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DYNAMIC BIOGEOGRAPHY OF PRAIRIE DOG (*CYNOMYS LUDOVICIANUS*) TOWNS NEAR THE EDGE OF THEIR RANGE

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Despite the broad and relatively stable distribution of the black-tailed prairie dog (*Cynomys ludovicianus*) throughout much of the Pleistocene and Holocene, anthropogenic activities have reduced the current range of this native grassland species and its associated biotic community to <5% of its historic range (approximately 1800—Miller et al. 1990, 1994). We studied the biogeography of the black-tailed prairie dog along the southeastern edge of its geographic range with 3 primary objectives: to assess the status of the species in this region and identify trends in town coverage and mean town size over the past century, to test whether town persistence was associated with area and isolation of towns, and to assess the protection status of towns >10 ha by comparing locations of extant towns to those of protected public lands. Prairie dog towns in this region now represent only 1% of presettlement estimates and continue to decline in total acreage because of advanced agricultural practices, systematic control measures, and outbreaks of plague. Further, <1% of the area now occupied by prairie dog towns >10 ha occurs within protected locations. As the total coverage of towns has declined, mean size of towns has decreased, and towns have become increasingly more isolated. Persistence of towns between 1989 and 1997 was highest for the largest and most isolated towns, even in regions that were not known to be influenced by plague.

Key words: area, biogeography, black-tailed prairie dog, conservation, *Cynomys ludovicianus*, endangered species, fragmentation, isolation

The geographic range of the black-tailed prairie dog (*Cynomys ludovicianus*) includes most of the Great Plains Region of North America from southern Saskatchewan in Canada south to northern Mexico, and from eastern Nebraska west to the foothills of the Rocky Mountains (Fig. 1). The range remained remarkably stable through the Pleistocene despite major climatic shifts associated with glacial–interglacial cycles. Although the geographic ranges of most other mammals contracted, expanded, and shifted substantially with each major climatic change (e.g., Graham 1986; Graham et al. 1996), the geographic range of the black-tailed prairie dog remained relatively stable over the past 40,000 years (Fig. 1). As a result, many species capitalized on and became adapted to habitats and resources characteristic of this ecosystem (Barko 1994; Barko et al. 1999; Kotilar et al. 1999; Miller et al. 1994; Sharps and Uresk 1990). A number of species prey on prairie dogs, whereas others find critical shelter in their burrows or benefit from grazing by prairie dogs, which maintains open, herbaceous habitats.

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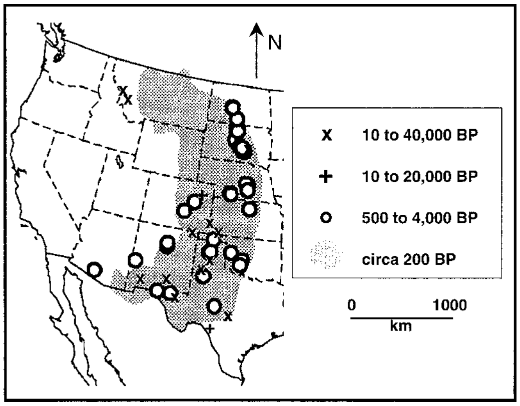

FIG. 1.—Until recent centuries, the geographic range of the black-tailed prairie dog remained remarkably stable throughout much of the Pleistocene and Holocene (Graham 1986; Graham et al. 1996; Graham and Lundelius 1994). Symbols represent paleontologic records of the species, whereas the shaded area represents a reconstruction of the historic range at 200 years ago.

The historically expansive and unusually stable geographic range of this species is related to 2 ecologic characteristics: a broad tolerance for climatic conditions, coupled with relatively narrow requirements for soils that permit extensive burrowing (Sharps and Uresk 1990; Whicker and Detling 1988). However, over the past 2 centuries, habitat conversion for agriculture, concurrent measures of control, and accidental introduction of plague (*Yersinia pestis*—Cully 2001) have reduced the geographic range of the black-tailed prairie dog to <5% of its entire historic (early 19th century) range (Kotilar et al. 1999; Miller et al. 1990, 1994). This includes the recent extirpation of this species in Arizona, and marked declines in town coverage and population levels of prairie dogs and associated species throughout their historic range (Clark et al. 1989; Miller et al. 1990, 1994). Populations of black-tailed prairie dogs likely constitute a metapopulation, a species comprising populations whose persistence largely depends on dispersal and recolonization among populations (Hanski and Gilpin 1997). If populations become smaller and more isolated, population persistence will decline, ultimately resulting in geographic range collapse of the species (Channell and Lomolino 2000a, 2000b).

The United States Fish and Wildlife Service recently designated the black-tailed prairie dog as a candidate species, warranted for listing as threatened, but precluded for administrative reasons (United States Fish and Wildlife Service, Department of the Interior 2000). Effective strategies for maintaining viable populations of prairie dogs and their associated communities must be based on a thorough understanding of factors influencing the biogeographic dynamics of prairie dog towns. Therefore, our purpose was 3-fold: to determine the current spatial extent of black-tailed prairie dogs in this region and assess trends in town coverage and mean size of towns during the past century, to test whether town persistence over the past decade was associated with town area and isolation, and to assess the protection status of towns by comparing locations of extant towns to those of protected public lands in this region.

MATERIALS AND METHODS

During summers (mid-May through August) of 1996–1998, we conducted road surveys for prairie dog towns within the historic range of this species in Oklahoma. In the panhandle of the state, this included exhaustive surveys along the mile-square grid system of roads that covers nearly all of that 3-county area (Beaver, Texas, and Cimarron counties). In the main part of the state, we surveyed roads ≤2 km from all sites across 32 counties where prairie dog towns had been mapped during surveys conducted in 1988–1989 (J. S. Shackford et al., in litt.). Road surveys were conducted with the observer driving along roads at about 56 km/h (35 miles/h) until encountering a prairie dog town, a site with a previously mapped town, or an otherwise appropriate habitat (i.e., a relatively flat area with little woody vegetation). The observer then stopped the vehicle and used binoculars or a spotting scope to view the site. If a town was detected, the observer recorded its location and

TABLE 1.—Characteristics of prairie dog towns in 4 different regions of Oklahoma in 1988–1989 (Fig. 3). For each focal town, isolation was measured as 1,000 minus the sum of the surface areas of other towns (excluding the focal town) ≤10 km from the focal town.

	Characteristics during 1988–1989			Percent
Region (ha)	Number of towns	Mean area (ha)	Mean isolation	persistence from 1989 to 1997
Body of state (16,631,091)[a]	156	10.1	980.1	49
Beaver County (468,270)	55	9.3	958.7	31
Texas County (528,358)	68	16.7	906.4	31
Cimarron County (477,076)	123	34.3	663.7	30

[a] Approximately 8,398,000 ha of this area in the body of the state is included within the historic range boundaries of the black-tailed prairie dog.

approximate shape, noted if it was active, and estimated its maximum length and width with a measuring wheel or, for large towns, with the vehicle's odometer.

Trends in coverage of towns over the entire state and within 4 regions of the state separately (Cimarron, Texas, and Beaver counties, and the remaining counties outside the panhandle; Table 1; Figs. 2 and 3), were quantified by comparing results of our surveys (1996–1998) with those conducted during previous surveys of 1988–1989 (J. S. Shackford et al., in litt.), 1972 and 1957 (Lewis and Hassien 1974), and presettlement figures (Koford 1958; Merriam 1902). Because surveys conducted in 1988–1989 also reported town size, we were able to assess trends in mean size of towns over the past decade.

We used logistic regression to test whether town persistence was influenced by town size and isolation. Logistic regression is used commonly to investigate the relationship between a proportion and ≥1 continuous independent variables (Sokal and Rohlf 1995). We conducted logistic regressions with SYSTAT (1997), with the dependent variable set to 0 or 1 for towns recorded during the 1st survey period that were absent or present in the 2nd survey period, respectively. Independent variables were town area and town isolation. Town area was log-transformed to reduce skewness; skewness of $\log_{10}$(area) ranged from 0.052 for towns in the main part of the state to 1.189 for towns in Texas County. We included an interaction term in the regression model to test whether effects of an independent variable on persistence differed with levels of the other variable.

Because town characteristics differed substantially among regions of the state (Table 1), we conducted separate analyses for each region. Town size for 1988–1989 was taken directly from information provided by J. Shackford (pers. comm.). We used two measurements of isolation: straight-line distance from each town (the focal town) to the nearest town and an inverse measurement of the coverage of other towns ≤10 km from the focal town during the 1988–1989 survey (n = 402 towns); Garrett and Franklin (1988) reported dispersal distances of radiocollared black-tailed prairie dogs ≤5.5 km, straight-line distance, and 6.7 km, actual distance traveled (cf. Knowles 1985). The coverage of towns in the adjacent landscape was a direct measurement of the number of potential immigrants. Therefore, we calculated landscape isolation as 1,000 minus the coverage in hectares of towns ≤10 km from the focal town (the choice of 1,000 was arbitrary, except that it exceeded the maximum value for coverage of adjacent towns, which was 893 ha). We used kriging to generate surface plots displaying the relationship between proportion of towns persisting and the independent variables town area and town isolation (SYSTAT 1997—method = angle, tension = 0.50). Kriging is a smoothing technique that uses generalized least-squares methods to interpolate and illustrate the relationship between a dependent variable (here, proportion of towns persisting) and ≥1 independent variables (area and isolation).

We assessed the protection level of towns in Oklahoma by comparing locations of protected lands within the state to the locations of towns ≥10 ha. We used ArcView (Environmental Systems Research Institute, Inc. 1999; Johnston 1998) to calculate the proportion and extent of large towns included within protected lands as defined by the National GAP Analysis Program (Scott et al. 1993; Table 2).

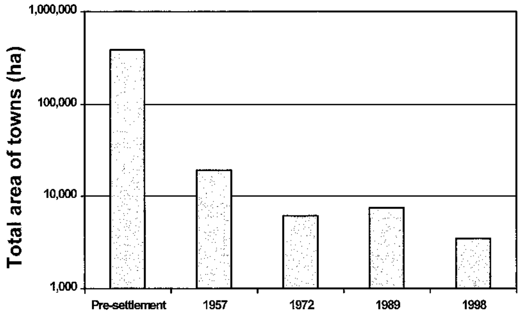

FIG. 2.—Changes in area of black-tailed prairie dog towns in Oklahoma from presettlement (roughly the early 1800s) to 1998 (note the logarithmic scale for area and the different time periods along the abscissa).

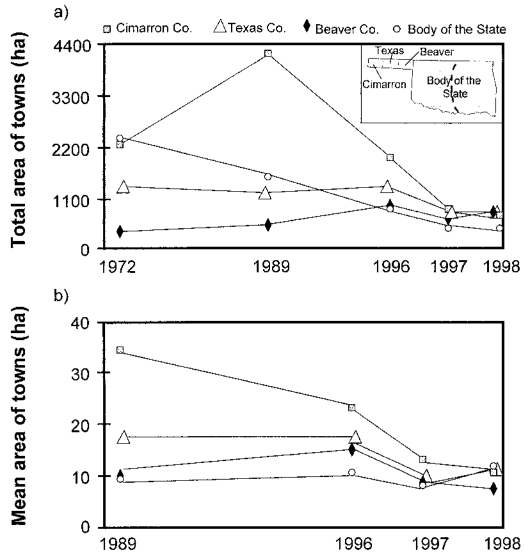

FIG. 3.—a) Trends in total coverage and b) mean size of black-tailed prairie dog towns in four regions of Oklahoma (see Table 1). The vertical dashed line on the state inset denotes the approximate eastern edge of the species' historic (and extant) range.

RESULTS

During 1998, we recorded 298 towns covering 3,255 ha across Oklahoma. That represented just 1% of the historic (presettlement) range of the species in Oklahoma (Fig. 2). Town coverage in 1998, as percentage of available land surface, was about 0.003% in the body of the state (0.006% within the historic range of this species), and 0.156%, 0.165%, and 0.159% within Beaver, Texas, and Cimarron counties, respectively. In contrast, the estimated presettlement extent of prairie dog towns across the state (385,000 ha—Koford 1958; Merriam 1902) was 3.9% of the total area within the historic range boundaries of the species in Oklahoma (Fig. 3, inset).

Most of the decline in prairie dog towns across Oklahoma seems to have occurred during the 1st half of the 20th century, after the westward spread of advanced agricultural practices (Ramankutty and Foley 1999) and systematic control measures. Outbreaks of plague likely contributed to this reduction but only in the 2 westernmost counties (Cimarron and Texas counties; plague outbreaks have never been recorded for other counties of Oklahoma—Cully 2001; Cully et al. 2000). Although the majority of prairie dog towns now persist in the panhandle region, during the 18th and 19th centuries some of the largest towns ever recorded occurred outside the panhandle. One town in central Oklahoma stretched 35 km (Strong 1960; Tyler 1968). Although no estimates of the total area of that town exist, it must have been a very large town indeed, one far exceeding the area of any extant town (maximum town size in 1998 was 427 ha; length = 2.1 km).

In recent decades, the decline in coverage of prairie dog towns has progressed from east to west (Fig. 3). The panhandle still contains the largest aerial extent of prairie dog towns, with the highest coverage during 1989 occurring in the westernmost county. However, over the past decade, those western towns have experienced the largest absolute declines in town coverage, and those declines continued even during our surveys (1996–1998). The area of towns in Cimarron County has now declined to essentially the same level as that of the other counties in the panhandle (Fig. 3a).

Concurrent with the decline in total cov-

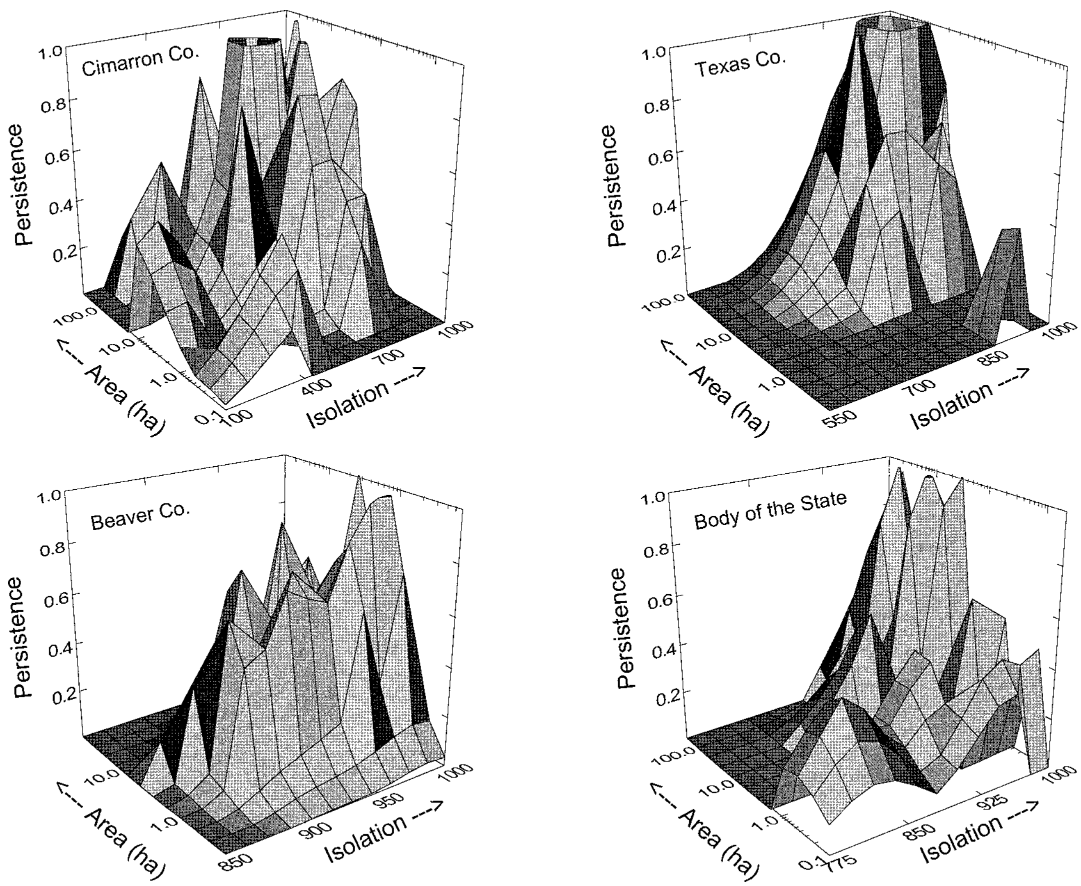

FIG. 4.—The relationship between persistence of black-tailed prairie dog towns (as proportion of towns surviving from 1989 to 1997) and town area and isolation (town isolation was measured as 1,000 ha minus coverage in hectares of other towns ≤10 km from the focal town). Surface plots were generated with SYSTAT's (1997) kriging routine (method = angle, tension = 0.50).

erage of towns across the state, mean town size also has decreased substantially over the past decade (Fig. 3b). Statewide, towns surveyed in 1988–1989 averaged 18.5 ha, whereas those surveyed in 1998 averaged just 10.9 ha. The decline was most severe in Cimarron County, where mean town size decreased from 34.3 ha in 1988–1989 to just 10.3 ha in 1998.

Across the entire state (i.e., all regions combined), persistence of towns between 1989 and 1997 increased significantly with landscape isolation and with town area (logistic regression, $P < 0.001$, $n = 402$). Because landscape isolation proved consistently superior to linear distance between towns in predicting town persistence, we restrict the following discussion to effects of landscape isolation. A significant interaction effect was found, indicating that the influence of 1 variable on persistence across the entire state varied with levels of the other variable; town persistence increased with area, but only for the more isolated towns (i.e., those with few and or relatively small towns in the adjacent landscape; Fig. 4). Even the largest towns, if not sufficiently isolated, suffered extinction.

Nonetheless, patterns of persistence differed among regions (Fig. 4). Persistence patterns in Cimarron and Texas counties were similar to that for the entire state for

TABLE 2.—Protection status of large (>10-ha) prairie dog towns in Oklahoma in 1997. Protection levels based on those of the National GAP Analysis Program (Scott et al. 1993).

Protection level	Number of towns	Area of large towns (ha)
Management plan in place	0	0.0
Managed for natural value	2	4.4
No permanent development	6	15.0
Unprotected lands	77	2,407.0

effects of landscape isolation, area, and the interaction term (P = 0.013, 0.081, and 0.068, respectively, for those effects in Cimarron County, n = 123; P = 0.034, 0.026, and 0.019, respectively, for those effects in Texas County, n = 68). However, outside the panhandle, persistence of towns was not correlated with landscape isolation per se but did increase significantly with town area. The interaction term was again significant, indicating that town persistence increased with area, but only for the more isolated towns ($P < 0.05$, n = 156; Fig. 4). Finally, although persistence of towns in Beaver County tended to increase with isolation (Fig. 4), none of the independent variables (landscape isolation, town area, or the interaction term) was correlated with persistence of towns ($P > 0.200$ in all cases).

Few extant towns currently receive any documented level of protection within the state (Table 2). In 1997, 85 towns in the panhandle exceeded 10 ha, accounting for 2,427 ha. However, only 8 of those towns and <1% of the total area of large towns were included in a location with some degree of documented protection (Table 2).

DISCUSSION

The anthropogenic decline in the geographic range of the black-tailed prairie dog, an ecological dominant of the Great Plains throughout much of the Pleistocene and early Holocene, has a geographic signature much like that of deforestation and other forms of fragmentation (Laurance and Bierregaard 1997; Lomolino and Perault 2000, 2001; Perault and Lomolino 2000). Concurrent with the decline in total aerial extent of these native ecosystems, remnant patches became both smaller and more isolated from each other. The likely effect of these biogeographic dynamics, whether fragmentation of old-growth forests or prairie dog towns, will likely be an overall decline in persistence of the entire metapopulation (Hanski and Gilpin 1997; M. Gilpin, in litt.). A relatively small number of populations, including those in some of the most isolated regions of the species' range, may persist through the 21st century. However, if isolation of remnant towns continues to increase, recolonization rates may decline to levels too low to compensate for local extinctions. Just as important, because diversity is directly correlated with area for nearly all types of ecosystems (Brown and Lomolino 1998; MacArthur et al. 1972; Rosenzweig 1995), regional and global diversity of native grasslands will experience substantial declines well before the last prairie dog town becomes extinct. Such declines in biological diversity are ongoing and evidenced by the documented declines of many town associates including burrowing owls (*Speotyto cunicularia*), ferruginous hawks (*Buteo regalis*), mountain plovers (*Charadrius montanus*), and swift fox (*Vulpes velox*—Barko 1994; Butts 1973; Desmond et al. 1995; Knopf 1996; Knowles et al. 1982; Miller et al. 1994) and the near extinction of black-footed ferrets (*Mustela nigripes*—Seal et al. 1989). For many of these species, town size may be just as important as town isolation or the total area of towns within a region (Lomolino et al. 2001).

The relatively high persistence for the most isolated populations in our study is consistent with the general patterns in range collapse observed for endangered species (Channell and Lomolino 2000a, 2000b; Lomolino and Channell 1995, 1998). These isolated populations are not necessarily more resistant to anthropogenic extinction forces or to plague (an exotic disease introduced to North America by humans—Cully 2001). Rather, the most isolated populations are likely the last ones encountered by anthropogenic factors that spread across native landscapes like a contagion. For an overwhelming majority of imperiled species of plants and animals, persistent populations are not necessarily those with historically high population densities, but they are usually the populations most isolated from the point of initial contact with anthropogenic disturbance (Channell and Lomolino 2000a, 2000b; Lomolino and Channell 1995, 1998). Therefore, areas along the periphery of the historic range of the black-tailed prairie dog should not be abandoned in future conservation efforts because they may provide valuable opportunities to maintain or reestablish populations of this important species. If anthropogenic extinction forces and plague can be controlled, persistence of prairie dog populations and associated species should be highest for the largest towns, whereas the likelihood of natural recruitment and recolonization should be highest for the least isolated ones.

The role that plague has played in the overall decline and biogeographic dynamics of prairie dog ecosystems remains a critical question for future studies. However, plague seemingly was not the primary cause of extinctions of prairie dog towns across most of Oklahoma. Note that lower persistence in less-isolated towns was evident not just for the westernmost county of the panhandle region, which suffered an outbreak of plague in the early 1990s, but also for other regions (including those not known to have experienced a plague outbreak at any time—Barnes 1982; Cully 2001; Cully et al. 2000; Hassien 1976; Shaw et al. 1993). Thus, the continuing statewide decline in prairie dog towns, and westward progression of this decline, cannot be attributed solely to plague, which expanded eastward from an initial establishment in California (Cully 2001). Rather, just as black-footed ferrets persisted in the extreme northwestern periphery of their historic range, the westward decline in prairie dog towns across Oklahoma is consistent with the westward expansion of human populations and advanced agricultural practices (Ramankutty and Foley 1999).

Taken together, the geographic trends in town size and isolation, and the ecologic association of many species with prairie dog towns, especially larger towns, clearly argue for development of conservation and recovery strategies to maintain and reestablish not just viable populations of prairie dogs, but viable communities of associated species. Although our analysis of protection levels indicates that few extant towns are protected, substantial tracts of public lands remain within the historic range of this species in Oklahoma and across the Great Plains. Such areas may hold great promise for conservation and recovery of this native grassland ecosystem.

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Literature Cited

Barko, V. A. 1994. Effect of the black-tailed prairie dog on avifaunal composition in southern shortgrass prairie. M.S. thesis, Oklahoma State University, Stillwater.

BARKO, V. A., J. H. SHAW, AND D. M. LESLIE, JR. 1999. Birds associated with black-tailed prairie dog colonies in southern shortgrass prairie. The Southwestern Naturalist 44:484–489.

BARNES, A. M. 1982. Surveillance and control of bubonic plague in the United States. Symposia of the Zoological Society of London 50:237–270.

BROWN, J. H., AND M. V. LOMOLINO. 1998. Biogeography. 2nd ed. Sinauer Associates, Inc., Publishers, Sunderland, Massachusetts.

BUTTS, K. O. 1973. Life history and habitat requirements of burrowing owls in western Oklahoma. M.S. thesis, Oklahoma State University, Stillwater.

CHANNELL, R., AND M. V. LOMOLINO. 2000a. Dynamic biogeography and conservation of endangered species. Nature 403:84–86.

CHANNELL, R., AND M. V. LOMOLINO. 2000b. Trajectories to extinction: spatial dynamics of the contraction of geographical ranges. Journal of Biogeography 27:169–179.

CLARK, T. W., D. HINCKLEY, AND T. RICH (EDS.). 1989. The prairie dog ecosystem: managing for biological diversity. Montana Bureau of Land Management Wildlife Technical Bulletin 2:1–55.

CULLY, J. F., JR., AND E. S. WILLIAMS. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. Journal of Mammalogy 82:894–905.

CULLY, J. F., JR., L. G. CARTER, AND K. L. GAGE. 2000. New records of sylvatic plague in Kansas. Journal of Wildlife Diseases 36:389–392.

DESMOND, M. J., J. A. SAVIDGE, AND T. F. SEIBERT. 1995. Spatial patterns of burrowing owl (*Speotyto cunicularia*) nests within black-tailed prairie dog (*Cynomys ludovicianus*) towns. Canadian Journal of Zoology 73:1375–1379.

ENVIRONMENTAL SYSTEMS RESEARCH INSTITUTE, INC. 1999. ArcView GIS 3.1.1. Environmental Systems Research Institute, Inc., Redlands, California.

GARRETT, M. G., AND W. L. FRANKLIN. 1988. Behavioral ecology of dispersal in the black-tailed prairie dog. Journal of Mammalogy 69:236–250.

GRAHAM, R. W. 1986. Response of mammalian communities to environmental changes during the late Quaternary. Pp. 300–313 in Community ecology (J. Diamond and T. Case, eds.). Harper and Row, New York.

GRAHAM, R. W., ET AL. 1996. Spatial response of mammals to late-Quaternary environmental fluctuation. Science 272:1601–1606.

GRAHAM, R. W., AND E. L. LUNDELIUS (EDS.). 1994. Faunmap: a database documenting late Quaternary distributions of mammal species in the United States. Illinois State Museum Scientific Papers, Springfield, Illinois.

HANSKI, I. A., AND M. E. GILPIN (EDS.). 1997. Metapopulation biology: ecology, genetics, and evolution. Academic Press, New York.

HASSIEN, F. D. 1976. A search for black-footed ferret habitat in the Oklahoma panhandle and adjacent areas and an ecological study of prairie dogs in Texas County, Oklahoma. M.S. thesis, Oklahoma State University, Stillwater.

JOHNSTON, C. A. 1998. Geographic information systems in ecology. Blackwell Science, Oxford, United Kingdom.

KNOPF, F. L. 1996. Mountain plover (*Charadrius montanus*). The birds of North America, No. 211 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, Pennsylvania, and the American Ornithologists' Union, Washington, D.C.

KNOWLES, C. J. 1985. Observations on prairie dog dispersal in Montana. The Prairie Naturalist 17:33–40.

KNOWLES, C. J., C. J. STONER, AND S. P. GIEB. 1982. Selective use of black-tailed prairie dog towns by mountain plovers. The Condor 84:71–74.

KOFORD, C. B. 1958. Prairie dogs, whitefaces, and blue grama. Wildlife Monographs 3:1–78.

KOTILAR, N. B., B. W. BAKER, A. D. WHICKER, AND G. PLUMB. 1999. A critical review of assumptions about the prairie dog as a keystone species. Environmental Management 24:177–192.

LAURANCE, W. F., AND R. O. BIERREGAARD, JR. (EDS.). 1997. Tropical forest remnants: ecology, management, and conservation of fragmented communities. The University of Chicago Press, Chicago, Illinois.

LEWIS, J. C., AND F. D. HASSIEN. 1974. Status of prairie dogs and black-footed ferrets in Oklahoma. Proceedings of the Oklahoma Academy of Science 54: 20–24.

LOMOLINO, M. V., AND R. CHANNELL. 1995. Splendid isolation: patterns of range collapse in endangered mammals. Journal of Mammalogy 76:335–347.

LOMOLINO, M. V., AND R. CHANNELL. 1998. Range collapse, reintroductions, and biogeographic guidelines for conservation: a cautionary note. Conservation Biology 12:481–484.

LOMOLINO, M. V., R. CHANNELL, D. R PERAULT, AND G. A. SMITH. 2001. Downsizing nature: anthropogenic dwarfing of species and ecosystems. Pp. 229–252 in Biotic homogenization: the loss of diversity through invasion and extinction (M. McKinney and J. Lockwood, eds.). Plenum Press, New York.

LOMOLINO, M. V., AND D. R. PERAULT. 2000. Assembly and dis-assembly of mammal communities in a fragmented temperate rain forest. Ecology 81:1517–1532.

LOMOLINO, M. V., AND D. R. PERAULT. 2001. Island biogeography and landscape ecology of mammals inhabiting fragmented, temperate rain forests. Global Ecology and Biogeography 10:113–132.

MACARTHUR, R. H., J. M. DIAMOND, AND J. KARR. 1972. Density compensation in island faunas. Ecology 53:330–342.

MERRIAM, C. H. 1902. The prairie dog of the Great Plains. Pp. 257–270 in Yearbook of the United States Department of Agriculture 1901. United States Government Printing Office, Washington, D.C.

MILLER, B., G. CEBALLOS, AND R. READING. 1994. The prairie dog and biotic diversity. Conservation Biology 8:677–681.

MILLER, B., C. WEMMER, D. BIGGINS, AND R. READING. 1990. A proposal to conserve black-footed ferrets and the prairie dog ecosystem. Environmental Management 14:763–769.

PERAULT, D., AND M. V. LOMOLINO. 2000. Corridors and mammal community structure across a frag-

mented, old-growth forest landscape. Ecological Monographs 70:401–422.
Ramankutty, N., and J. A. Foley. 1999. Estimating historical changes in land cover: North American croplands from 1850 to 1992. Global Ecology and Biogeography 8:381–396.
Rosenzweig, M. L. 1995. Species diversity in space and time. Cambridge University Press, New York.
Scott, M. J., et al. 1993. GAP analysis: a geographical approach to protection of biological diversity. Wildlife Monographs 123:1–41.
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, Connecticut.
Sharps, J. C., and D. W. Uresk. 1990. Ecological review of black-tailed prairie dogs and associated species in western South Dakota. Great Basin Naturalist Memoirs 50:339–345.
Shaw, J. H., W. McAbee, T. S. Carter, and D. M. Leslie, Jr. 1993. Assessment of black-tailed prairie dog colonies for reintroduction of black-footed ferrets in western Oklahoma. Proceedings of the Oklahoma Academy of Science 73:47–52.
Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. W. H. Freeman and Company, New York.
SYSTAT, Inc. 1997. SYSTAT for Windows: statistics, version 7.0.1. SYSTAT, Inc., Evanston, Illinois.
Strong, W. E. 1960. Canadian river hunt. University of Oklahoma Press, Norman.
Tyler, J. D. 1968. Distribution and vertebrate associates of the black-tailed prairie dog in Oklahoma. Ph.D dissertation, University of Oklahoma, Norman.
United States Fish and Wildlife Service, Department of the Interior. 2000. Endangered and threatened wildlife and plants; 12-month finding for a petition to list the black-tailed prairie dog as threatened. Federal Register 65:5476–5488.
Whicker, A. D., and J. K. Detling. 1988. Ecological consequences of prairie dog disturbances. BioScience 38:778–785.

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