



4-30-2004

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Shaughnessy, Michael J. Jr. and Cifelli, Richard L. (2004) "Influence of black-tailed prairie dog towns (*Cynomys ludovicianus*) on carnivore distributions in the Oklahoma Pandhandle," *Western North American Naturalist*. Vol. 64 : No. 2 , Article 5.

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INFLUENCE OF BLACK-TAILED PRAIRIE DOG TOWNS
(*CYNOMYS LUDOVICIANUS*) ON CARNIVORE DISTRIBUTIONS
IN THE OKLAHOMA PANHANDLE

Michael J. Shaughnessy, Jr.,^{1,3} and Richard L. Cifelli²

ABSTRACT.—Carnivores were recorded at prairie dog towns and non-prairie dog town paired sites in the Oklahoma Panhandle over 4 sampling sessions from October 1995 to February 1997. We established carnivore presence through the use of baited tracking plates dusted with chalk and matched with infrared-triggered cameras. Five carnivore species were recorded at both prairie dog towns and paired sites across the Oklahoma Panhandle. Of these, 4 were recorded with sufficient regularity to permit analyses. Carnivores were analyzed at prairie dog towns across the entire Panhandle and in the Panhandle's westernmost county (Cimarron County) only. Canids showed no significant preference for prairie dog towns or other areas. In the Oklahoma Panhandle and Cimarron County only, occurrence of swift fox (*Vulpes velox*) between prairie dog towns and control sites was insignificant. Badgers (*Taxidea taxus*) and spotted skunks (*Spilogale putorius*) occurred significantly more often at prairie dog towns in Cimarron County but not in the Panhandle. No single mustelid species showed a significant association with either prairie dog towns or non-prairie dog town habitats. Our results indicate that whereas prairie dog towns do attract some carnivore species, the presumption that prairie dogs are "keystone species" for so many organisms (especially threatened or endangered species) in the current plains ecosystem may not be as clear as previously thought.

Key words: prairie dog town, keystone species, carnivore, swift fox, coyote, badger, skunk.

The ability of black-tailed prairie dogs (*Cynomys ludovicianus*) to broadly alter biotic and abiotic characteristics of their environment has been the focus of intense scientific investigation over the last 20 years (Bonham and Lerwick 1976, Clark et al. 1982, Garrett et al. 1982, O'Meila et al. 1982, Coppock et al. 1983, Agnew et al. 1986). More recently, research has been directed to questions regarding the specific effects black-tailed prairie dog activities have on other prairie organisms (Clark et al. 1982, Knowles et al. 1982, Agnew et al. 1986, Whicker and Detling 1988, Sharps and Uresk 1990, Miller et al. 1994, Barko 1997). Their ability to alter their environment has led to the suggestion that black-tailed prairie dogs may function as "keystone species" (a species having a dominating influence on the composition of a community [Ricklefs 1997]) in the prairie ecosystem, creating patches of more suitable or even preferred habitat for other prairie organisms (Clark et al. 1982, Forrest et al. 1988, Seal et al. 1989, Sharps and Uresk 1990, Knowles and Knowles 1994, Miller et al. 1994,

Hoogland 1995, Barko 1997). In Oklahoma, 48 species of vertebrates have been reported to be associates of black-tailed prairie dog towns; 22 of these species are considered rare and/or protected by federal or state legislation (Shackford and Tyler 1991).

Since the turn of the century, black-tailed prairie dog populations have experienced periods of decline and recovery due to numerous factors ranging from disease to federal and private control practices (Miller et al. 1994). The area presently covered by black-tailed prairie dog towns in the central plains may have been reduced by as much as 99% since the turn of the century (Miller et al. 1994). Structure and arrangement of black-tailed prairie dog towns in the environment have changed as well. In the past black-tailed prairie dog towns were typically large and continuous (Marsh 1984). With the reduction in black-tailed prairie dog populations, towns in some areas have become increasingly fragmented, smaller, and isolated (Marsh 1984). As a keystone species, the black-tailed prairie dog would be expected to have a

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disproportionate effect on species assemblages wherever they occur. This change in landscape dynamics could be expected to significantly affect those species associated with black-tailed prairie dog towns.

Populations of black-tailed prairie dogs have declined in Oklahoma, particularly in the region known as the Panhandle (Osborn and Allan 1949, Shaw et al. 1991). Populations in the Panhandle also are unstable, as illustrated by the fact that only 39% of black-tailed prairie dog towns mapped in 1967 survived to 1989 (Shaw et al. 1991). During 1991 some of the largest black-tailed prairie dog towns in the Panhandle were decimated by sylvatic plague (*Yersinia pestis*; Shaw et al. 1991). This reduction of populations and town sizes has provided an increased incentive to study the relationships between black-tailed prairie dogs and their vertebrate associates.

Among the associates reported for black-tailed prairie dog towns, mammalian carnivores have the potential to be some of the most severely affected by decreases in population size and town area. As upper trophic-level consumers, mammalian carnivores may depend upon prairie dog towns to provide food sources, both prairie dogs themselves and small mammals and birds they may attract (Koford 1958, Forrest et al. 1988, Sharps and Uresk 1990, Hoogland 1995). Mammalian carnivores also may exploit prairie dog burrows as potential denning sites, particularly on the edges of prairie dog towns. Smaller carnivores also may depend upon the burrows of prairie dogs as escape routes when pursued by larger carnivores. The black-footed ferret (*Mustela nigripes*), a mammalian carnivore known to be highly associated with prairie dogs, suffered high losses when prairie dogs in Wyoming died from sylvatic plague (Forrest et al. 1988, Seal et al. 1989). In Oklahoma, the 3-county Panhandle region supports 17 mammalian carnivore species (14 extant, 3 historically) in 5 families (Caire et al. 1989). Four of these mammalian carnivores are reported to be associated with black-tailed prairie dog towns (Shackford and Tyler 1991).

The purpose of this research was to examine carnivore occurrence and activity at black-tailed prairie dog towns in the Oklahoma Panhandle. We also investigated whether these carnivores occur at black-tailed prairie dog

towns more often than they occur in surrounding habitats. These questions were intended to provide a better understanding of the role of black-tailed prairie dogs in structuring local and regional carnivore assemblages.

STUDY AREA

We conducted research on prairie dog towns and carnivores in the Oklahoma Panhandle, which is adjacent to the northwesternmost part of the body of the state and is approximately 267 km long (east–west) and 55 km wide (north–south). Three counties (Cimarron, Texas, Beaver) of approximately equal size comprise the Panhandle.

Historically, the Panhandle was a shortgrass prairie dominated by blue grama (*Boteloua gracilis*), buffalograss (*Buchloe dactyloides*), and prairie three-awn (*Aristida oligantha*; Shaughnessy 2003). Prairie dog towns occurred in all habitat types throughout the Panhandle (Shackford and Tyler 1991). Panhandle prairie dog towns also were reported to be continuous, spreading unbroken for miles (Shackford and Tyler 1991). Historically and currently, several major riparian areas cut through the landscape. These are dominated by large eastern cottonwoods (*Populus deltoides*) and taller grasses (Shaughnessy 2003). A mesa habitat, characterized by sand sagebrush (*Artemisia filifolia*), juniper (*Juniperus scopulorum*), prickly pear and/or cholla (*Opuntia* spp.), and two-needle pinyon (*Pinus edulis*; Shaughnessy 2003), dominates the northwest corner of the Panhandle.

Over time the Panhandle environment has been altered by human activities (Shaughnessy 2003). Agricultural, livestock, and fossil fuel interests have come to dominate the landscape (Shaughnessy 2003). Although historical habitat types still persist, the quality and quantity of habitats have changed. Grassland, mesa, and riparian areas are now almost entirely grazed by domestic cattle or converted to other agricultural uses, and little remains of the original, extensive shortgrass prairie (Shaughnessy 2003). Prairie dog towns also have been reduced in numbers and sizes due to periodic episodes of plague (*Yersinia pestis*) and eradication efforts of landowners (Marsh 1984, Shaw et al. 1991). Presently, the total area covered by prairie dog towns in the Oklahoma Panhandle is approximately 562 ha (Shaughnessy 2003).

MATERIALS AND METHODS

We determined the presence and distribution of carnivores by using baited tracking plates at preestablished tracking stations applying the method described in Shaughnessy (2003). Stainless steel tracking plates (approximately 1 m × 1 m) were placed at tracking stations and sprayed with a mixture of isopropyl alcohol and carpenter's chalk. A 1-inch hole was drilled through the center of each plate, allowing it to be placed directly over a stake that permanently marked the tracking station (Shaughnessy 2003). Bait, consisting of canned mackerel and/or beef scraps, was placed in the middle of the plate or on the stake. We examined the plates for tracks and moved them at the end of the 3-night sampling period (Egoscue 1956, Orloff et al. 1986).

Ninety permanent tracking stations were established previously throughout the Panhandle in a stratified random design as part of a broader project examining Panhandle carnivore distributions (Shaughnessy 2003). Stations were established based first on county area and then on area covered by major habitats (Shaughnessy in press). Habitats were identified by vegetation, physiographic features, and/or land use (Shaughnessy 2003). Of 90 stations, 16 were established at prairie dog towns and 16 at control sites located in habitats adjacent to the prairie dog town stations. In almost all instances control sites were located within about 15 km of tracking stations at prairie dog towns. Because of this, we could reasonably expect that any carnivores detected at one site could potentially be detected at that site's pair (Zoellick and Smith 1992). In all instances control sites were placed in habitats similar to or nearly identical to those in which the prairie dog town sites occurred, and control sites were paired with prairie dog town sites as part of the statistical design.

We conducted 4 tracking plate surveys in the Panhandle from October 1995 to February 1997, one survey during each season to minimize within-season variation in carnivore detections. Panhandle counties were surveyed in staggered succession, offset by 1 day per county. We completed all surveys within 7 days of their initiation. Tracking plates at prairie dog towns were operated for 163 functional plate nights across the Panhandle and for 155 functional plate nights at paired sites. Cimarron

County reported the most consistent and highest numbers of carnivore detections at both prairie dog towns and non-town sites. As a result, we analyzed separately data from Cimarron County where we recorded for 53 functional plate nights (5 plates total) at prairie dog towns and 51 functional plate nights (5 plates total) at paired sites. A functional plate night is defined as 1 tracking plate operated for 1 night without rain.

Statistical Methods

Due to the ordinal nature of the data (2-sample ranked test), we used nonparametric statistics. All data for carnivore counts at prairie dog towns and paired sites were analyzed with a Wilcoxon paired-sample test. This test was chosen because the sampling and statistical design had paired prairie dog towns with adjacent non-prairie dog town control sites before we initiated data collection. We felt that these a priori pairings appropriately linked the 2 sampling designations. As a result, the Wilcoxon paired-sample test was determined to be the most rigorous and appropriate for these analyses.

The westernmost county in the Oklahoma Panhandle (Cimarron) accounted for most carnivore detections during all phases of this study. Two separate analyses were conducted, 1 analyzing data for the entire Panhandle and a 2nd analyzing data only for Cimarron County. The 2 analyses would help determine what effect, if any, the skewed detection frequencies had on data analyses and interpretation. All statistical tests were computed according to protocol described in Zar (1984).

The nature of the data generated by tracking plates was such that individual carnivores of the same species could not be distinguished. As a result, it was impossible to determine if multiple detections of the same species of carnivore at the same site resulted from visits by different carnivores or a single carnivore that visited the site many times. Analyses did not require this type of differentiation though, as data were not used to estimate carnivore numbers. Rather, data were used to measure carnivore activity between 2 habitat types (prairie dog towns and non-prairie dog town areas). Carnivore-preferred habitats would necessarily generate more detections, either by attracting many carnivores or by retaining just a few carnivores over time.

RESULTS

Five carnivore species were identified at black-tailed prairie dog towns (*Vulpes velox*, *Canis latrans*, *Spilogale putorius*, *Taxidea taxus*, and *Lynx rufus*). We detected 4 of these carnivores often enough to permit individual analyses: *Vulpes velox* (6 detections at prairie dog towns, 15 detections at paired sites), *Canis latrans* (9, 3), *Spilogale putorius* (7, 4), and *Taxidea taxus* (3, 0). The bobcat, *Lynx rufus*, was not detected often enough to permit individual analysis (0, 1), but data on bobcats were included in analyses of all carnivores at prairie dog towns. A single striped skunk, *Mephitis mephitis*, was detected at 1 paired site in the Panhandle during this study, but no striped skunks were detected at prairie dog towns.

At prairie dog towns we recorded 25 carnivore detections over the course of the study. Twenty-five detections were also recorded at paired sites during this same period. Analysis using a Wilcoxon paired-sample test revealed no significant differences between carnivore detections at prairie dog towns and non-prairie dog town paired sites ($n = 11$; $T_+ = 32.5$, $T_- = 30.5$; $P \geq 0.05$; Fig. 1). Data in figures are presented as indices of activity expressed as the number of detections divided by functional plate nights.

Seventeen carnivore track detections (in 4 species) were recorded at prairie dog town sites in Cimarron County and 14 (in 5 species) at paired sites: *Vulpes velox* (6 detections at prairie dog towns, 10 detections at paired sites), *Canis latrans* (4, 1), *Taxidea taxus* (3, 0), *Spilogale putorius* (4, 2), *Lynx rufus* (0, 1). Again, the analysis using Wilcoxon paired-sample tests revealed no significant differences in carnivore detections between prairie dog towns and their paired sites in Cimarron County ($n = 5$; $T_+ = 9$, $T_- = 5$; $P \geq 0.05$; Fig. 1).

We analyzed canids as a group with respect to their occurrence at prairie dog towns and paired sites. Of 2 canid species detected (*Canis latrans* and *Vulpes velox*), we recorded 15 track detections at prairie dog towns and 18 at paired sites. Wilcoxon paired-sample analysis revealed no significant differences in detections of canids between prairie dog towns and paired sites ($n = 10$; $T_+ = 24$, $T_- = 31$; $P \geq 0.05$; Fig. 2).

Analysis of canid data for Cimarron County also resulted in no significant differences in canid detections at prairie dog towns and

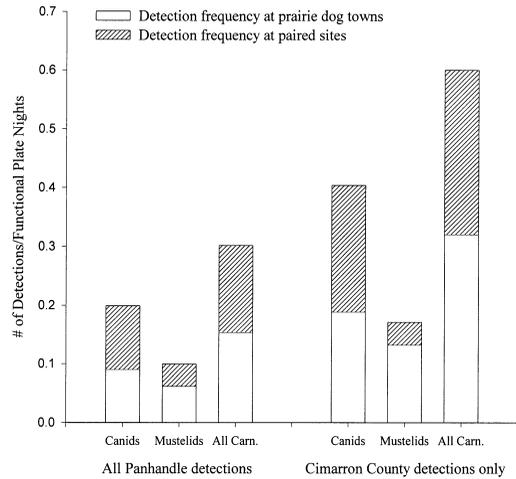


Fig. 1. Comparison of canid, mustelid, and all carnivore detection frequencies at prairie dog towns and control sites in the Oklahoma Panhandle, 1995–1997.

paired sites ($n = 5$; $T_+ = 6$, $T_- = 9$; $P \geq 0.05$; Fig. 2). Ten canids were recorded at prairie dog towns whereas 11 were recorded at paired sites.

Individual species also were analyzed for differences in occurrence between prairie dog towns and non-prairie dog town sites. In our analysis of coyote (*Canis latrans*) detections at prairie dog towns and paired sites across the Panhandle, we found no significant differences between coyote occurrences at prairie dog towns and at paired sites ($n = 5$; $T_+ = 13.52$, $T_- = 1.5$; $P \geq 0.05$; Fig. 2). However, 9 coyotes detections were recorded at prairie dog towns in contrast to only 3 at paired sites. Coyote occurrences at prairie dog towns and paired sites in Cimarron County only were not analyzed because the data set was too small and the distribution of the data across the Panhandle was not as skewed.

Across the Panhandle, 6 swift foxes were recorded at prairie dog towns whereas 15 were recorded at paired sites. The Wilcoxon paired-sample analysis of these data was insignificant ($n = 7$; $T = 5$; $P \geq 0.05$). When we analyzed data for swift foxes detected in Cimarron County only, results were also insignificant ($n = 5$; $T = 4$; $P \geq 0.05$; Fig. 2). In Cimarron County, 6 swift foxes were recorded at prairie dog towns compared with 10 at non-prairie dog town paired sites.

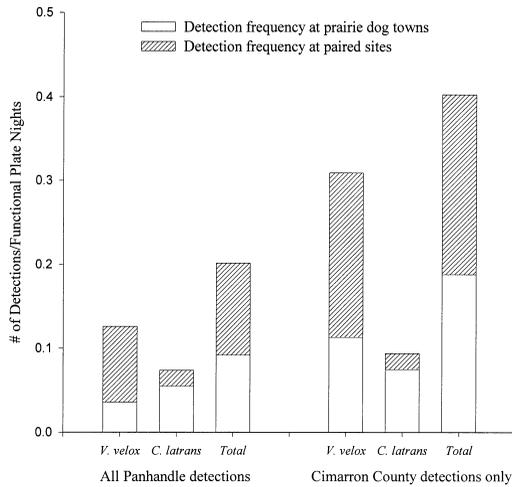


Fig. 2. Comparison of *Vulpes velox* and *Canis latrans* detection frequencies at prairie dog towns and control sites in the Oklahoma Panhandle, 1995–1997.

Mustelids were analyzed as a group as well. Across the Oklahoma Panhandle, we recorded 10 mustelids in 2 species at prairie dog towns and 6 mustelids in 3 species at non-prairie dog town paired sites. Mustelids did not occur significantly more often at prairie dog towns across the Panhandle than at the non-prairie dog town paired sites ($n = 8$; $T_+ = 25$, $T_- = 11$; $P \geq 0.05$; Fig. 3). In Cimarron County mustelids were significantly associated with prairie dog towns ($n = 4$; $T = 0$; $P \leq 0.05$; Fig. 3). Seven mustelids were recorded at prairie dog towns in Cimarron County whereas only 2 were recorded at paired sites.

The spotted skunk (*Spilogale putorius*) was the mustelid we most often recorded at prairie dog towns and paired sites. Spotted skunks were recorded 7 times at the former sites and 5 times at the latter sites across the Panhandle. Spotted skunks, however, were not significantly associated with either prairie dog towns or paired sites ($n = 8$; $T = 7$; $P \geq 0.05$; Fig. 3). In Cimarron County spotted skunks again were not significantly associated with either prairie dog towns or paired sites ($n = 4$; $T_+ = 3$, $T_- = 0$; $P \geq 0.05$; Fig. 3). Four spotted skunks were recorded at prairie dog towns in Cimarron County and only 2 at paired sites.

The badger (*Taxidea taxus*) was the only other mustelid we detected at prairie dog towns. No badgers were recorded at paired sites, nor

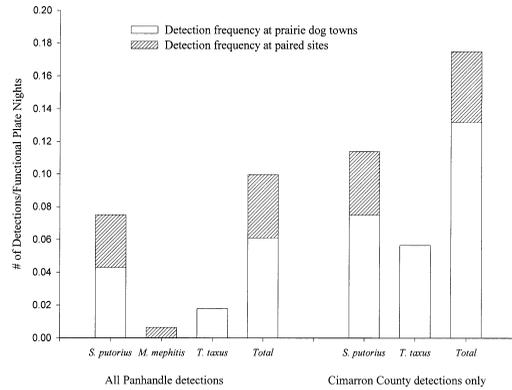


Fig. 3. Comparison of mustelid species at prairie dog towns and control sites in the Oklahoma Panhandle, 1995–1997.

were they detected outside Cimarron County. However, we recorded 3 badgers at prairie dog town sites in Cimarron County (Fig. 3). Due to the small sample size, we performed no statistical tests on these data. The data are presented here merely to illustrate a trend of badgers toward prairie dog towns.

DISCUSSION

Sample sizes and visitation rates at permanent tracking stations were low, which is not uncommon for tracking studies (Humphrey and Zinn 1982, Conner et al. 1983). However, the low numbers of data could have had an effect on the power of the tests to detect significant differences. The paired-sample design and the use of nonparametric procedures for analyzing the data addressed some of these deficiencies, but the small nature of the data set must be kept in mind for any interpretations.

In general, carnivore species detected during this study did not show a significant affiliation with black-tailed prairie dog towns in the Oklahoma Panhandle. Total numbers of carnivore detections at prairie dog towns and paired sites were very similar for the entire Panhandle (Fig. 1) and for Cimarron County as well, which was, in terms of total detections and frequency of detections, the county in which carnivores were most abundant (Fig. 1).

There were variations among canids with respect to affiliation with prairie dog towns. The 2 canids detected during the study (coyote and swift fox) showed divergent patterns in

association with prairie dog towns. When combined, canids were not significantly associated with prairie dog towns either in Cimarron County alone or across the entire Panhandle. Individually, however, certain trends were apparent. Coyotes, while not statistically significantly associated with prairie dog towns, trended toward higher numbers of detections at prairie dog towns (Fig. 2).

Swift foxes trended away from prairie dog towns in Cimarron County and across the entire Panhandle (Fig. 2). These results do not seem to support the long-held assumption that prairie dog towns are important resource areas for sensitive species like the swift fox.

Interference competition, aggression, and even predation have been documented between canids in many different ecosystems (Carbyn 1982, Rudzinski et al. 1982, Sargeant et al. 1987, Harrison et al. 1989, Bailey 1992, Peterson 1995, Dayan and Simberloff 1996, Johnson et al. 1996). Because larger canids harass and threaten smaller canids, some resources or areas become unavailable to the smaller canids. Small canids persist in the environment by behaviorally avoiding those areas that are most likely to contain larger canids (Carbyn 1982, Sargeant et al. 1987, Harrison et al. 1989, White and Ralls 1993, White et al. 1994, Ralls and White 1995, Gese et al. 1996).

It is possible that this dynamic is at work between swift foxes and coyotes in the Oklahoma Panhandle at black-tailed prairie dog towns. Coyotes and swift foxes trended in opposite directions at prairie dog towns and paired sites. Prairie dog towns may be areas rich in resources that canids recognize and attempt to exploit. However, smaller canids, such as swift foxes, may perceive an increased risk of predation at prairie dog towns due to increased coyote presence. Thus, they avoid prairie dog towns, confining their activity away from towns to areas of lower coyote densities. Across broader Panhandle habitats, swift foxes were detected more frequently in range and mesa habitats, away from prairie dog towns (Shaughnessy 2003). Coyotes were detected infrequently in the broader range and mesa non-prairie dog town areas (Shaughnessy 2003). Swift foxes in the Oklahoma Panhandle may be forgoing prairie dog towns as resource areas in favor of the more "coyote depauperate" range and mesa habitats. While prairie dog towns

may be important areas for coyotes, in this instance, interspecific interactions, which affect canid distributions in the broader prairie ecosystem, may be operating at prairie dog towns.

Mustelids also exhibited interesting occurrence patterns between prairie dog towns and paired sites. Although mustelids were significantly associated with prairie dog towns in Cimarron County, they were not significantly associated with prairie dog towns across the Panhandle (Fig. 3). Three mustelids were detected during this study, but only 2 (badger and spotted skunk) were detected at prairie dog towns. Striped skunks were not detected at the prairie dog town stations during any part of the study and were detected only once at a control site. Even with poor representation of striped skunks, mustelids still exhibited a significant association with prairie dog towns in Cimarron County and a preference for prairie dog towns across the Panhandle. No single mustelid species exhibited a significant association with either prairie dog towns or paired sites across the Oklahoma Panhandle or in Cimarron County alone.

We detected badgers only at prairie dog towns and never at paired sites during the course of this study. The occurrence of badgers exclusively at prairie dog towns appears to be the reason mustelids, in general, were determined to be significantly associated with these areas. The total absence of badgers at paired sites suggests that badgers have a strong association with prairie dog towns. Badgers have long been known to be associated with prairie dog towns and are, in fact, major predators of prairie dogs and ground squirrels (*Spermophilus tridecilineatus*) in Oklahoma (Caire et al. 1989).

Spotted skunks also were detected at prairie dog towns in slightly disproportionate (although not significant) numbers (7 detections at towns, 5 at paired sites). However, these trends are not sufficiently large enough to permit interpretation.

Prairie dog towns appear to be important resource areas for carnivores (particularly mustelids in general) in the Oklahoma Panhandle. Nonetheless, their overall importance and the strength of carnivore associations with prairie dog towns (particularly for some rarer carnivores) may not be as clear as previously thought for specific species. Swift foxes persist

in other parts of the Oklahoma Panhandle (Shaughnessy 2003) despite their lower frequency of detection at prairie dog towns (possibly due to the heightened coyote presence in these areas).

This is not to say that prairie dog towns are not vital habitats of the plains ecosystem. Prairie dog towns in the plains ecosystem are undeniably unique areas. Their role in structuring and influencing prairie communities has been well documented for many species (Clark et al. 1982, Whicker and Detling 1988, Sharps and Uresk 1990, Miller et al. 1994, Hoogland 1995). They increase species richness, mix topsoil and subsoil, and have large overall effects on ecosystems and biodiversity in the plains (O'Meila et al. 1982, Coppcock et al. 1983, Hoogland 1995). Other carnivores are also known to be highly associated with prairie dog towns (e.g., black-footed ferret and badger). However, it is equally important not to overlook or underestimate other species interactions that may be as important or even more important in influencing organismal and, in this instance, carnivore distributions in prairie environments. This research provides indications that, whereas prairie dog towns do appear to be favored by some carnivores (coyotes and mustelids), other interactions (e.g., interspecific interactions) between organisms may be as important in determining distributions of carnivores (swift fox and coyote) in the Oklahoma Panhandle.

Ultimately, the role of prairie dogs in the ecosystem of the Great Plains is dependent upon the definition of "keystone species." Traditionally, a keystone species has been designated as one whose presence or absence in an ecosystem overrides other interactions within the system and regulates the structure and dynamics of the entire community (Feldhamer et al. 1999). The role of prairie dogs as keystone species in the plains has recently been questioned (Stapp 1998, Barko et al. 1999). With respect to carnivores (and specifically canids) in the Oklahoma Panhandle, prairie dogs may not exert the single overriding influence determining carnivore occurrence. At least one type of interaction (interspecific) other than the presence of prairie dogs seems to be involved in determining carnivore presence in the Panhandle. As a result, the assignment of prairie dogs as keystone species in the plains

environment should be reexamined as it relates to carnivores.

ACKNOWLEDGMENTS

We express our most sincere thanks to the following people who were influential in the completion of this manuscript: J. Thompson, L. Toothaker, K. Pandora, N. Czaplowski, and M. Jakubauskas, as well as C. Vaughn and M. Kaspari for their assistance, guidance, and advice over the course of this study. Sincere thanks are extended to all landowners and ranchers in the Oklahoma Panhandle who permitted us access to their land to perform fieldwork. We also thank graduate students of the Zoology Department at the University of Oklahoma. We express our gratitude to D. Legates who helped design the statistical analyses. These studies were supported, in part, by funding through Section 6 of the Endangered Species Act to M. Lomolino and the Oklahoma Department of Wildlife Conservation

LITERATURE CITED

- AGNEW, W., D.W. URESK, AND R.M. HANSEN. 1986. Flora and fauna associated with prairie dog colonies and adjacent ungrazed mixed-grass prairie in western South Dakota. *Journal of Range Management* 39: 135–139.
- BAILEY, E.P. 1992. Red foxes, *Vulpes vulpes*, as biological control agents for introduced arctic foxes, *Alopex lagopus*, on Alaskan islands. *Canadian Field-Naturalist* 106:200–205.
- BARKO, V.A. 1997. History and policies concerning the black-tailed prairie dog: a review. *Proceedings of the Oklahoma Academy of Sciences* 77:27–33.
- BARKO, V.A., J.H. SHAW, AND D.M. LESLIE, JR. 1999. Birds associated with black-tailed prairie dog colonies in southern shortgrass prairie. *Southwestern Naturalist* 44:485–490.
- BONHAM, C.D., AND A. LERWICK. 1976. Vegetation changes induced by prairie dogs on shortgrass range. *Journal of Range Management* 29:221–225.
- CAIRE, W., J.D. TYLER, B.P. GLASS, AND M.A. MARES. 1989. *Mammals of Oklahoma*. University of Oklahoma Press, Norman. 567 pp.
- CARBYN, L.N. 1982. Coyote population fluctuations and spatial distribution in relation to wolf territories in Riding Mountain National Park, Manitoba. *Canadian Field-Naturalist* 96:176–183.
- CLARK, T.W., T.M. CAMPBELL III, T.M. SOCHIA, AND D.E. CASEY. 1982. Prairie dog colony attributes and associated vertebrate species. *Great Basin Naturalist* 42: 577–582.
- CONNER, M.C., R.F. LABISKY, AND D.R. PROGULSKE, JR. 1983. Scent-station indices as measures of population abundance for bobcats, raccoons, gray foxes and opossums. *Wildlife Society Bulletin* 11:125–129.

- COPPOCK, D.L., J.K. DETLING, J.E. ELLIS, AND M.I. DYER. 1983. Plant-herbivore interactions in a North American mixed-grass prairie. I. Effects of black-tailed prairie dogs on intraseasonal above-ground plant biomass and nutrient dynamics and plant species diversity. *Oecologia* 56:1-9.
- DAYAN, T., AND D. SIMBERLOFF. 1996. Patterns of size separation in carnivore communities. *In*: J.L. Gittleman, editor, *Carnivore ecology, behavior and evolution*. Volume 2. Cornell University Press, Ithaca, NY. 644 pp.
- EGOSCUE, H.J. 1956. Preliminary studies of the kit fox in Utah. *Journal of Mammalogy* 37:351-357.
- FELDHAMER, G.A., L.C. DRICKAMER, S.H. VESSEY, AND J.F. MERRITT. 1999. *Mammalogy: adaptation, diversity, and ecology*. WCB/McGraw-Hill, Boston, MA. 563 pp.
- FORREST, S.C., D.E. BIGGENS, L. RICHARDSON, T.W. CLARK, T.M. CAMPBELL III, K.A. FAGERSTONE, AND E.T. THORNE. 1988. Population attributes for the black-footed ferret (*Mustela nigripes*) at Meeteetse, Wyoming, 1981-1985. *Journal of Mammalogy* 69:261-273.
- GARRETT, M.G., J.L. HOOGLAND, AND W.L. FRANKLIN. 1982. Demographic differences between an old and new colony of black-tailed prairie dogs (*Cynomys ludovicianus*). *American Midland Naturalist* 108:51-59.
- GESE, E.M., T.E. STOTTS, AND S. GROTHE. 1996. Interactions between coyotes and red foxes in Yellowstone National Park, Wyoming. *Journal of Mammalogy* 77:377-382.
- HARRISON, D.J., J.A. BISSONETTE, AND J.A. SHERBURNE. 1989. Spatial relationships between coyotes and red foxes in eastern Maine. *Journal of Wildlife Management* 53:181-185.
- HOOGLAND, J.L. 1995. *The black-tailed prairie dog: social life of a burrowing mammal*. University of Chicago Press. 557 pp.
- HUMPHREY, S.R., AND T.L. ZINN. 1982. Seasonal habitat use by river otters and Everglades mink in Florida. *Journal of Wildlife Management* 46:375-381.
- JOHNSON, W.E., T.K. FULLER, AND W.L. FRANKLIN. 1996. Sympatry in canids: a review and assessment. *In*: J.L. Gittleman, editor, *Carnivore ecology, behavior and evolution*. Volume 2. Cornell University Press, Ithaca, NY. 644 pp.
- KNOWLES, C.J., AND P.R. KNOWLES. 1994. Additional records of Mountain Plovers using prairie dog towns in Montana. *Prairie Naturalist* 16:183-186.
- KNOWLES, C.J., C.J. STONER, AND S.D. GEIB. 1982. Selective use of black-tailed prairie dog towns by Mountain Plovers. *Condor* 84:71-74.
- KOFORD, C.B. 1958. Prairie dogs, whitefaces and blue grama. *Wildlife Monographs* 3:1-78.
- MARSH, R.E. 1984. Ground squirrels, prairie dogs and marmots as pests on rangeland. Pages 195-208 *in* Proceedings of the conference for organization and practice of vertebrate pest control, Hampshire, England, 30 August-3 September 1982. Plant Protection Division, Fernherst, England.
- MILLER, R.E., G. CEBALLOS, AND R. READING. 1994. The prairie dog and biotic diversity. *Conservation Biology* 8:677-681.
- O'MEILA, M.E., F.L. KNOPE, AND J.C. LEWIS. 1982. Some consequences of competition between prairie dogs and beef cattle. *Journal of Range Management* 35:580-585.
- ORLOFF, S., F. HALL, AND L. SPIEGEL. 1986. The distribution and habitat requirements of the San Joaquin kit fox in the northern extreme of their range. *Transactions of the Western Section Wildlife Society* 22:60-70.
- OSBORN, B., AND P.F. ALLAN. 1949. Vegetation of abandoned prairie dog towns in tall grass prairie. *Ecology* 30:322-332.
- PETERSON, R.O. 1995. Wolves as interspecific competitors in canid ecology. *In*: L.N. Carbyn, S.H. Fritts, and D.R. Seip, editors, *Ecology and conservation of wolves in a changing world*. Canadian Circumpolar Institute, Occasional Publication 35. 642 pp.
- RALLS, K., AND P.J. WHITE. 1995. Predation on San Joaquin kit foxes by larger canids. *Journal of Mammalogy* 76:723-729.
- RICKLEFS, R.E. 1997. *The economy of nature*. 4th edition. W.H. Freeman and Company, New York. 678 pp.
- RUDZINSKI, D.R., H.B. GRAVES, A.B. SARGEANT, AND G.L. STORM. 1982. Behavioral interactions of penned red and arctic foxes. *Journal of Wildlife Management* 46:877-884.
- SARGEANT, A.B., S.H. ALLEN, AND J.O. HASTINGS. 1987. Spatial relations between sympatric coyotes and red foxes in North Dakota. *Journal of Wildlife Management* 51:285-293.
- SEAL, U.S., E.T. THORNE, M.A. BOGAN, AND S.H. ANDERSON. 1989. *Conservation biology and the black-footed ferret*. Yale University Press, New Haven, CT. 302 pp.
- SHACKFORD, J.S., AND J.D. TYLER. 1991. Vertebrates associated with black-tailed prairie dog colonies in Oklahoma. Report submitted to the Oklahoma Department of Wildlife Conservation. 24 pp.
- SHARPS, J., AND D.W. URESK. 1990. Ecological review of black-tailed prairie dogs and associated species in western South Dakota. *Great Basin Naturalist* 50:339-345.
- SHAUGHNESSY, M.J., JR. 2003. Swift fox detection methods and distribution in the Oklahoma Panhandle. *In*: L. Carbyn and M. Sovada, editors, *Ecology and conservation of swift foxes in a changing world*. Canadian Circumpolar Institute, University of Alberta, Edmonton, Alberta, Canada.
- SHAW, J.H., T.S. CARTER, AND D.M. LESLIE, JR. 1991. Black-footed ferret reintroduction assessment in Oklahoma. Final report to the Oklahoma Department of Wildlife Conservation. 14 pp.
- STAPE, P. 1998. A reevaluation of the role of prairie dogs in Great Plains grasslands. *Conservation Biology* 12:1253-1259.
- WHICKER, A.K., AND J.K. DETLING. 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38:778-785.
- WHITE, P.J., AND K. RALLS. 1993. Reproduction and spacing patterns of kit foxes relative to changing prey availability. *Journal of Wildlife Management* 57:861-867.
- WHITE, P.J., K. RALLS, AND R.A. GARROTT. 1994. Coyote-kit fox interactions as revealed by telemetry. *Canadian Journal of Zoology* 72:1831-1836.
- WHITE, P.J., K. RALLS, AND C.A. VANDERBILT WHITE. 1995. Overlap in habitat and food use between coyotes and San Joaquin kit foxes. *Southwestern Naturalist* 40:342-349.

- ZAR, J.H. 1984. Biostatistical analysis. 2nd edition. Prentice-Hall, Englewood Cliffs, NJ. 718 pp.
- ZOELLICK, B.W., AND N.S. SMITH. 1992. Size and spatial organization of home ranges of kit foxes in Arizona. *Journal of Mammalogy* 73:83–88.

Received 12 June 2002

Accepted 7 May 2003