival.

3.7.2. Optimize release methods and timing. Release strategies continue to be refined and investigated. Release methods should be considered for publication in wildlife journals. New literature will be reviewed and incorporated into reintroduction plans and reports.

3.7.3. Continue to improve ferret monitoring techniques. Post-release monitoring is essential to judge the overall success of individual

reintroduction projects, and is a required element of all reintroduction projects.

3.7.4. Continue to improve survey techniques. Reintroduction partners should continue efforts to improve spotlight survey efficacy and investigate alternative survey techniques.

3.7.5. Continue to evaluate methodologies for counting or estimating ferrets at recovery sites. A method for accurately estimating ferret numbers is critical to assessing progress at each recovery site, which will in turn allow the reassessment of objectives, priorities and allocation of resources for each site. As recovery sites expand or resource availability changes, it is likely that methods or rigor for estimating ferrets at individual sites will change. The Service and BFFRIT will continue to refine survey methodologies and estimation parameters to assess progress towards recovery goals.

3.7.6. Continue to improve telemetry equipment and techniques. Radio-telemetry is the only technique that has provided meaningful data on causes of mortality for free-ranging ferrets. Nevertheless, telemetry is problematic due to costs, short transmitter life, and increased risks of injury to individuals. Improved telemetry should be considered to address specific questions at certain reintroduction areas.

3.7.7. Continue to improve techniques for habitat monitoring and habitat evaluation. The principal technique for determining how many ferrets can be supported by a given prairie dog complex is to survey active prairie dog burrows by standardized transects, estimate how many prairie dogs are present, and how many ferret families could exist. An understanding of the relationship of prairie dog density and the associated spatial use of prairie dog complexes by ferrets will continue to be evaluated.

- 3.7.8. Support disease monitoring and management capabilities.** Methods of controlling plague in free-ranging populations through the use of vaccines, flea powders, growth inhibitors, or sterilants will continue to be explored. Regular monitoring for canine distemper in sympatric predators at reintroduction sites should continue.
- 3.7.9. Improve understanding of ferret demography and genetics.** The benefits of translocation of wild animals into other recovery areas are important program considerations. Program partners need to ensure adequate monitoring of donor, recipient, and control populations and coordinate such activities with the Service through the Black-footed Ferret Recovery Coordinator.
- 3.7.10. Consider population viability, including potential effects of inbreeding, interspecific interactions, and disease.** Data are accumulating from reintroduction sites that could be used to identify different habitat effects.
- 3.8. Enforce all laws protecting established populations.** Most ferrets have been reintroduced in non-essential experimental population areas as set forth in section 10(j) of the ESA. More recently, ferrets have been released under provisions of recovery permits (section 10(a)(1)(A) of ESA). Other ESA tools such as Safe Harbor Agreements are under development and should be considered as potential ferret reintroduction options. All applicable State, Federal, and tribal laws regarding the protection of ferrets will be followed.
- 3.9. Review the reintroduction program annually.** An evaluation of reintroduction success is required for each site on an ongoing basis. The ultimate measure of reintroduction success is the documented growth of a population through natural recruitment to a level that becomes self-sustaining and requires no further augmentation or fully occupies the available habitat. Success is evaluated via post-release monitoring of the reintroduced population and varies among

reintroduction sites. Post-release monitoring is necessary to identify causes and rates of mortality, characterize dispersal, and refine current recovery strategies. Information from monitoring efforts should be shared.

3.9.1. Produce annual site reports. Recovery partners will summarize monitoring data and research results, evaluate the efficacy and efficiency of their efforts, and make appropriate modifications to their procedures based on new information.

3.9.2. Include demographic and/or genetic manipulation needs for each population. Individual recovery partners should be involved with day-to-day management for established ferret populations. A broad management strategy should also be employed to ensure that ferrets are managed in a metapopulation context. Wild-born ferrets may be periodically exchanged between reintroduced populations to achieve demographic and/or genetic management goals. Demographic manipulations may include stocking, translocation, or removal of individuals from donor populations.

3.9.3. Evaluate and update site monitoring and research efforts. A routine level of periodic ferret population monitoring is required in a long-range management plan for each reintroduction site. The Service will periodically reviews site plans and monitoring efforts.

3.9.4. Update reintroduction strategy and protocols as needed. The Service will update the reintroduction program and protocols as necessary based upon successful results from individual reintroduction sites.

Action 4. Ensure sufficient habitat to support a wide distribution of self-sustaining ferret populations. Black-footed ferret habitat is synonymous with areas occupied by several species of prairie dogs. Ferret habitat has been destroyed, modified, and curtailed through conversion for agricultural use, eradication of prairie dog populations through poisoning, and introduction of sylvatic plague. These combined impacts have resulted in

the loss of approximately 96 percent of prairie dog occupied habitat and consequently the loss of approximately 96 percent of potential ferret habitat.

Since the early 1980s, program partners have invested considerable resources in the recovery of this species. To date, ferret reintroduction projects have predominantly occurred on Federal or tribal lands. The development of recovery partnerships with more private landowners is essential to recovery of the species. The Service and BFFRIT partners should continue to support and manage established ferret reintroduction sites, whether or not reintroduction efforts are presently active. In addition, new partnerships are encouraged, to expand reintroduction opportunities across the historical range of the species into additional sites in other States and on other tribal lands.

Some loss of breeding vigor may be occurring in the captive breeding program, in part due to the inherent limitations of captive breeding. Individuals breeding in the wild likely have a higher breeding vigor. Therefore, we believe it essential to the survival of the species to establish additional sites as quickly as possible to allow wild breeding. This will require use of sites in the near term that may not have yet gained sufficient size or may not yet have the potential for sufficient numbers of prairie dogs to support a viable self-sustaining ferret population over the long term.

This action and its associated tasks will identify and conserve current and potential habitat for the black-footed ferret. This action addresses all of the factors considered a threat to the species by managing habitat to minimize potential adverse impacts from plague, poisoning, and inadequate management; and by encouraging participation from Federal, State, tribal, and private landowners.

4.1 Estimate the amount and configuration of habitat required to support ferret populations that meet downlisting and delisting criteria. We estimate that a minimum of approximately 191,000 ac (77,000 ha) of black-tailed prairie dog occupied habitat and 56,000 ac (23,000 ha) of white-tailed and Gunnison's prairie dog occupied habitat will be required to meet downlisting criteria. Similarly, a minimum of 383,000 ac (154,000 ha) of black-tailed prairie dog occupied habitat

and 112,000 ac (46,000 ha) of white-tailed and Gunnison's prairie dog occupied habitat will be required to meet delisting criteria (see discussion on pp. 65–66). These estimates will be adjusted as necessary.

4.1.1. Improve guidelines for determining ferret habitat requirements. It is crucial to establish and maintain as many ferret populations as possible in native habitats. For example, in cases where the amount of available habitat is smaller, or subject to periodic effects of plague, more on-going human intervention and management may be required to maintain populations. The Service should consider the density of prairie dogs needed to support ferrets, the effects of territoriality on ferret density, and the effect of patchiness of prairie dog habitat on ferret density.

4.1.2. Assess progress toward meeting downlisting and delisting criteria. In order to estimate the amount of additionally purposefully managed habitat required for recovery, partners will evaluate progress toward recovery objectives. This action will require estimates of purposefully managed habitat and an assessment of demographic data of reintroduced populations.

4.1.3. Estimate the amount and configuration of habitat necessary to support downlisting and delisting objectives. Analyzing ferret population growth based on data from each reintroduction site can provide a means for determining progress toward reintroduction goals and coordinating between ferret population objectives and supporting habitat objectives. Preliminary estimates of the amount of habitat required to downlist and delist the ferret are provided in Table 6.

4.2. Identify and manage ferret habitats to support recovery goals. Managing habitat for ferret recovery does not necessarily preclude other habitat uses. Efforts to fund incentive programs for expanding existing habitat on private and tribal lands will be identified and implemented.

- 4.2.1. Consult Federal, State, tribal, and private entities with jurisdiction over historical ferret habitats to develop jurisdiction-specific habitat goals and habitat management plans.** In order to achieve recovery objectives for distributing sufficient numbers of ferret populations across the historical range of the species, large recovery areas that can be managed as long-term ferret reintroduction sites will be identified. Many sites currently supporting only small prairie dog populations could ultimately be expanded to create suitable ferret reintroduction areas. Other areas that historically supported prairie dog populations but are currently unoccupied could be restored via prairie dog translocations. State and Federal land and wildlife management agencies and tribes have ultimate authority and responsibility for implementing habitat conservation measures needed to recover the ferret. Close coordination will be maintained between the Service, the BFFRIT, and prairie dog management groups. The BFFRIT and land and wildlife management agencies will investigate opportunities to develop cooperative reintroduction efforts with private landowners.
- 4.2.2. Recover and maintain sufficient ferret habitat to support recovery goals.** Ferret recovery depends on the conservation and management of prairie dog populations. Many State and Federal agencies and tribes have developed management plans to maintain viable prairie dog populations. Efforts to manage prairie dogs will continue to be evaluated. States and tribes should describe the impact of prairie dog population control activities on ferret management objectives. EPA label restrictions on rodenticide application should be enforced.
- 4.2.3. Engage relevant government agencies currently not participating in ferret recovery.** A few State and Federal agencies have participated minimally in ferret recovery efforts. Fiscal or administrative constraints

may have kept some tribes, with suitable habitat, from participating more fully. The Service and other active members of BFFRIT will continue to reach out to these agencies and tribes. They will be invited to annual BFFRIT committee meetings and their input and review will be requested on potential recovery efforts within their jurisdictions.

Action 5. Reduce disease-related threats in wild populations of ferrets and associated species. Disease continues to be a primary factor inhibiting recovery of the black-footed ferret in the wild. The threat of catastrophic loss of prairie dogs and ferrets from sylvatic plague is significant. Plague may also periodically impact reestablished populations. Increasing evidence suggests that some levels of enzootic plague may result in negative growth rates for prairie dog and ferret populations. Ferret populations that are otherwise self-sustaining may require intervention where plague maintains a chronic effect. Other diseases such as canine distemper, coccidiosis, and cryptosporidiosis are less likely to threaten ferret persistence. There are several methods currently employed to monitor plague and other diseases.

This action and its associated tasks will improve plague management and encourage appropriate disease research. This action addresses the threat of modification of habitat due to plague and the direct threat of disease to ferrets and prairie dogs.

5.1. Maintain a clearinghouse for disease research and information related to ferrets and associated species. Currently, there are many agencies, institutions and individuals researching various aspects of plague. A clearinghouse/repository of plague-related data, possibly internet based, should be developed to promote continued coordination and define further research needs.

5.1.1. Develop a list of disease research needs. The coordination of ongoing studies and data sharing to further research needs will be considered by the BFFRIT.

- 5.1.2. Develop a list of bibliographies of relevant publications and projects relative to disease.** As noted in task 1.4.4., a list of plague researchers has been compiled with contact information.
- 5.1.3. Synthesize relevant information and research results.** Periodic literature reviews and syntheses regarding the ecology of sylvatic plague will continue.
- 5.1.4. Report epizootics to the Centers for Disease Control, the National Wildlife Health Laboratory, and other appropriate disease research facilities.** Coordination will be maintained with research institutions to follow-up on any case histories of disease outbreaks in prairie dog populations and ferret recovery areas as noted in task 1.4.5. Field biologists should characterize the extent of impact and recovery of areas affected by any apparent diseases. Additional background investigations will be considered at sites experiencing significant losses.
- 5.2. Minimize the threat of sylvatic plague in ferrets and associated species.** Plague remains a significant factor in the direct mortality of black-footed ferrets and the loss of habitat. Many plague issues need further research including flea ecology, mammalian reservoirs, management methods (e.g., vaccines), effects on ferrets (both direct and indirect), methods to control fleas (e.g. insecticides, growth inhibitors, biological factors), and effects of plague on different species of prairie dogs.
- 5.2.1. Develop and implement as appropriate prophylactic methods for controlling sylvatic plague.** Methods for prophylactic control of plague now focus on flea control and protective vaccines. Flea control via use of Deltamethrin powder inserted into prairie dog burrows appears to provide an effective deterrent for transmission of both enzootic and epizootic plague, but the application of insecticidal dust is costly and highly labor-intensive. Recent testing indicates a prairie dog bait containing

Imidacloprid (insecticide) provided some flea reduction in prairie dogs. Research is ongoing to determine field management applicability of this product. An experimental plague vaccine based on the F1 and V antigens provides effective protection for ferrets. However, its delivery under field conditions is currently limited. Development of a bait-deliverable vaccine for prairie dogs is underway, and field trials have been conducted. Development of this vaccine has implications for future management of prairie dog habitats and recovery of the ferret. Obtaining funds for plague research is an ongoing effort.

5.2.2. Develop and implement ecological methods for control of sylvatic plague in ferret recovery areas, including methods based on manipulation of ferret habitats or associated species communities.

Research into the ecology of plague in prairie dog communities should be expanded to help identify reservoir hosts, identify low levels of plague, determine factors in the geographic expansion of plague, measure transmission modes and speed, determine differential susceptibility among hosts, investigate the varying roles of different flea species in plague ecology, and determine the potential impacts from climate change. This task will require collaboration of partners from reintroduction sites and research institutions.

5.3. Continue to address the threat of canine distemper in ferrets and associated species and take management actions as appropriate. Canine distemper research will continue as part of ongoing widespread vaccination efforts.

5.3.1. Continue to implement prophylactic methods for control of canine distemper. An effective canine distemper vaccine has been developed and is in widespread use in the ferret recovery program, both in captivity and at some sites in the field. We will continue to employ vaccination as a management strategy unless the best available information indicates vaccination is no longer necessary or appropriate.

5.3.2. Continue to implement ecological methods for control of canine distemper in ferret recovery areas, including methods based on manipulation of ferret habitats or associated carnivore communities.

Natural epizootics should be fully documented to provide a greater understanding of disease flow through ferret populations. Reintroduction sites should be regularly monitored for canine distemper through predator surveys.

5.4. Periodically synthesize available disease data and disease research results, and re-evaluate disease management strategies. Continue to adapt management procedures as new information becomes available.

5.4.1. Conduct periodic symposia and workshops to exchange information on diseases. Such workshops will encourage synergism between disease research being conducted on ferret habitat and research being conducted on other species worldwide. This is especially true of plague, which has received much attention in other countries.

5.4.2. Maintain public support for ferret reintroduction efforts at sites with disease issues. Public support can be lost due to confusion about why ferrets are being released into areas where they are at risk of being infected with diseases. Public education about the nature of the disease issues facing ferrets and other species in the prairie ecosystem, as well as humans, will help maintain support in the face of disease related mortalities.

Action 6. Support partner involvement and conduct adaptive management through cooperative interchange. This action addresses the need for continued development of recovery partnerships and strategies. Progress toward black-footed ferret recovery requires sustained program momentum. Among listed species, the ferret has one of the longest histories of endangerment and cooperative recovery efforts. The conservation of

sufficient habitat will require increased efforts by many Federal, State, tribal, and private entities. Continued public and private involvement should be encouraged through frequent communication of recovery program status. The historical ferret range included lands now within the jurisdiction of Mexico, Canada, 12 States, several tribes, several Federal agencies, many local governments, and myriad private landowners. Currently, ferrets have been reintroduced on Federal, State, tribal, and private lands within eight States, on private and communal lands within Chihuahua, Mexico, and on Federal and private lands in Canada.

This action and its associated tasks will encourage participation by Federal, State, tribal, private, and foreign entities. This action addresses the threat to the black-footed ferret from a lack of proactive management.

6.1. Engage partners in review, analysis, and updates to program direction on a regular basis. Participants in the recovery program will continue an open process for review of recovery activities.

6.1.1. Support review and analysis of program progress. Research objectives and priorities will be assessed and competitive proposals from outside groups will be encouraged and evaluated. Regular evaluation of the progress in captive breeding, disease monitoring and management, habitat recovery and management, reintroduced ferret populations, and outreach efforts will be conducted.

6.1.2. Coordinate program components and update program direction as appropriate based on reviews addressed in task 6.1.1. This revised recovery plan will provide a framework for adaptive management, based on rapid and reasoned response to population needs, rather than specific protocols. Communication between the Service, the SSP® and the BFFRIT to coordinate kit production and supply animals for reintroduction efforts will continue.

- 6.1.3. Formally report on progress toward recovery objectives on a five-year basis.** Progress on the actions specified in this plan will be assessed on a regular basis. External review will occur at longer intervals. Responsibility of assigning tasks is left to the funding entities and is coordinated by the Service. The most recent 5-year review was completed by the Service in 2008.
- 6.1.4. Use the Black-footed Ferret Recovery Implementation Team to help identify problems and solutions.** The Service consults with the BFFRIT to address specific problems and solutions. The structure and operations of the BFFRIT will be periodically reviewed and appropriate changes implemented. Annual meetings for the EC and all subcommittees are arranged by the Service.
- 6.1.5. Encourage the formation of jurisdictional and topical working groups to identify problems and solutions.** State working groups are site-specific implementation teams that provide recommendations on the management of local ferret recovery projects. The establishment of the BFFRIT has promoted improved technical support and the exchange of information by both involved partners and interested/affected parties, including tribes. Partners and other interested parties will be updated as appropriate on activities undertaken by various subcommittees.
- 6.2. Communicate program status, direction, and needs to potential recovery partners.** Communication is an important function of the Service. All partners should be kept informed of the latest developments and important issues facing the program. Public, political, and private support will be maintained to the extent possible through appropriate education and public relations efforts, including demonstration of progress toward ferret recovery. All ferret recovery activities will be organized on an annual basis. Recovery Program priorities and activities may change from year to year based on analysis of new data. Therefore, the organization and coordination of recovery activities may also change from

year to year. Administrators should be aware of these dynamics and be prepared to coordinate and administer the program accordingly.

6.2.1. Maintain an up-to-date website describing the ferret recovery program and partnership opportunities. Ferret-related websites are maintained by the Service as well as many other affected agencies and organizations. Current information regarding the ferret is available from websites maintained by the Service (www.fws.gov/endangered/) and by the BFFRIT (www.blackfootedferret.org).

6.2.2. Promote recovery partnerships through the formation of jurisdictional and topical working groups. Working groups will be organized to address local recovery efforts and specific research tasks as appropriate.

6.2.3. Encourage the exchange of scientific information and technical advice. The Service encourages sound experimental approaches and broad partner input to help ensure an effective and cost-efficient recovery program. Scientific exchange is facilitated by broad distribution of pertinent planning documents, recovery program progress, technical research results, and accurate information on the effect of reintroduction projects on area land uses and other points of program controversy. Technical meetings are conducted annually by each of the BFFRIT subcommittees. Workshops on disease management, field techniques, anesthesia, breeding techniques, etc. are regularly conducted to meet program needs.

6.3. Support site-specific ferret reintroduction efforts and develop an outreach plan to stakeholders that support ferret recovery. The BFFRIT OIS should facilitate the exchange of ferret recovery information through web sites, media contacts, and other means.

- 6.3.1. Support the efforts of States, tribes, and other organizations to recover the ferret.** Community education and outreach programs have been established in most States that are active in ferret reintroductions. Partnerships among agencies and organizations can increase the visibility of ferret recovery efforts and will be encouraged.
- 6.3.2. Encourage public support for ferret recovery through strategically focused outreach efforts.** Outreach activities provide information on the status of the ferret, its history and habitat, and the unique efforts to save it. Emphasis should be placed on generating interest, understanding, and appreciation among active recovery participants. Specific constituencies will also be targeted according to their proximity to and possible involvement in the Recovery Program (i.e., western States, tribes, ranchers, policy makers, and educators). Constituencies who are adverse to the Recovery Program should also be identified. The benefits of maintaining this ecosystem and the species it supports should be conveyed.
- 6.3.3. Provide ferret recovery information to Non-Government Organizations currently supporting recovery and solicit the assistance of other NGOs who could aid species recovery.** Conservation organizations have participated in ferret recovery activities since before the discovery of the last wild population at Meeteetse and are vital to the continued success of ferret recovery. Other organizations with similar wildlife and habitat conservation charters could potentially become involved to help accelerate public awareness and physical recovery efforts. The Service and the BFFRIT should frequently update national conservation organizations through personal contact and seek additional support or assistance where warranted.
- 6.3.4. Support participation and coordination among government agencies with jurisdiction over programs related to ferret recovery.** The

Service will encourage appropriate Federal, State, and tribal government agencies to participate in ferret recovery. All Federal government agencies should be aware of ESA section 7 responsibilities, including the affirmative conservation mandate found in section 7(a)(1) of the Act directing all Federal agencies to use their authorities to conserve listed species.

6.3.5. Maintain updated information on the contributions of SSP® captive breeding facilities. Annual assessment of the expenditures and contributions of animals in terms of SSP® management and field recovery efforts will be conducted.

6.4. Consider funding needs for national and international ferret recovery.

Funding needs for ferret recovery will be prioritized and updated as appropriate.

PART III. IMPLEMENTATION SCHEDULE

The Implementation Schedule outlines actions and estimated costs for recovery of the black-footed ferret, as set forth in this recovery plan. It is a guide for meeting the recovery goals outlined in this plan. This schedule indicates action priorities, action numbers, action descriptions, duration of actions, parties responsible for actions (either funding or carrying out), and estimated costs. Parties with authority, responsibility, or expressed interest to implement a specific recovery action are identified in the Implementation Schedule. When more than one party has been identified, the proposed lead party is indicated by an asterisk (*). The listing of a party in the Implementation Schedule does not require the identified party to implement the action(s) or to secure funding for implementing the action(s).

Recovery priorities (column 1) are defined as follows:

- Priority 1: An action that should be taken to prevent extinction or to prevent the species from declining irreversibly in the foreseeable future.
- Priority 2: An action that should be taken to prevent a significant decline in species population or habitat quality, or to prevent some other significant negative impact short of extinction.
- Priority 3: All other actions to consider during reclassification and eventual full recovery of the species.

Responsible parties (column 4) include:

USFWS	U.S. Fish and Wildlife Service
BFFRIT	Black-footed Ferret Recovery Implementation Team (comprised of State and Federal agencies, tribes, and conservation organizations)
SSP®	American Zoo Association Species Survival Plan Partners
States	State wildlife agencies with ongoing or proposed reintroduction sites
Tribes	Tribes with ongoing or proposed reintroduction sites
NPS	U.S. National Park Service
USFS	U.S. Forest Service
BLM	U.S. Bureau of Land Management
USGS	U.S. Geological Survey – Biological Resources Division
APHIS	Animal and Plant Health Inspection Service

Table 7. Implementation schedule for the Black-footed Ferret Recovery Plan

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
1	1.1	Maintain an SSP Husbandry Manual that provides up-to-date protocols for the care, propagation, preconditioning, and transportation of captive ferrets	SSP®*, BFFRIT, USFWS	250	200	200	650
1	1.2	Provide adequate facilities for breeding ferrets in captivity, pursuant to Husbandry Manual guidelines	USFWS*, SSP®*	1400	1000	1000	3400
1	1.4.1	Maintain multiple captive populations located in at least three separate geographic locations to avoid catastrophic loss at a single facility	SSP®*, USFWS	1370	980	980	3330
1	1.4.2	Follow protocols for disease prevention described in the Husbandry Manual	SSP®*, USFWS*	400	300	300	1000
1	1.4.3	Develop disease outbreak contingency plans	SSP®*, USFWS, BFFRIT	550	400	400	1350
1	1.4.5	Support appropriate disease research	BFFRIT*, USFWS, USGS, APHIS	800	600	600	2000

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
1	1.5.5	Provide optimal stock for reintroduction purposes	USFWS*, SSP®	700	500	500	1700
1	2.1	Use recent prairie dog surveys to identify and prioritize habitats with potential as future ferret reintroduction sites	USFWS*	90	60	60	210
1	3.3.1	Work with site managers, landowners, and stakeholders to develop long-term site management assurances for potential new reintroduction sites	USFWS*, NPS, USFS, BLM, States, Tribes	300	240	240	780
1	3.3.3	Include site-specific prairie dog management plans in evaluation of new recovery sites	USFWS*, NPS, USFS, BLM, other Federal agencies, States, Tribes	1050	840	840	2730
1	3.3.4	Conduct site-specific monitoring of ferret populations and environmental variables	USFWS*, BFFRIT	300	240	240	780

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
1	3.4.2	Assess site conditions prior to ferret releases	USFWS*, BFFRIT	600	480	480	1560
1	3.5.1	Release sufficient numbers of ferrets to meet downlisting criteria of establishing 1500 free-ranging adults distributed among at least 10 populations, with no less than 30 breeding adults in each population	USFWS*, BFFRIT	1140	0	0	1140
1	3.5.2	Continue releases to meet the delisting criteria	USFWS*, BFFRIT	0	1140	1680	2820
1	3.5.3	Represent all founders as equally as possible in each released population	USFWS*, BFFRIT, SSP®	300	240	240	780
1	3.5.4	Support the use of wild-born ferrets for reintroduction at other sites	USFWS*, BFFRIT, SSP®	900	720	720	2340

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
1	3.6.1	Monitor ferrets	USFWS*, BFFRIT, NPS, USFS, BLM, USGS, States, Tribes	1500	1200	1200	3900
1	3.6.2	Monitor and evaluate changes in prairie dog density and distribution	USFWS*, BFFRIT, NPS, USFS, BLM, States, Tribes	300	240	240	780
1	3.6.3	Monitor disease dynamics	USFWS*, USGS, NPS, USFS, APHIS, BLM, States, Tribes	300	240	240	780
1	3.6.4	Monitor and evaluate changes in the site environment	USFWS*, BFFRIT, NPS, USFS, BLM, States, Tribes	300	240	240	780

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
1	3.7.7	Support disease monitoring and management capabilities	USFWS*, USGS, APHIS	400	920	920	2240
1	3.7.8	Improve understanding of ferret demography and genetics	USFWS*, BFFRIT, USGS, SSP®	350	280	280	910
1	3.7.9	Consider population viability, including potential effects of inbreeding, interspecific interactions, and disease	USFWS*, USGS, SSP®, BFFRIT	350	280	280	910
1	3.8	Enforce all laws protecting established populations	USFWS*, NPS, USFS, BLM, other Federal agencies, States, Tribes	300	840	840	1980
1	3.9.1	Produce annual site reports	USFWS*, BFFRIT	300	240	240	780
1	3.9.2	Include demographic and/or genetic manipulation needs for each population	USFWS*, SSP®, BFFRIT, USGS	300	840	840	1980

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
1	3.9.4	Update reintroduction strategy and protocols	USFWS*, BFFRIT	300	240	240	780
1	4.1.1	Improve guidelines for determining ferret habitat requirements	USFWS*, BFFRIT, USGS	2000	1600	1600	5200
1	4.1.3	Estimate the amount and configuration of habitat necessary to support downlisting and delisting objectives	USFWS*, BFFRIT, USGS	1000	800	800	2600
1	4.2.1	Consult Federal, State, tribal, and private entities with jurisdiction over historical ferret habitats to develop jurisdiction-specific habitat goals and habitat management plans	USFWS*, BFFRIT, NPS, USFS, BLM, other Federal agencies, States, Tribes	10000	10000	10000	30000

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
1	4.2.2	Recover and maintain sufficient ferret habitat to support recovery goals	USFWS*, BFFRIT, NPS, BLM, USFS, other Federal agencies, States, Tribes	5500	4400	4400	14300
1	4.2.3	Engage relevant government agencies currently not participating in ferret recovery	USFWS*, BFFRIT, NPS, USFS, BLM, other Federal agencies, States, Tribes	4000	4800	4800	13600
1	5.2.1	Develop and implement prophylactic methods for controlling sylvatic plague	USGS*, USFWS, APHIS,	3800	2700	2700	9200

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
1	5.2.2	Develop and implement ecological methods for control of sylvatic plague in ferret recovery areas, including methods based on manipulation of ferret habitats or associated species communities	USFWS*, BFFRIT, NPS, USGS, USFS, BLM, other Federal agencies, States, Tribes	3500	1700	1700	6900
1	5.4.2	Maintain public support for ferret reintroduction efforts at sites with disease issues	USFWS*, BFFRIT, USGS	150	100	100	350
2	1.5.2	Conduct and evaluate efforts to improve reproductive output to support genetic management and reintroduction efforts	SSP®*, USFWS	270	180	180	630
2	1.5.3	Continue management efforts to balance the genetic representation of founders in the captive population	SSP®*, USFWS	450	300	300	1050
2	1.5.4	Evaluate the reproductive fitness, genetics, and demography of the captive population	USFWS*, SSP®	510	340	340	1190

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
2	3.1	Maintain a list of research needs related to reintroduction and population monitoring	BFFRIT*, USFWS	50	40	40	130
2	3.2	Maintain a standardized ranking procedure for allocating ferrets to candidate reintroduction sites	USFWS*, BFFRIT	50	40	40	130
2	3.3.2	Collect information for site screening and baseline data purposes	USFWS*, NPS, USFS, BLM, other Federal agencies, States, Tribes	225	180	180	585
2	3.3.5	Standardize annual site monitoring and reporting to the extent practical	USFWS*, BFFRIT	150	120	120	390
2	3.4.1	Comply with obligations of the ESA, NEPA, and other laws	USFWS*, NPS, USFS, BLM, USGS, other Federal agencies, States, Tribes	50	40	40	130

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
2	3.4.3	Schedule and prepare ferrets for releases	USFWS*, SSP®	150	120	120	390
2	3.7.1	Continue the use of ferret preconditioning techniques	USFWS*, SSP®	50	40	40	130
2	3.7.2	Optimize release methods and timing	USFWS*, BFFRIT	50	40	40	130
2	3.7.3	Continue to improve ferret monitoring techniques	USFWS*, BFFRIT, NPS, USGS, USFS, BLM, other Federal agencies, States, Tribes	50	40	40	130
2	3.7.6	Continue to improve techniques for habitat monitoring and habitat evaluation	USFWS*, BFFRIT, USGS, USFS, BLM, other Federal agencies, States, Tribes	50	40	40	130

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
2	3.9.3	Evaluate and update site monitoring and research efforts	USFWS*, BFFRIT, USGS	100	80	80	260
2	4.1.2	Assess progress toward meeting downlisting and delisting criteria	USFWS*, BFFRIT	500	400	400	1300
2	5.1.2	Develop a list of bibliographies of publications and projects relevant to disease	USGS*, USFWS	30	20	20	70
2	5.1.3	Synthesize relevant information and research results	USFWS*, USGS	30	20	20	70
2	5.1.4	Report epizootics to the Centers for Disease Control, the National Wildlife Health Laboratory, and other appropriate disease research facilities	USFWS*, BFFRIT	60	40	40	140
2	5.4.1	Conduct periodic symposia and workshops to exchange information on diseases	USFWS*, BFFRIT, USGS	150	100	100	350
2	6.1.1	Support review and analysis of program progress	USFWS*, SSP®, BFFRIT	4000	2900	2900	9800

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
2	6.1.2	Coordinate program components and update program direction as appropriate based on reviews addressed in task 611	USFWS*, BFFRIT, USGS, SSP®	1340	940	940	3220
2	6.1.3	Formally report on progress toward recovery objectives on a five-year basis	USFWS	60	60	60	180
2	6.1.4	Use the BFFRIT to help identify problems and solutions	USFWS*, BFFRIT	350	250	250	850
2	6.4	Consider funding needs for national and international ferret recovery	USFWS*, BFFRIT	290	210	210	710
3	1.3	Provide a description of research needs related to genetic and demographic management of captive populations	USFWS*, SSP®, BFFRIT, USGS	60	40	40	140
3	1.4.4	Maintain a list of disease research contacts	USFWS*, SSP®, BFFRIT, USGS	60	40	40	140
3	1.5.1	Conduct regular reviews of breeding strategies	SSP®*, USFWS, BFFRIT	120	80	80	280

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
3	1.6	Establish policies for the use and handling of dead, non-reproductive, or otherwise excess ferrets	USFWS	60	40	40	140
3	2.2	If a remnant population is located, develop a plan to integrate any population into the recovery program	USFWS	0	0	0	0
3	3.7.4	Continue to improve survey techniques	USGS*, USFWS	175	140	140	455
3	3.7.5	Continue to improve telemetry equipment and techniques	USGS*, USFWS	50	40	40	130
3	5.1.1	Consider development of a list of disease research needs	USGS*, USFWS	30	20	20	70
3	5.3.1	Continue to implement prophylactic methods for control of canine distemper	USGS*, USFWS	150	100	100	350

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
3	5.3.2	Continue to implement ecological methods for control of canine distemper in ferret recovery areas, including methods based on manipulation of ferret habitats or associated carnivore communities	BFFRIT*, USGS, USFWS	210	140	140	490
3	6.1.5	Encourage the formation of jurisdictional and topical working groups to identify problems and solutions	USFWS*, BFFRIT	60	40	40	140
3	6.2.1	Maintain an up-to-date website describing the ferret recovery program and partnership opportunities	USFWS*, BFFRIT	60	40	40	140
3	6.2.2	Promote recovery partnerships through the formation of jurisdictional and topical working groups	USFWS*, BFFRIT	60	40	40	140
3	6.2.3	Encourage the exchange of scientific information and technical advice	USFWS*, BFFRIT	120	80	80	280

PRIORITY #	TASK #	ACTION DESCRIPTION	LEAD* & RESPONSIBLE PARTIES	COST ESTIMATES (\$1,000'S)			
				FY 10-20	FY 21-30	FY 31-40	TOTAL
3	6.3.1	Support the efforts of States, tribes, and other organizations to recover the ferret	USFWS*, BFFRIT	90	60	60	210
3	6.3.2	Encourage public support for ferret recovery through strategically focused outreach efforts	USFWS*, BFFRIT	440	300	300	1040
3	6.3.3	Provide ferret recovery information to Non-Government Organizations currently supporting recovery and solicit the assistance of other NGOs who could aid species recovery	USFWS*, BFFRIT	60	40	40	140
3	6.3.4	Support participation and coordination among government agencies with jurisdiction over programs related to ferret recovery	USFWS*, BFFRIT	60	40	40	140
3	6.3.5	Maintain updated information on the contributions of SSP® captive breeding facilities	USFWS*, BFFRIT, SSP®	60	40	40	140

PART IV. LITERATURE CITED

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

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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.

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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 interspersed of Douglas fir (*Pseudotsuga menziesii*), spruce (*Picea engelmannii*), 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,

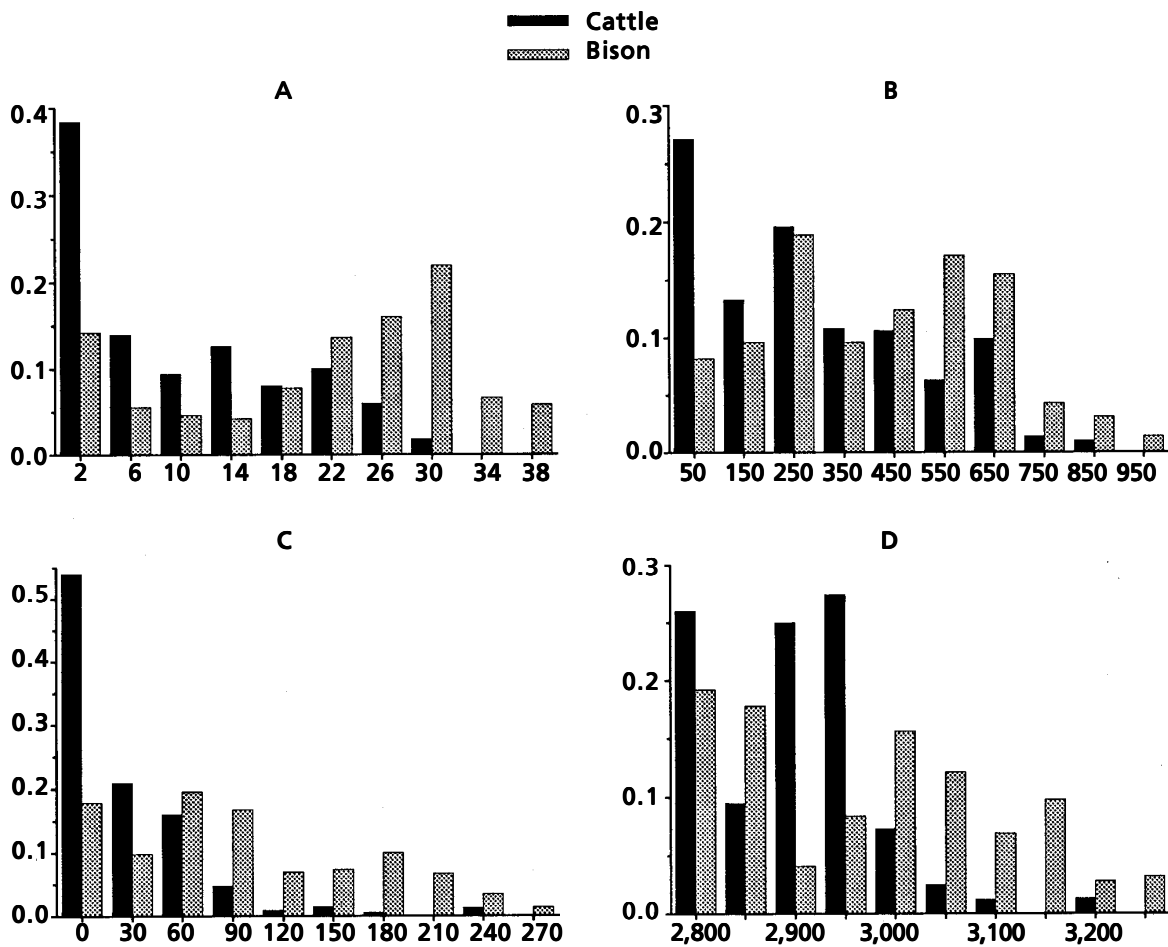


Fig. 1. Proportion of observations of foraging bison and cattle in relation to: A. Slope, in degrees; B. Horizontal distance from water, in m; C. Vertical distance from water, in m; D. Elevation, in m, at the headwaters of South Creek, Henry Mountains, Utah.

Fig. 1. Proporción de observaciones de forrajeo del bison y del ganado vacuno en relación con: A. Inclinação 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

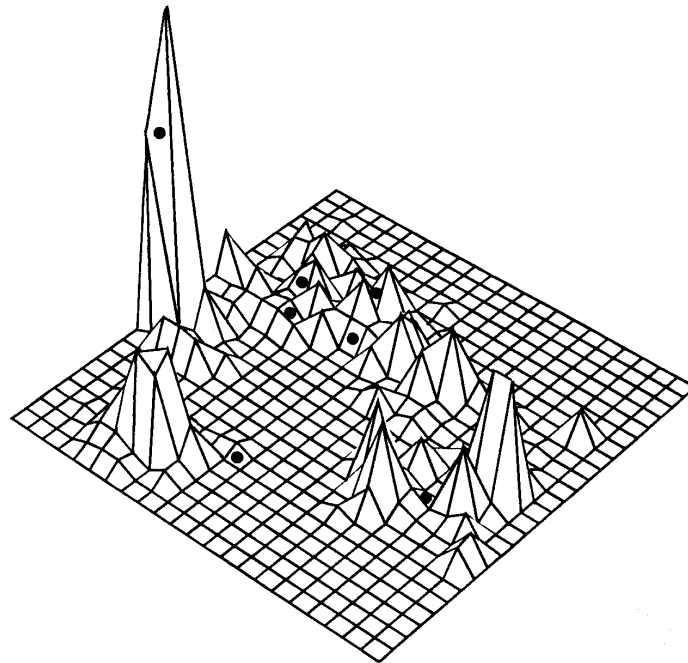
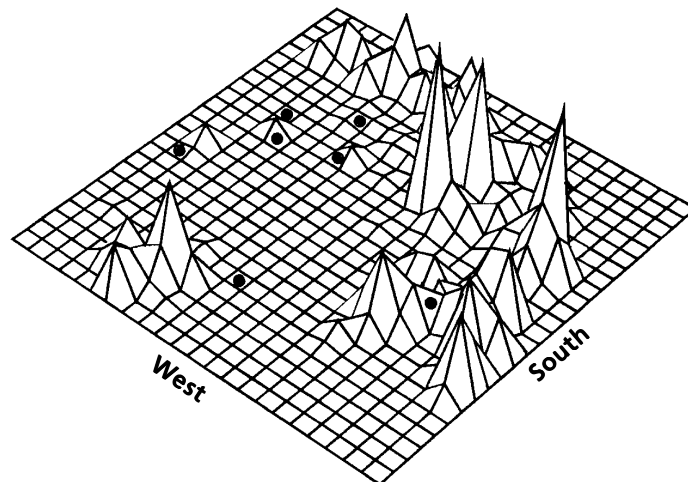
Cattle**Bison**

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.

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