

# Terrestrial vertebrate communities at black-tailed prairie dog (*Cynomys ludovicianus*) towns

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## Abstract

We capitalized on a regional-scale, anthropogenic experiment—the reduction of black-tailed prairie dog (*Cynomys ludovicianus*) towns across the Great Plains of North America—to test the hypothesis that decline of this species has led to declines in diversity of native grassland vertebrates of this region. We compared species richness and species composition of non-volant mammals, reptiles and amphibians at 36 prairie dog towns and 36 paired sites in the Panhandle Region of Oklahoma during the summers and falls of 1997, 1998 and 1999. We detected 30 species of mammals, 18 species of reptiles and seven species of amphibians. Comparisons between communities at prairie dog towns and paired sites in the adjacent landscape indicated that while richness per se was not necessarily higher in towns, they did harbor significantly more rare and imperiled species. Species that were positively associated with prairie dog towns during one or both seasons (summer and fall) included badgers (*Taxidea taxus*), eastern cottontails (*Sylvilagus floridanus*), coyotes (*Canis latrans*), grasshopper mice (*Onychomys leucogaster*), swift fox (*Vulpes velox*), pronghorn antelopes (*Antilocapra americana*), striped skunks (*Mephitis mephitis*), white-tailed deer (*Odocoileus virginianus*), cattle, thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*), black-tailed jackrabbits (*Lepus californicus*), barred tiger salamanders (*Ambystoma tigrinum*), plains spadefoot toads (*Scaphiopus bombifrons*), Great Plains toad (*Bufo cognatus*), Woodhouse's toad (*Bufo woodhousii*), prairie rattlesnakes (*Crotalis viridis*), western plains garter snakes (*Thamnophis radix*), Texas horned lizards (*Phrynosoma cornutum*), and ornate box turtles (*Terrapene ornata*).

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## 1. Introduction

The terms “ecosystem engineer” and “keystone species” are interrelated in that they refer to species and factors influencing the organization, assembly, and disassembly of ecological communities (Paine, 1969, 1995; Mills et al., 1993; Brown, 1995; Lawton and Jones, 1995; Power et al., 1996). Unfortunately, both terms carry some burdensome political and semantic baggage. Yet, as the ecological dominance of our own species intensifies, these concepts become increasingly relevant for conserving diversity of native ecosystems. Semantic

issues aside, the simplest and most relevant criterion for a “keystone species” is taken from their architectural derivations. While all stones in a Roman arch are interdependent and contribute to its integrity, it is the keystone that is believed to complete and stabilize the structure. The most obvious and important application of this for conservation biologists is that, in comparison to most other species, removal of a “keystone” species will have a highly disproportionate effect on community structure.

Keystone species may include those whose effects are direct—i.e. through predation and other interspecific interactions (Paine, 1969), or indirect through their actions as ecosystem engineers, altering succession and composition of native landscapes or seascapes (Brown, 1995; Lawton and Jones, 1995). Some species may act in both ways. For conservation biologists, the relevance of

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these related concepts is far more than academic. When such species become extirpated, the effects may cascade across trophic levels, resulting in the collapse of native communities, often to be replaced by assemblages of species adapted to the expanding matrix of anthropogenic habitats (see Fox, 1987; Lomolino and Perault, 2000; Mikkelsen, 1993). Such species substitutions may result in little change in alpha diversity, while both beta diversity and global diversity may decline as the earth's biotas become homogenized (Lockwood and McKinney, 2001; Lomolino et al., 2001). It is clear that conservation biologists should focus, not just on richness per se, but on diversity and distributions of native, imperiled species.

Ecologists often view manipulative experiments as the most rigorous means of testing these and related concepts in community assembly. Such experiments, however, may be both logistically infeasible (if performed at the appropriate temporal and spatial scales) and unethical, especially in the realm of conservation biology (Diamond, 1986; Brown, 1995). Unfortunately, native landscapes are now replete with unplanned, but none-the-less instructive, manipulative “experiments” that have reduced or removed populations of putative keystone species and ecological engineers.

On the Great Plains of North America, black-tailed prairie dogs (*Cynomys ludovicianus*) once ranged across

as much as 40,000,000 ha of short and mixed-grass prairie (Fig. 1; see Miller et al., 1994, 2000). Today, agricultural development, poisoning, shooting, and sylvatic plague (*Yersinia pestis*) have combined to reduce prairie dog populations to less than 5% of these historic estimates (Miller et al., 1994, 2000; Miller and Cully, 2001). Black-tailed prairie dogs are now extirpated from Arizona, and colonies in other areas continue to be reduced in size and fragmented. In Oklahoma, for example, the mean town size is about 10 ha and even the largest towns are less than 500 ha (Lomolino and Smith 2001). Such fragmentation, isolation and downsizing of towns may lead to continued declines of this putative ecosystem engineer along with a variety of other species thought to be associated with prairie dog towns in different regions (see Pizzimenti, 1981; Wilcox and Murphy, 1985; Hanski and Gilpin, 1997; Wuerthner, 1997; Miller et al., 1994; Lomolino et al., 2001).

Although use of the terms “keystone species” and “ecosystem engineer” for prairie dogs has been debated (Stapp, 1998; Kotliar et al., 1999; Kotliar, 2000; Miller et al., 2000), there is little doubt that prairie dogs have measurable effects on soil structure and chemistry, plant community composition and primary productivity and, in turn may influence the structure of animal communities (Koford, 1958; Bonham and Lerwick, 1976;

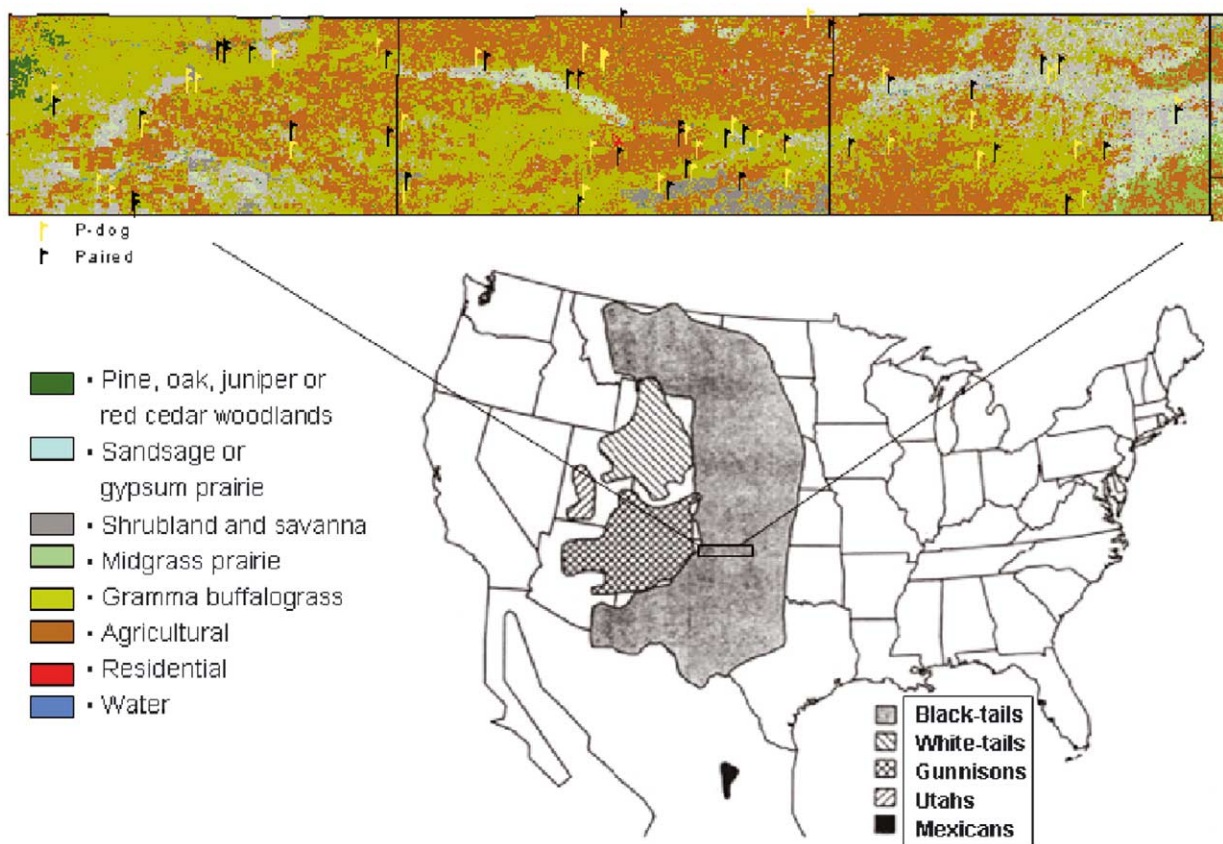


Fig. 1. Geographic distribution of the five prairie dog species (Hoogland, 1995, p. 12) in North America and map of the Panhandle region of Oklahoma indicating locations of sites surveyed in this study and principal, macrohabitats.

O'Melia et al., 1982; Agnew et al., 1986; Krueger, 1986; Whicker and Detling, 1988; Clark et al., 1989; Reading et al., 1989; Sharps and Uresk, 1990; Weltzin et al., 1997; Ceballos et al., 1999; Manzano-Fischer et al., 1999). There remains a critical need, however, to document the ecological role of prairie dogs and test whether particular vertebrates, especially rare and imperiled species, are significantly associated with prairie dog towns.

The geographic range of black-tailed prairie dogs, although dynamic, remained extensive throughout much of the late Pleistocene and early Holocene (Goodwin, 1995). Many species came to depend on these stable and predictable habitats, refugia and microclimates offered by burrows, or the abundance of prairie dogs and associated prey species (Benedict et al., 1996). Thus, the anthropogenic decline of this native ecosystem constitutes a regional scale "experiment" that is of heuristic value to ecologists and vital interest to conservation biologists.

Here we capitalize on this anthropogenic experiment to test the hypothesis that prairie dogs influence the structure of terrestrial vertebrate communities. Specifically, we focus on non-volant mammals, reptiles and amphibians and test whether community structure (species richness and composition) at black-tailed prairie dog towns differs significantly from that at paired sites in the adjacent landscape.

## 2. Methods

### 2.1. Study sites and field methods

All field work was conducted in the Oklahoma Panhandle, which constitutes a transition zone from the mixed grass prairies in the east to short grass prairies of the west. The Panhandle is a three county area stretching approximately 270 km east–west, covering 14,737 km<sup>2</sup>, and surrounded by the bodies of the states of Oklahoma, Kansas, Colorado, New Mexico, and Texas. Historically, much of this area was short-grass plains dominated by buffalo grass (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*), along with dense concentrations of sand sage (*Artemisia* spp.) in the east. Over the past two centuries, agricultural development and cattle ranching have expanded westward across this region (Morris et al., 1986), leaving only remnants of native ecosystems in the form of much reduced and sparsely distributed prairie dog towns, riparian habitats, and rocky mesas in the extreme western portions of the Panhandle.

Surveys for non-volant, terrestrial vertebrates were conducted during summer (mid-May to early August) and fall (mid-November to mid-December) of 1997, 1998 and 1999. Prairie dog towns, which ranged from

9.0 to 211.0 ha, were located on maps developed during our previous roadside surveys of this region (Lomolino and Smith, 2001) along with information from land owners and Game Wardens. Permission from land-owners was obtained for each site surveyed.

We conducted simultaneous surveys for terrestrial vertebrates at 36 prairie dog towns and 36 paired sites (Fig. 1) utilizing identical survey protocols. Paired sites were chosen such that they were between 0.6 and 8.0 km from the focal, prairie dog town and were comprised of habitat that covered an area at least as extensive as the focal town. Paired sites were located within one of the major macrohabitats that constituted the anthropogenic matrix of this region: rangeland, scrubland, CRP (Conservation Reserve Program, primarily dominated by an Old World bluestem, *Bothriochloa ischaemum*), and cleared fields.

We surveyed 12 towns and their 12 paired sites during each summer and repeated surveys at half of these sites during fall. Thus, over three years we conducted a total of 108 surveys for terrestrial vertebrates at 72 sites (36 of these sites were surveyed over two seasons). Mammal species were recorded by live-trapping, surveying for sign, photographing with infra-red triggered cameras, tracking, and direct observation. At each prairie dog town, between three and five trapping stations were set-up, spaced 100 m apart and no closer than 75 m from the edge of the town. Trapping stations consisted of one chipmunk-sized Tomahawk live-trap [12.7×12.7×40.8 cm (5.0×5.0×6.0 inches); Tomahawk Live Trap, Tomahawk, Wisconsin] located at the center of the station and surrounded by one large Sherman live-trap [10.2×11.4×38.1 cm (4.0×4.5×15.0 inches); H.B. Sherman Traps, Tallahassee, Florida] and three small Sherman live-traps [7.6×7.6×22.9 cm (3.0×3.0×9.0 inches)] placed at the four cardinal directions approximately 5 meters from the station center. Approximately 10 m from the center of each station, we placed a 5 m drift fence of garden edging. Sealed, 2-Liter plant pots (pit-falls) were buried at each end and at the center of the fence and filled 1/4 full with water.

Tomahawk traps were baited with mackerel, apples, cracked corn, and a mixture of peanut butter and oats. Sherman traps were baited with apples and peanut butter and oats. A small wad of cotton was added to each Sherman trap during the trapping session to provide insulation and bedding material for any captures. Pit-falls were baited with peanut butter and oats. Traps were locked open for a 5-day pre-bait period, then unlocked, rebaited, and checked daily for 7 days. All small mammals captured were identified to species, weighed, measured, sexed, aged, marked by toe clipping, and released. Relative frequencies for each trapped species were determined by dividing the number of unique individuals captured by the number of functional trap nights. Functional trap nights were calculated by

subtracting from the total potential number of trap nights 1.0 for traps that were not functional and 0.5 for traps that were disturbed, missing bait, or contained a recaptured individual (Songer et al., 1997).

At each site, 100 m from the center trapping station, we set up one baited station to record tracks and photographs of mammals. The tracking station consisted of a 1 m<sup>2</sup>, galvanized steel tracking plate paired with an infra-red triggered camera unit. The stations were baited with beef and mackerel to attract carnivores, and peanut butter and oats, corn, and apples for herbivores. Each plate was sprayed with a 2:5 mixture of carpenter's chalk and 70% isopropyl alcohol. The alcohol quickly evaporated leaving the plate covered with a thin and even layer of chalk allowing prints to be recorded. Tracking/camera stations were checked periodically during the 12-day session to identify prints and sign, replace film, rebait, and check for proper functioning of the equipment.

Presence of reptiles and amphibians at towns and their paired sites were determined by active searches in and under appropriate microhabitats at each site, and concurrently with live and pitfall trapping for mammals and surveys for mammal sign. Walking searches for reptiles and amphibians were conducted during the 12-day trapping sessions at each site. During 3 years of field surveys (summer and fall combined), 522 mammal stations were established, totaling 37,062 potential trap nights, and just over 54 h of herpetile surveys were conducted.

At each trap station, 13 local environmental variables were recorded during each session. A 10-m rope, knotted at 1-m intervals, was laid on the ground along each cardinal direction from the center of the station. Therefore, there were 40 measurement points (4–10 m lines with 10 knots per line). Under each knot, we recorded the presence of grass, forbs, bare soil, litter, cacti, yucca, cattle dung, shrubby/woody vegetation, rock, and other material. We also recorded presence of vegetation reaching the following height categories: 11–25 cm; 26–50 cm; > 50 cm. Measurements of these local environmental characteristics were converted into a percentage of sampling points containing a particular vegetation type or belonging to a particular height category.

The survey protocol, including number of stations within a site, spacing among stations, complement of traps set at each station, and protocols for herpetile surveys, tracking and camera surveys, and habitat assessments at each town was exactly duplicated on its paired site.

## 2.2. Analytical methods

We compared species richness at each prairie dog town to that of its paired site, and then counted the number of paired comparisons where richness was

higher at the town or at its paired site. We then used binomial tests to calculate the probability that these results could be due to chance (two-tailed binomial test with cumulative probability function and conditional probability of 0.5). For these analyses, we also included data from our concurrent studies of avian communities at these sites. In addition to conducting these analyses for all species of terrestrial vertebrates, we repeated them for the subset of species including just those of conservation priority (see Table 1).

Given the multifactorial nature of ecological communities, we used discriminant function analyses and multiple correspondence analysis to investigate differences in environmental characteristics and species composition among macrohabitats (towns, rangeland, scrubland, CRP and cleared fields). We used multiple discriminant analysis (SYSTAT version 10, SPSS, Inc. 2000) to test the statistical significance of differences in habitat characteristics and community structure based on the composition of mammal and herpetile communities. Discriminant function analyses were conducted using data from those species that occurred on at least three of the sites studied. We used multiple correspondence analysis (SYSTAT version 10, SPSS, Inc. 2000) to compare differences in species assemblages among communities within the five principal macrohabitats, again based on incidences of those species that occurred on at least three of the study sites.

## 3. Results

### 3.1. Local habitat

Environmental characteristics differed significantly among the five macrohabitats (prairie dog towns, rangeland, scrubland, CRP and cleared fields) during both summer and fall surveys [based on discriminant function analysis (DFA) of 13 habitat variables; between group  $F$ -values > 5.00,  $P < 0.001$ ; overall  $F$ -values = 7.61 and 7.26 for analyses using summer or fall data, respectively]. Thus, the macrohabitats can be considered distinct landscape-level treatments in subsequent analyses. Based on the jackknifed classification matrix of DFA of local habitat variables, prairie dog towns and scrublands were the most distinct macrohabitats we studied (% classification success for prairie dog towns and scrublands = 94 and 100% during summer, and 100 and 80% during fall).

### 3.2. Species richness among seasons and macrohabitats

Thirty species of mammals, 18 species of reptiles, and seven species of amphibians were detected during our surveys (Table 1). For each of these faunal groups, richness was significantly higher during summer than fall ( $P = 0.040$  for mammals,  $P < 0.001$  for reptiles, and

Table 1  
Non-volant, terrestrial vertebrate species detected during biological surveys in Oklahoma's Panhandle region in 1997, 1998 and 1999 (\* denotes species with conservation status at the state or federal levels)

Common name	Scientific name
<b>Mammals</b>	
Least Shrew	<i>Cryptotis parva</i>
Eastern Mole	<i>Scalopus aquaticus</i>
Black-tailed Jackrabbit	<i>Lepus californicus</i>
Desert Cottontail	<i>Sylvilagus audubonii</i>
Eastern Cottontail	<i>Sylvilagus floridanus</i>
Hispid Cotton Rat	<i>Sigmodon hispidus</i>
Hispid Pocket Mouse	<i>Chaetodipus hispidus</i>
House Mouse	<i>Mus musculus</i>
N. Grasshopper Mouse	<i>Onychomys leucogaster</i>
Deer Mouse	<i>Peromyscus maniculatus</i>
Western Harvest Mouse	<i>Reithrodontomys megalotis</i>
Ord's Kangaroo Rat	<i>Dipodomys ordii</i>
Plains Harvest Mouse	<i>Reithrodontomys montanus</i>
Plains Pocket Mouse	<i>Perognathus flavescens</i>
Prairie Vole	<i>Microtus ochrogaster</i>
Silky Pocket Mouse	<i>Perognathus flavus</i>
Southern Plains Woodrat	<i>Neotoma micropus</i>
Black-tailed Prairie Dog*	<i>Cynomys ludovicianus</i>
Spotted Ground Squirrel	<i>Spermophilus spilosoma</i>
Thirteen-lined Ground Squirrel	<i>Spermophilus tridecemlineatus</i>
American Badger	<i>Taxidea taxus</i>
Coyote	<i>Canis latrans</i>
Swift Fox*	<i>Vulpes velox</i>
Striped Skunk	<i>Mephitis mephitis</i>
Raccoon	<i>Procyon lotor</i>
Yellow-faced Pocket Gopher	<i>Pappogeomys castanops</i>
Pronghorn	<i>Antilocapra americana</i>
Mule Deer	<i>Odocoileus hemionus</i>
White-tailed Deer	<i>Odocoileus virginianus</i>
Cattle	<i>Bos taurus</i>
<b>Reptiles</b>	
Bull Snake	<i>Pituophis melanoleucus</i>
Checkered Garter Snake	<i>Thamnophis marciatus</i>
Coachwhip	<i>Masticophis flagellum</i>
Ground Snake	<i>Sonora semiannulata</i>
Ornate Box Turtle*	<i>Terrapene ornata</i>
Plains Blackhead Snake	<i>Tantilla nigriceps</i>
Western Hognose Snake	<i>Heterodon nasicus</i>
Prairie Rattlesnake*	<i>Crotalus viridis</i>
Western Plains Garter Snake	<i>Thamnophis radix haydeni</i>
Kansas Glossy Snake	<i>Arizona elegans elegans</i>
Racer	<i>Coluber constrictor</i>
Racerunner	<i>Cnemidophorus sexlineatus</i>
Earless Lizard*	<i>Holbrookia maculata</i>
Eastern Collared Lizard	<i>Crotaphytus collaris</i>
Fence Lizard	<i>Sceloporus undulatus</i>
Texas Horned Lizard*	<i>Phrynosoma cornutum</i>
Ground Skink	<i>Scincella lateralis</i>
Great Plains Skink	<i>Eumeces obsoletus</i>
<b>Amphibians</b>	
Barred Tiger Salamander*	<i>Ambystoma tigrinum</i>
Great Plains Toad	<i>Bufo cognatus</i>
Plains Spadefoot Toad	<i>Scaphiopus bombifrons</i>
Western Green Toad	<i>Bufo debilis</i>
Woodhouse's Toad	<i>Bufo woodhousii</i>
Plains Leopard Frog	<i>Rana blairi</i>
Great Plains Narrow-mouthed Toad	<i>Gastrophryne olivacea</i>

$P < 0.001$  for amphibians; based on comparisons of richness at the 36 sites surveyed both during the summer and fall; binomial tests excluding ties). The seasonal difference in mammalian richness was largely due to a significant, seasonal decline in richness at prairie dog towns ( $P = 0.011$ , binomial test across seasons; cleared fields were not surveyed during fall, and CRP lands were surveyed too infrequently during fall to justify statistical analyses).

Four species of mammals [house mouse (*Mus musculus*), eastern mole (*Scalopus aquaticus*), thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*) and desert cottontail (*Sylvilagus audubonii*)] were detected solely during summer surveys, while no mammals were detected only during fall surveys (house mice and eastern moles were detected just once during the 3-year period of our studies and were not included in analyses). Among the herpetiles, all 20 species of reptiles and five species of amphibians were detected during the summers, while only two species [fence lizard (*Sceloporus undulatus*) and prairie rattlesnake (*Crotalus viridis*)] were detected during fall surveys. Therefore, subsequent statistical analyses of herpetile data will be limited to those derived from summer surveys.

Patterns in species richness were markedly different for analyses including all species versus those limited to species of conservation priority (i.e. rare and otherwise imperiled species; Table 1). During summer, prairie dog towns and paired sites had similar diversities of mammals, reptiles and amphibians, while avian richness was significantly higher on towns than at paired sites ( $P = 0.025$ , binomial test based on the number of pairings where richness was higher in prairie dog towns or paired sites; Fig. 2). On the other hand, mammalian richness during fall was significantly lower at prairie dog towns than at paired sites ( $P = 0.0461$ , binomial test). Note, however, that in the fall we did not attempt to detect hibernating species, such as thirteen-lined ground squirrels, which were common at towns during summer surveys.

When we restricted our analyses to species of conservation priority, however, prairie dog towns consistently included a significantly higher diversity of these species (Fig. 3). In addition, cattle activity (measured as frequency of cattle dung detected during habitat surveys; see Section 2.1) was significantly higher on prairie dog towns than their paired sites.

### 3.3. Species composition

Implicit in the previous result is that species composition of vertebrates varied significantly between prairie dog towns and paired sites. DFA and multiple correspondence analysis (MCA) indicated that prairie dog towns and paired sites were inhabited by different assemblages of vertebrates. Despite the significant decline in mammalian richness at prairie dog towns from summer to fall, species composition of mammalian communities was more similar between seasons than

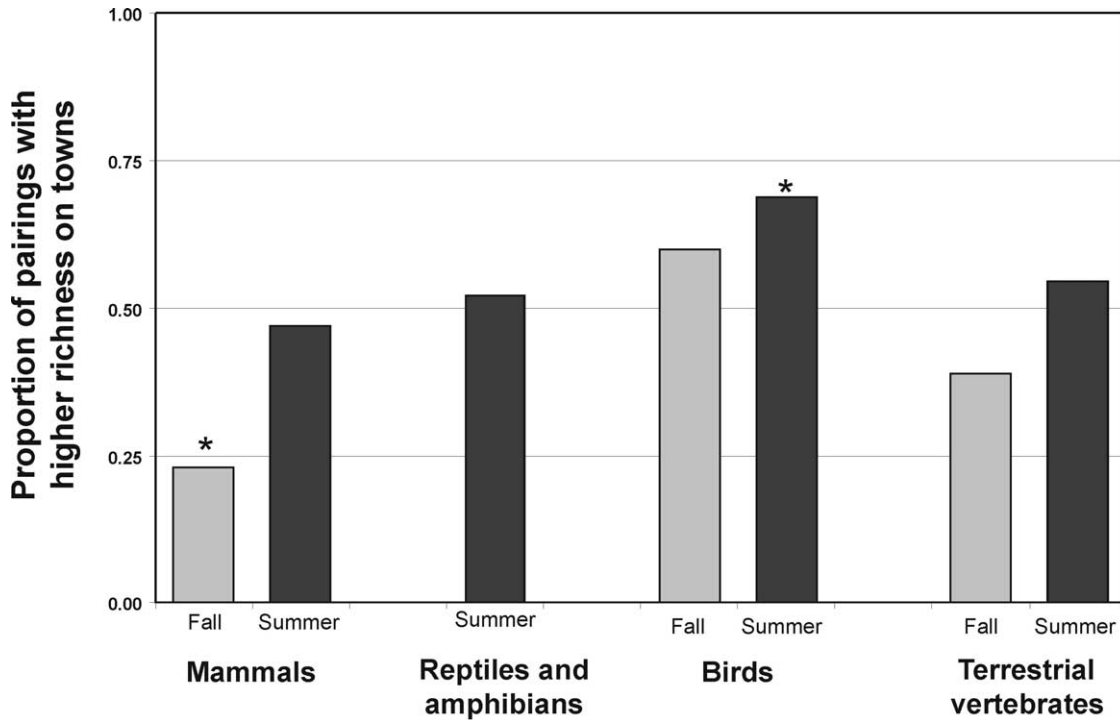


Fig. 2. Comparisons of species richness of terrestrial vertebrates at prairie dog towns and paired sites in the adjacent landscape of the Oklahoma Panhandle during summer and fall of 1997, 1998, and 1999 (36 prairie dog towns and 36 paired sites during summer, 18 prairie dog towns and 18 paired sites during fall). (\* $P < 0.05$ ; binomial test, two-tailed, cumulative probability excluding ties.)

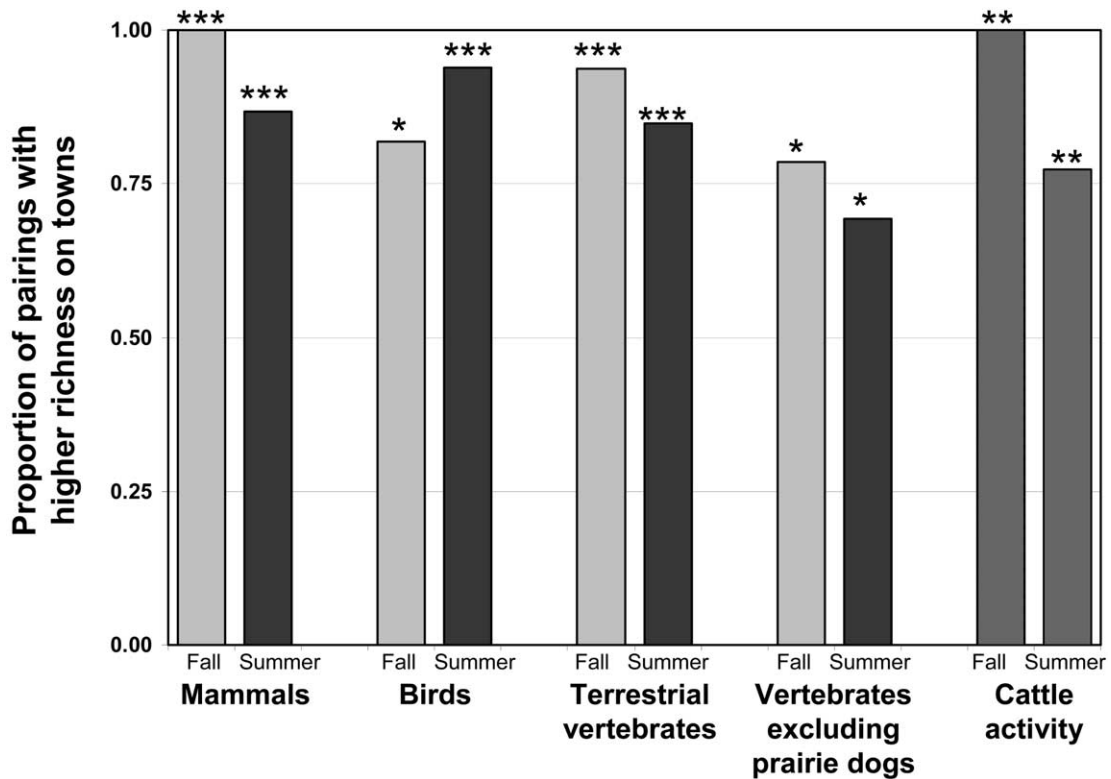


Fig. 3. Comparisons of species richness of terrestrial vertebrates of conservation priority occurring at prairie dog towns and paired sites in the adjacent landscape of the Oklahoma Panhandle during summer and fall of 1997, 1998, and 1999 (36 prairie dog towns and 36 paired sites during summer, 18 prairie dog towns and 18 paired sites during fall). (\* $P < 0.05$ ; binomial test, two-tailed, cumulative probability excluding ties.)

between treatments (prairie dog towns versus paired sites; Fig. 4). That is, mammalian species composition at prairie dog towns varied little from summer to fall, but different assemblages of species were associated with prairie dog towns and their paired sites (overall  $F_{72,242}=5.024$ , DFA excluding species occurring at fewer than three sites). Inspection of variable loadings in DFA and of ordination plots from MCA indicates that prairie dog town associates across both seasons included badgers (*Taxidea taxus*), thirteen-lined ground squirrels, cattle (*Bos* spp.), eastern cottontails (*Sylvilagus floridanus*), coyotes (*Canis latrans*), grasshopper mice (*Onychomys leucogaster*), swift fox (*Vulpes velox*) and pronghorn (*Antilocapra americana*).

During summer, each of the five macrohabitats was inhabited by distinct assemblages of mammals (overall  $F_{96,176}=2.83$ ,  $P<0.001$ , DFA). Of the communities inhabiting the five macrohabitats, those at prairie dog towns tended to be most distinct, exhibiting the highest between group  $F$ -values ( $=3.21$ – $4.73$  for comparisons to prairie dog towns, versus  $0.80$ – $2.72$  for other comparisons) and the highest jackknifed classification success (89%, followed by 83% for cleared fields). Town associates during summers included badgers, striped skunks (*Mephitis mephitis*), coyotes, white-tailed deer (*Odocoileus virginianus*), cattle, grasshopper mice, thirteen-lined ground squirrels, eastern cottontails and, to a lesser extent, black-tailed jackrabbits (*Lepus californi-*

*cus*) and swift fox (Fig. 5). Mammalian community patterns were similar during fall (Fig. 6), again exhibiting significant differences in species composition between macrohabitats (DFA; overall  $F_{66,33}=4.16$ ,  $P<0.001$ ). As in analyses for summer surveys, mammalian communities at prairie dog towns during fall appeared to be more distinct than those from other macrohabitats (based on between group  $F$ -values and on jackknifed classification success, which = 72% for prairie dog towns, followed by 64% for range habitats). Town associates during fall included swift fox, pronghorn, cattle, badgers, grasshopper mice, coyotes and eastern cottontails. Again, thirteen-lined ground squirrels may be added to this list as they were common on towns during summers, but we did not attempt to detect them in their hibernacula during fall.

Similar to the results for mammals, herpetile species composition during summer differed significantly among the five macrohabitats (overall  $F_{64,205}=1.45$ ,  $P=0.027$ , DFA based on species occurring in at least three sites; Fig. 7). In this case, however, herpetile communities at cleared fields and CRP sites tended to be most distinct, followed by prairie dog towns (jackknifed classification success = 50, 33 and 28%, respectively). Prairie dog town associates included barred tiger salamander (*Ambystoma tigrinum*), plains spadefoot toad (*Scaphiopus bombifrons*), Great Plains toad (*Bufo cognatus*), Woodhouse's toad (*Bufo woodhousii*), prairie

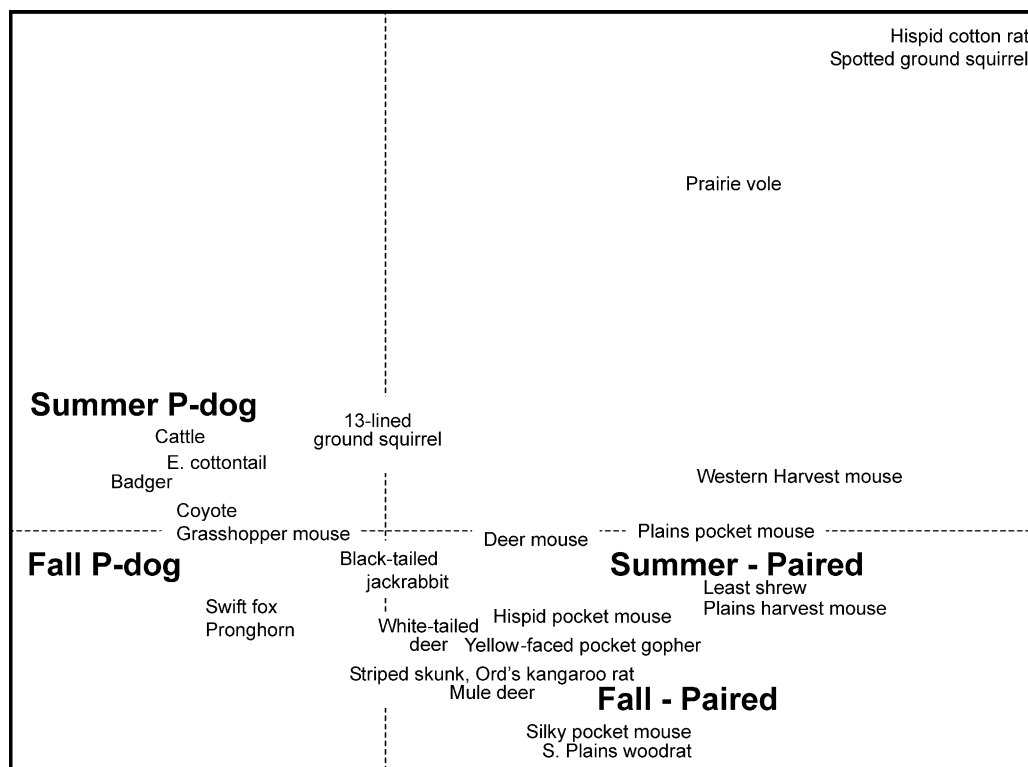


Fig. 4. Differences in assemblages of non-volant mammal communities at prairie dog towns and paired sites across two seasons in the Oklahoma Panhandle during 1997, 1998, and 1999 (36 prairie dog towns and 36 paired sites during summer, 18 prairie dog towns and 18 paired sites during fall). (Plot based on multiple correspondence analysis including just those species occurring on at least three sites.)

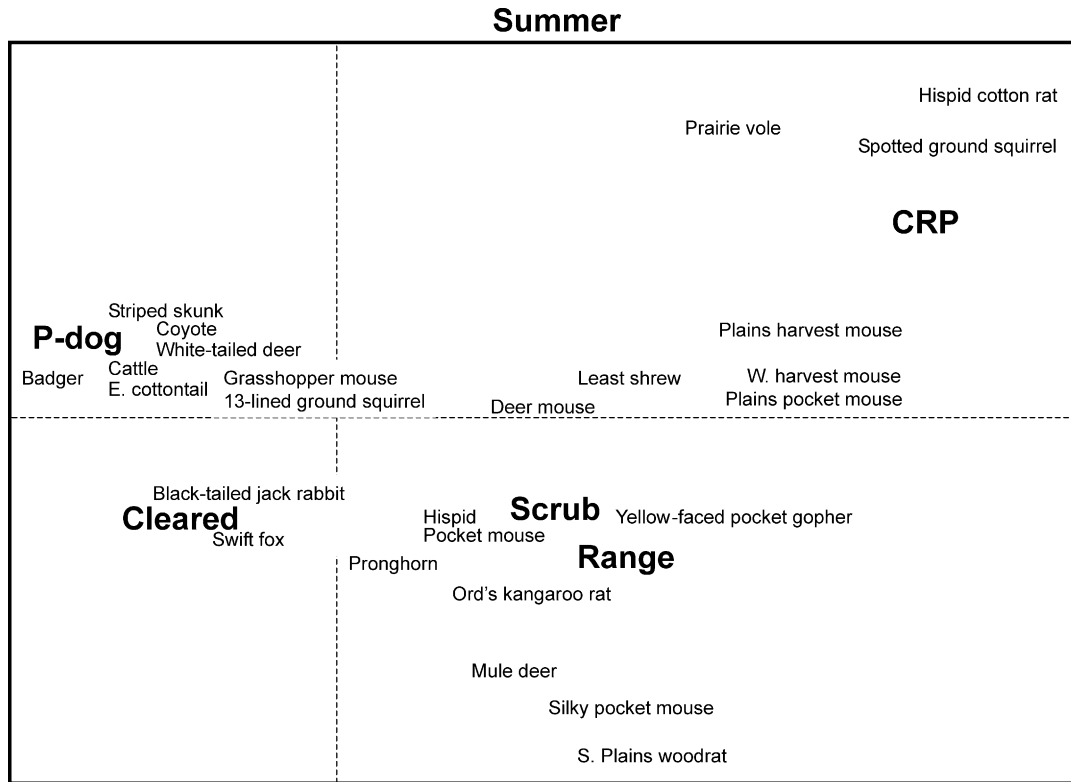


Fig. 5. Differences in assemblages of non-volant mammal communities at 36 prairie dog towns and 36 paired sites during summers of 1997, 1998, and 1999 in the Oklahoma Panhandle (based on multiple correspondence analysis including just those species occurring on at least three sites).

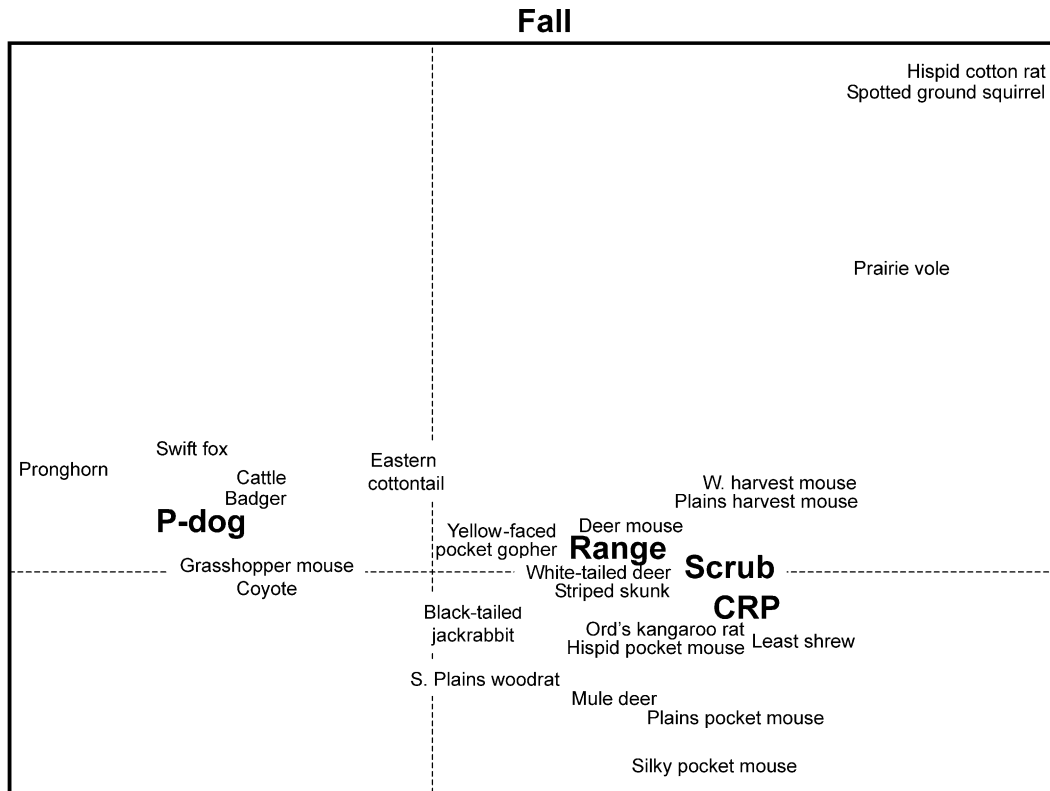


Fig. 6. Differences in assemblages of non-volant mammal communities at 18 prairie dog towns and 18 paired sites during falls of 1997, 1998, and 1999 in the Oklahoma Panhandle (based on multiple correspondence analysis including just those species occurring on at least three sites).



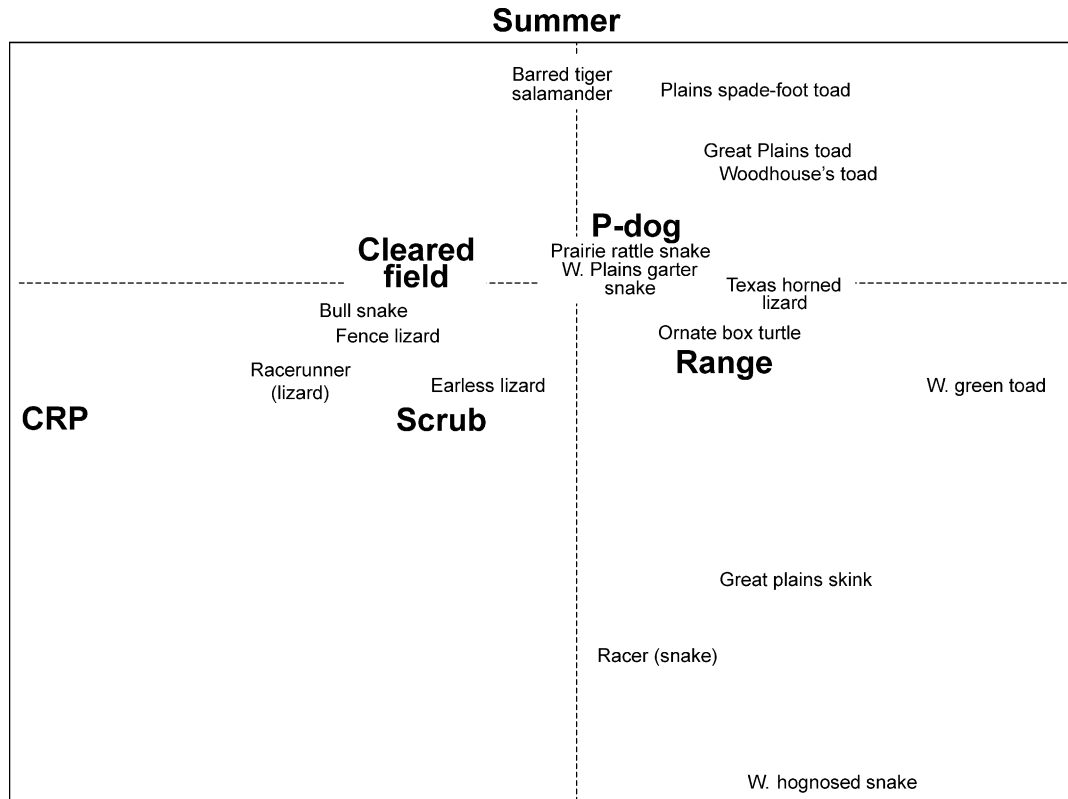


Fig. 7. Differences in assemblages of reptile and amphibian communities at 36 prairie dog towns and 36 paired sites during summers of 1997, 1998, and 1999 in the Oklahoma Panhandle (based on multiple correspondence analysis including just those species occurring on at least three sites).

rattlesnake, western plains garter snake (*Thamnophis radix*), Texas horned lizard (*Phrynosoma cornutum*) and ornate box turtle (*Terrapene ornata*) (Fig. 7).

#### 4. Discussion

Patterns reported here for non-volant terrestrial vertebrates are consistent with those obtained during our concurrent studies of avian communities at these sites (Smith and Lomolino, submitted for publication). That is, prairie dog towns were inhabited by a highly distinct assemblage of bird species, including burrowing owls (*Athene cunicularia*), killdeer (*Charadrius vociferus*), horned larks (*Eremophila alpestris*), meadowlarks (*Sturnella spp.*), scissor-tailed flycatchers (*Tyrannus forficatus*), brown-headed cowbirds (*Molothrus ater*), and lark sparrows (*Chondestes grammacus*) during summer, and ferruginous hawks (*Buteo regalis*), horned larks, longspurs (*Calcarius spp.*), and loggerhead shrikes (*Lanius ludovicianus*) during fall. Just as we observed for mammal and herpetile communities, avian communities in prairie dog towns tended to be most similar to those of cleared fields in contrast to those of rangeland, shrubland or CRP habitats.

Thus, town ecosystems, created and maintained by one species, continue to be inhabited by distinct assemblages

of terrestrial vertebrates, both volant and non-volant. The fact that vertebrate assemblages at black-tailed prairie dog towns remain distinct, despite substantial variation in species composition between seasons, highlights the ecological role of this species as well as the seasonal context of patterns in community assembly. Given the ongoing anthropogenic declines of prairie dog ecosystems (e.g. see Miller et al., 2000; Lomolino and Smith, 2001), these results also portend the likely, continuing declines of native communities across the Great Plains. Anthropogenic disassembly of imperiled communities is most often reported for fragmentation of forested landscapes (Fox, 1987; Lomolino and Perault, 2000; Mikkelsen, 1993), but prairies and other native landscapes may be just as subject to non-random loss of their native species.

The ecological role of prairie dog towns may also be variable and contextual, not just from summer to fall, but over longer time periods and greater spatial scales as well. Multi-annual variation in climate strongly influences the environmental characteristics of ecosystems across the Great Plains, affecting matrix habitats along with regional species pools. For example, distinctness of prairie dog town habitats tends to be much more pronounced during periods of significant precipitation when vegetation becomes more lush. Consistent with this, distinctness of animal communities among prairie

dog towns and the adjacent matrix tends to be highest during periods of moderate to high rainfall (Barko et al., 1999; Winter et al., 1999).

Perhaps even more important for the conservation and potential restoration of native North American species is the more long-term, historical context of these ecological interactions. Towns can only attract and support those species that remain in the regional species pool. Yet species pools have been transformed, reduced or homogenized by anthropogenic activities, replacing native species such as black-footed ferrets (*Mustela nigripes*) and American bison (*Bison bison*) with commensals, exotics and other species associated with anthropogenic habitats. Had our studies been conducted before the dramatic declines of prairie dog towns, it is very likely that ferrets would be added to our species list. Thus, the actual list and total number of town associates would have exceeded the numbers reported here. Just as important, the entire historic range of the black-tailed prairie dog encompasses many regions, including those where other species, although absent from our study area, still persist and continue to be strongly associated with prairie dog towns. Despite this, prairie dog towns harbored significantly higher numbers of rare and otherwise imperiled vertebrates.

Habitat associations of large herbivores provide some especially important insights into the contextual nature of ecological associations with prairie dog towns. The only two grazing ungulates detected, pronghorn antelope and cattle, were positively associated with prairie dog towns. This was especially evident for cattle during both seasons, and for pronghorn during fall, i.e. when grass and herbaceous vegetation would be most limiting. The two browsing ungulates—white-tailed deer and mule deer (*O. hemionus*)—exhibited quite different associations during our studies. In both fall and summer surveys, mule deer were most frequently detected in matrix habitats (rangeland, scrubland and CRP), i.e. habitats with much more shrub biomass than found in prairie dog towns or cleared fields. While the same was true for white-tailed deer during fall surveys, they shifted toward prairie dog towns in the summer. The highly significant and positive association of cattle with prairie dog towns is important both with respect to ranching practices and conservation of native grassland vertebrates. Given this commensalistic, and possibly mutualistic relationship, future programs to develop a range-wide reserve program for prairie dog communities may well include managed grazing by cattle.

Black-tailed prairie dogs maintained an expansive geographic range across much of the Great Plains for at least the past 50,000 years (Goodwin, 1995). Therefore, a number of now extirpated or extinct species may have been associated with towns during the Pleistocene and prior to our rise to ecological dominance in these eco-

systems. The plains bison was just one of the last remnants of a diverse assemblage of megafaunal herbivores, predators, and scavengers that ranged across the Great Plains and may have been associated with habitats maintained by prairie dogs (Benedict et al., 1996; Byers, 1997). These “ghosts of species past” compromise our ability to evaluate the ecological role of prairie dogs in their now altered, anthropogenic landscapes. These confounding challenges are, of course, not unique to the Great Plains ecosystem, but common to nearly all terrestrial and aquatic ecosystems around the world.

Despite the regional, historic and prehistoric context of prairie dog ecosystems, and the spatial and temporal limits of our current study, the influence of prairie dog towns on the structure of native communities is clear and compelling. While these and similar studies provide interesting insights for community ecologists, landscape ecologists and biogeographers, they are especially relevant for conservation biologists. The list of imperiled vertebrates (i.e. species with at least some federal or state protection or conservation designation) of the Great Plains includes several species generally believed to be associated with, or in some way dependent on, prairie dog towns: tiger salamanders, prairie rattlesnakes, Texas horned lizards, ornate box turtles, burrowing owls, mountain plovers (*Charadrius montanus*), ferruginous hawks, Swainson’s hawks (*B. swainsoni*), prairie falcons (*Falco mexicanus*), golden eagles (*Aquila chrysaetos*), lesser prairie-chickens (*Tympanuchus pallidicinctus*), long-billed curlews (*Numenius americanus*), black-footed ferrets and swift fox (Tyler, 1968; Butts, 1976; Knowles et al., 1982; Agnew et al., 1986; Shackford and Tyler, 1991; Miller et al., 1994; Allison et al., 1995; Desmond et al., 1995; Knopf, 1996; Barko et al., 1999). In our own studies, we detected all of these species except black-footed ferrets, and all but lesser prairie-chickens were positively associated with prairie dog towns.

Even within these highly altered landscapes, the remaining small and isolated prairie dog towns continue to attract terrestrial vertebrates, especially the rare and otherwise imperiled species of the Great Plains. Again, we can only speculate on the structure and function of unaltered, expansive and highly connected prairie ecosystems prior to our arrival. Whether we call it a keystone species or an ecosystem engineer, it is clear that prairie dog towns, even in their highly reduced and heavily fragmented condition, provide a valuable opportunity to conserve the native, Great Plains biota.

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