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Prairie Dogs in the Chihuahuan Desert: History, Ecology, Conservation

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Abstract—The region we know as the Chihuahuan Desert has supported black-tailed prairie dogs (*Cynomys ludovicianus*) for at least 40,000 years, more widely in the late Pleistocene than since. In the past, prairie dog populations expanded and contracted with the abundance of large grazers, control efforts by people, episodes of sylvatic plague, and recently in some areas, habitat loss to agriculture. Chihuahuan Desert populations may be more sensitive than those elsewhere to human persecution and intensity of grazing, but the hot, dry climate may help insulate populations from sylvatic plague. With prudent management of livestock in rangelands, the Chihuahuan Desert may be as well or better suited than some other regions for long-term maintenance of prairie dog populations, albeit at lower densities, and associated species.

Resumen—La región que conocemos como el Desierto Chihuahuense ha mantenido a los perros llaneros (*Cynomys ludovicianus*) por al menos 40,000 años, de manera más amplia durante en el Pleistoceno que posteriormente. En el pasado, las poblaciones de perros llaneros se expandieron y contrajeron con la abundancia de los grandes animales pastoreadores, con los esfuerzos de control por parte de la gente, con los episodios de peste bubónica, y recientemente en algunas áreas, por la pérdida del hábitat debido a la agricultura. Las poblaciones del Desierto Chihuahuense pueden ser más sensibles a la persecución humana y a la intensidad del pastoreo por el ganado que las que se encuentran en otros sitios, pero el clima seco y caliente puede ayudar a aislar a las poblaciones de la peste bubónica. Con un manejo ganadero prudente en los pastizales, el Desierto Chihuahuense puede encontrarse en una mejor situación que otras regiones para el mantenimiento a largo plazo de las poblaciones de perros llaneros, aunque en menores densidades.

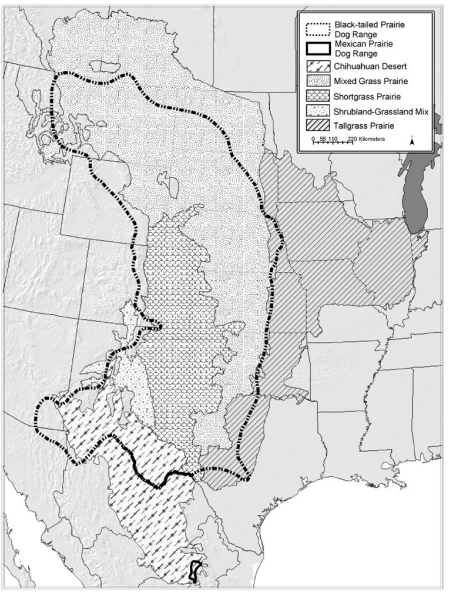

FIG. 1—Historical distributions of black-tailed prairie dogs (*Cynomys ludovicianus*) and Mexican prairie dogs (*C. mexicanus*) (Hall, 1981) with respect to major vegetation types (adapted from Bailey et al., 1994).

The black-tailed prairie dog (*Cynomys ludovicianus*), our primary focus herein, is the most abundant and widely distributed of the five prairie dog (*Cynomys*) species. Its populations occur from Canada to Mexico in the central and southwestern grasslands of North America (Fig. 1). The only other prairie dog in the Chihuahuan Desert (except for small numbers of Gunnison's prairie dog [*C. gunnisoni*] at the northwestern margin) is the black-tailed prairie dog's close relative, the Mexican prairie dog (*C. mexicanus*). Black-tailed prairie dogs are highly social animals that live in colonies ranging in size from a fraction of a hectare to many square kilometers.

Black-tailed prairie dogs survive poorly where vegetation grows tall and dense because they depend on good visibility to avoid predation. Thus they occupy primarily shortgrass steppe, mixed-grass prairie, and desert grassland environments, but usually not tallgrass prairie (Koford 1958; Hubbard and Schmitt 1984; Truett 2003) (Fig. 1). Regardless of grassland type, grazing by large herbivores usually benefits prairie dogs if the dominant vegetation grows taller than about 20 cm (Knowles 1982). This includes not only most of the species' range in the Great Plains (Truett 2003) but also at least parts of its Chihuahuan Desert range (Truett and Savage 1998).

Colonies of prairie dogs attract an array of other species that prey on them, use their burrows for shelter, or both. One species, the endangered black-footed ferret (*Mustela nigripes*), historically coexisted with *C. ludovicianus*, *C. leucurus,* and *C. gunnisoni,* and apparently cannot survive in the wild without prairie dogs. Other species, such as the burrowing owl (*Athene cunicularia*) and ferruginous hawk (*Buteo regalis*), also benefit greatly from prairie dogs (Desmond et al. 2000; Cook et al. 2003) but are not prairie dog obligates. In the Chihuahuan Desert, black-tailed prairie dogs benefit burrowing owls (Berardelli 2003), ferruginous hawks (Manzano-Fischer et al. 1999; Bak et al. 2001), kit foxes (*Vulpes macrotis*) (List and Macdonald 2003; List et al. 2003), and probably

numerous other species (List 1997; Manzano-Fischer et al. 1999; Ceballos et al. 1999; Desmond 2004).

Currently in the Chihuahuan Desert, more black-tailed prairie dogs exist in México than in the United States despite the greater historical range and likely greater historical numbers (see Bailey 1931) in the United States. Differential intensities of control probably were responsible. The group of colonies, or colony "complex," between Janos and Casas Grandes in Chihuahua (see Fig. 2) contains a large majority of the species in México; the complex occupied about 55,250 ha in 1988 (Ceballos et al. 1993), but declined in area about 36% (to about 35,360 ha) between 1998 and 2000 (Marcé 2001). New Mexico contains an estimated 400 ha of colonies (G. Schmitt, A. Ernst, and J. Truett, unpublished data), and Trans-Pecos Texas an estimated 5,162 ha (Texas Parks and Wildlife, unpublished data). Black-tailed prairie dogs have been extirpated from Arizona (Van Pelt 1999). Thus the total colony acreage in the Chihuahuan Desert probably is about 41,000 ha, with more than 85% of the total in México.

Prairie dog populations in the Chihuahuan Desert (as elsewhere) have declined dramatically in the last 100 years. Purposeful control by humans has been the main

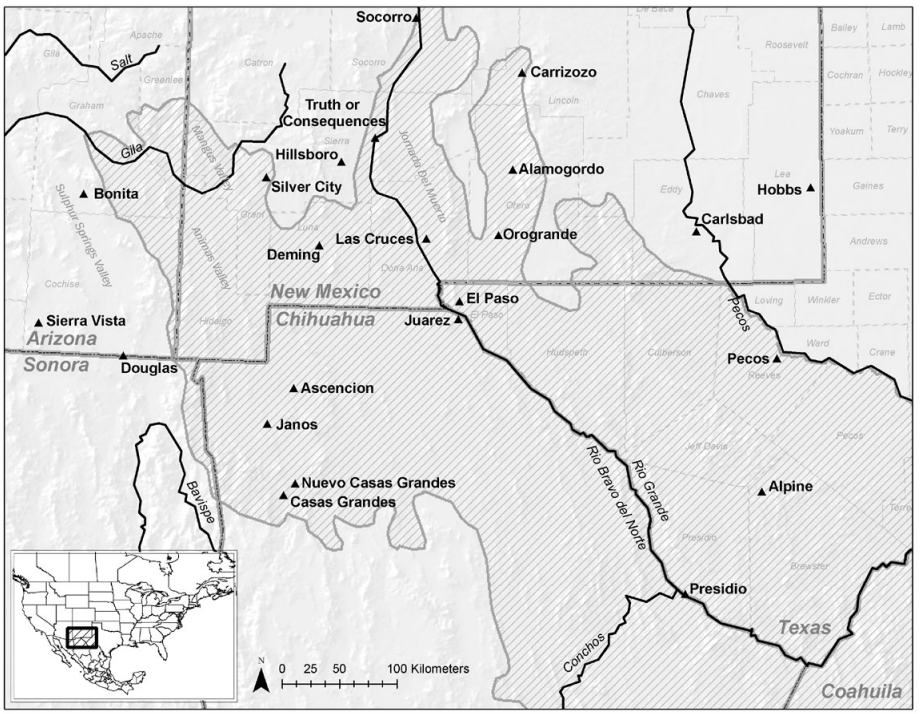

Fig. 2—The northern portion of the Chihuahuan Desert (cross-hatched, adapted from Schmitt, 1979) and place names referenced in text.

cause (Hubbard and Schmitt 1984; Oakes 2000), but conversion of habitat to farmland recently has been influential in some locations (List 1997; Marcé 2001). Sylvatic plague has decimated many populations in western portions of the Great Plains (Cully and Williams 2001), but may be less of a threat in the Chihuahuan Desert than in some other regions, as discussed below.

Prairie dog control programs have used primarily toxicants applied at burrows. In New Mexico and Arizona, government-sponsored poisoning campaigns became important in the early 1900s, peaking in the 1930s and early 1940s (Hubbard and Schmitt 1984; Oakes 2000). By 1960, nearly all black-tailed prairie dog colonies that historically had existed west of the Rio Grande in these two states (Fig. 3) had been eliminated, and in 1972 the last colony succumbed (Oakes 2000). East of the Rio Grande, in southeastern New Mexico and Trans-Pecos, Texas, populations plummeted, but not to extinction (Cottam and Caroline 1965; Schmidly 1977; Hubbard and Schmitt 1984). Poisoning commenced in Chihuahua at least as early as the 1930s (Bailey 1932),

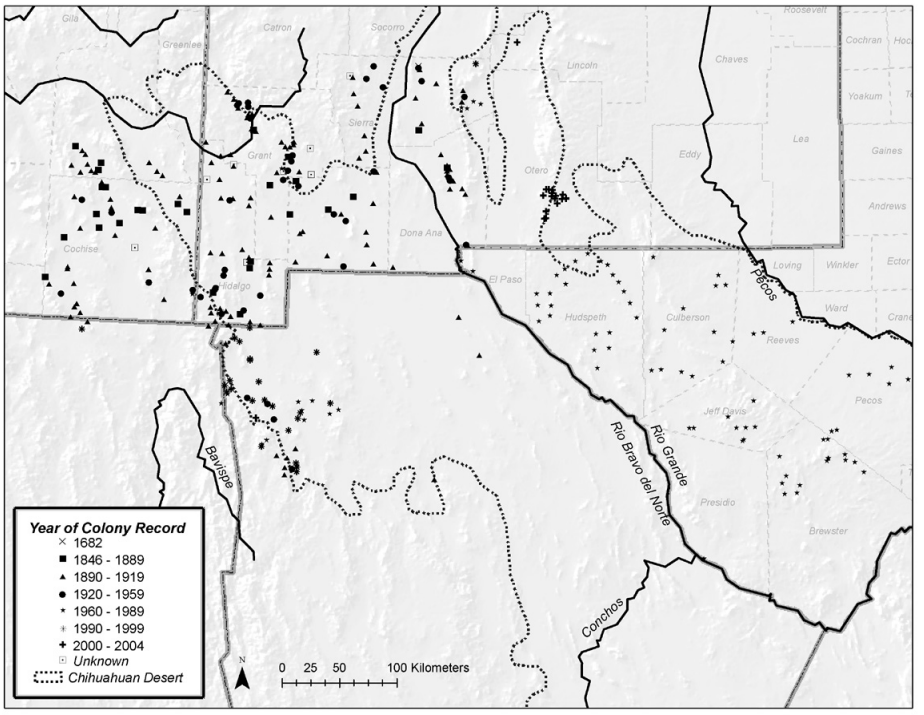

Fig. 3—Locations of black-tailed prairie dogs (*Cynomys ludovicianus*) reported during 1682 to 2004 in and near the Chihuahuan Desert. Locations are based on specimen records and reliable reports (adapted from Schmidly 1977; Ceballos et al. 1993; Knyazhnitskiy et al. 2000; Oakes 2000).

although the impacts were far less extensive than in the United States, as evidenced by the persistence of a large prairie dog complex to the present in the Janos-Casas Grandes region (Ceballos et al. 1993; List 1997). Poisoning in México was common in the late 1980s and early 1990s (List 1997).

Conversion of prairie dog habitat to agriculture recently has expanded in parts of the Chihuahuan Desert. This threat has been most obvious in México, where agriculture has encroached upon existing colonies in the Janos-Casas Grandes region (List 1997). Because most historical prairie dog habitat in the United States portion of the Chihuahuan Desert has not supported prairie dogs for decades (Schmidly 1977; Hubbard and Schmitt 1984), agricultural development therein may seem less of a threat. However, encroachment of farming into historically occupied areas (discussed below) has been extensive in some places such as the Sulphur Springs Valley south of Bonita in Arizona, the Deming area in Luna County, New Mexico, and to a lesser extent the Animas Valley in southern Hidalgo County, New Mexico (J. Truett, pers. observation). Such development reduces the potential for prairie dog restoration.

Since the mid-1900s plague has decimated many *Cynomys* populations in southern grasslands west of about the 100th meridian (Cully and Williams 2001). However, several lines of evidence suggest plague is less common in the Chihuahuan Desert part of this region than farther north. Barnes (1983) noted the relatively low incidence of plague (as antibodies in blood samples) among wild carnivores in southern Arizona; he suggested the hot, dry climate may have played a role. Brand (2002) noted the low numbers of human cases of plague in Chihuahuan Desert areas (counties in southern Arizona and New Mexico) compared with the high numbers immediately to the north. Parmenter et al. (1999) reported a direct correlation between precipitation amount and plague incidence in humans in New Mexico; these authors suggested that low soil moisture resulting from low precipitation (both common in the Chihuahuan Desert) may reduce survival and reproduction of fleas known to transmit plague. J. F. Cully, Jr. (Kansas State University, pers. comm.) failed to find evidence of plague in recent samples of fleas from rodents in and near the Janos-Casas Grandes complex in Chihuahua, and plague never has been reported from this large complex.

Early History—The species group we call prairie dogs evolved in the central grasslands of North America, the genus *Cynomys* first appearing in the Pliocene about 2 million years ago (Goodwin 1995). The various species (including some now extinct) evolved primarily in the Pleistocene, 1.8 million to 0.01 million (=10,000) years ago. Remains identifiable as *C. ludovicianus* appear as far back as the Farmdalian interval of the

last (Wisconsin) glaciation 40,000 to 22,000 years ago. The Mexican prairie dog (*C. mexicanus*), a species presently restricted to a small region near the southern tip of the Chihuahuan Desert (Fig. 1), closely resembles *C. ludovicianus* and probably is a relictual species derived from it during or since the late Pleistocene (Goodwin 1995).

The evolutionary environment of the black-tailed prairie dog probably helps explain why it prospers under a regime of short grass. Such an adaptation seems reasonable for a short-statured, vision-dependent animal coexisting with a diversity of large grazers such as dominated Pleistocene grasslands (Graham and Lundelius 1984). This evolutionary context probably accounts for the positive response of the species in tall, dense stands of grass to grazing and trampling by modern-day large herbivores (see Koford 1958; Knowles 1986; Cincotta et al. 1988). Viewing the species in this light can give potential insight into prehistoric and historic changes in its distribution and abundance in the Chihuahuan Desert.

The black-tailed prairie dog appears to have occurred much more widely in the southwestern United States and México in the late Pleistocence (40,000 to 10,000 years ago) than it did recently. The species' remains from the late Pleistocene, though geographically sparse, suggest it occupied not only historic range (Fig. 3) but also regions at least 200 km farther west (in what is now the Sonoran Desert) and 1,000 km farther south in México (Goodwin 1995). We suggest two potential reasons for the contraction in range since the end of the Pleistocene: climate change and loss of large grazers.

Vegetation remains in packrat (*Neotoma*) middens in the Chihuahuan Desert point to a late Pleistocene climate more mesic and equable than now, with less seasonal variation in temperature (Van Devender 1986, 1990, 1995; Van Devender et al. 1987). Documented responses of grasses to climate, coupled with the species composition of grass remains in the packrat middens, indicate that a more productive grassland existed in the late Pleistocene than now. Given that the modern Chihuahuan Desert represents the most xeric environment in the range of the black-tailed prairie dog (as measured by evapotranspitation potential and precipitation amount and distribution—see McClaran 1995; Lauenroth et al. 1999), the more favorable climate in the late Pleistocene could have facilitated the species' wider distribution then.

However, a more mesic climate and the resulting taller and denser stands of grass probably would have been unfavorable to prairie dogs. Large Pleistocene grazers probably improved the quality of such grasslands for prairie dogs, and indeed their grazing may have been necessary in many areas for prairie dogs to persist. The extinction of large grazers at Pleistocene's end thus could have prompted the extinction of

prairie dogs from southern portions of the Chihuahuan Desert. A similar grazing-based scenario has been proposed for the historic waning and waxing of prairie dog populations in the Great Plains with the demise of bison and the subsequent influx of European cattle (Truett 2003).

The early-historic distribution of bison, the only large (> 400 kg) grazer to survive the end-of-Pleistocene extinctions in North America, coincides roughly with the historic distribution of prairie dogs (Fig. 1, Fig. 3) in the Chihuahuan Desert. Bison (like prairie dogs) appear to have been long absent from most southern reaches of the Chihuahuan Desert when cattle entered (Reed 1955; Roe 1970) but persisted in some northern parts. Cabeza de Vaca in 1535 found tribes hunting and eating bison on one or both sides of the Rio Grande west of the Pecos River, probably in the vicinity of or upstream from the Rio Grande-Rio Conchos junction at Presidio, Texas (Krieger 2002). DiPeso et al. (1974) provided archaeological evidence that people at Casas Grandes in northwestern Chihuahua depended on bison for a large part of their subsistence until the entry of cattle in the 1600s. Agenbroad and Haynes (1975) excavated remains of a bison cow with fetus dating A.D. 1610 to 1700 in extreme southeastern Arizona. Dobie (1953) provides reliable evidence of people hunting bison in Coahuila, probably the northern part, around 1806. Lew Wallace, a past governor of New Mexico, hunted bison in ranching country in southern Coahuila in 1866 (Wallace 1866). (The Mexican prairie dog persists only in a small region [Fig. 1] surrounding the southern tip of Coahuila [Ceballos et al. 1993], not far from where Wallace hunted bison.) Despite these records, most lines of evidence suggest that bison were scarce in the Chihuahuan Desert when Europeans and their cattle arrived (Schmidly 1977; Truett 1996).

Faunal remains (usually bones) of black-tailed prairie dogs at archaeological sites show the species existed in northern parts of the Chihuahuan Desert in the millenium prior to the coming of Europeans. Quantitative interpretation of such remains can be problematic—bones can confirm presence but, when used alone, not population levels. To get some idea of populations, the abundance of prairie dog bones can be compared with that of similar-sized species known to be ubiquitous and common, e.g., cottontails (*Sylvilagus*) and jackrabbits (*Lepus*). This yields a ratio of abundance, a tool commonly used by archaeologists to index actual abundance.

The most abundant and useful faunal records come from remains of sedentary (farming) cultures that lived near historic prairie dog habitat during the millennium before European entry. When interpreting these records, one probably can assume that where prairie dogs were found, they existed (as now) in greater densities than cottontails or jackrabbits. Furthermore, the behavior and sedentary nature of prairie

dogs probably made them easy for aboriginal people to capture as a food source. Thus if large colonies existed near prehistoric villages, one would expect their remains to be relatively common in archaeological excavations at the village sites.

Surprisingly, remains of black-tailed prairie dogs show up not at all or sparingly in late prehistoric trash middens where historical data suggest they should have been abundant. Consider the following archaeological-historical contradictions:

- DiPeso et al.'s (1974) excavations at Casas Grandes, Chihuahua (covering the period A.D. 650 to 1660), disclosed no prairie dog bones but 44 bones of cottontails and 121 of jackrabbits. In contrast, Escudero (1834) reported prairie dogs in this area in the early 1800s, Tinker (1978:97) found prairie dog "infestations" there in the early 1900s, Oakes (2000) described historic colonies within a few kilometers, and in 1988 a very large complex existed about 15 km to the northwest (Ceballos et al. 1993).
- Woosley and McIntyre's (1996) report of excavations at Wind Mountain in Mangas Valley, 15 km southwest of Silver City, New Mexico, revealed seven prairie dog bones compared with 1,294 of cottontails and 1,522 of jackrabbits during A.D. 300 to 1150. In contrast, a century ago Bailey (1906) found prairie dogs to be "common…in Mangus Valley."
- M. Nelson and M. Hegmon (Arizona State University Department of Anthropology, unpublished data) reported four prairie dog bones compared with 2,048 cottontail bones and 388 jackrabbit bones at an Animas Creek, New Mexico, site near Hillsboro dated A.D. 1300 to 1450. During the early 1900s within 5 km of this site, prairie dogs occupied extensive colonies in valley bottoms (Oakes 2000).

These and other archaeological excavations in prairie dog habitat in the Chihuahuan Desert (e.g., Anyon and LeBlanc 1984; Shaffer 1991), viewed in the context of historical reports, suggest prairie dogs were much less abundant before European entry than afterward. But note that factors other than prairie dog abundance could have influenced the abundance of their remains.

In contrast to the low relative abundance of black-tailed prairie dogs in Chihuahuan Desert archaeological sites, bones of Gunnison's prairie dogs over an 800-year period at the prehistoric settlement of Chaco Canyon in northwestern New Mexico were 20 to 100% as abundant as cottontail and jackrabbit bones (Akins 1984). Why would Gunnison's prairie dogs, which live in usually lower densities than black-tailed prairie dogs (Knowles 2002), have been so much more abundant than black-tails in prehistoric times? As in the Chihuahuan Desert, no evidence of locally abundant bison appeared

in the Chaco Canyon excavations. However, Gunnison's prairie dogs are more tolerant of tall vegetation than black-tails (Hoogland 1981). Moreover, grasslands in Gunnison's prairie dog habitat surrounding Chaco Canyon may have been naturally more open than those in Chihuahuan Desert prairie dog habitat (see Dick-Peddie 1993).

Another indication that prairie dogs may have been less common in the Chihuahuan Desert before the introduction of cattle than afterward is the distibution of historical records of black-footed ferrets. The Chihuahuan Desert shows a conspicuous lack of such records in comparison with substantial numbers elsewhere in black-tailed prairie dog range (Anderson et al. 1986; Truett et al. 2006). This is not readily explainable given the abundance of prairie dogs historically (Bailey 1931) and presently (List 1997) in some parts of the Chihuahuan Desert, unless prairie dog abundance was a relatively recent (post-cattle) phenomenon that ferrets had not been able to exploit by dispersal from elsewhere (north and east) in their historic range. Ferrets did occupy at least parts of the Chihuahuan Desert region during the late Pleistocene (Messing 1986).

Coming of Cattle—Early last century, Merriam (1902) and Bailey (1905) noted the proliferation of prairie dogs following the stocking of Great Plains grasslands with cattle. They believed predator control, which occurred during the same period, stimulated the prairie dog population expansion. Only later, with more careful investigation (e.g. Osborn and Allan 1949; Koford 1958; Smith 1967), did the connection between grazing and prairie dog abundance become clear. More recent studies (e.g. Snell and Hlavachick 1980; Knowles 1982, 1986; Cincotta et al. 1988) elaborated on this connection. Predation presumably was involved, but changes in the vegetation structure and not the predator abundance apparently was the most important factor.

The idea that entry of livestock into the Chihuahuan Desert might have brought about the abundance of prairie dogs observed in the late 1800s and early 1900s by Mearns (1907), Bailey (1931), and others (Oakes 2000) (Fig. 3) seems consistent with the coincidence in time and space of large numbers of cattle and prairie dogs. The earliest reports of prairie dog colonies in the Chihuahuan Desert discussed by Oakes (2000) came from the Jornada del Muerto along the first major livestock thoroughfare in the region—El Camino Real paralleling the Rio Grande between Las Cruces and Socorro, New Mexico. Apparently the most expansive populations of prairie dogs that Mearns (1907) encountered in southeastern Arizona in 1885 occupied the range near present-day Bonita, where the Sierra Bonita, largest of the early Spanish ranches in Arizona, was located in the late 1700s and early 1800s (Haskett 1935). The Animas Valley in southwestern New Mexico, noted by Bailey (1931:124) to be occupied by

prairie dogs in 1908 its "entire length and breadth," may have had numerous cattle in the late 1700s, though it probably saw a reduction in numbers after 1820 because of Apache depredations (see Haskett 1935). However, it received a tremendous influx of new arrivals in the 1880s that quickly overgrazed the range (Hilliard 1996). Rangelands in the region of Casas Grandes (northwestern Chihuahua), that historically and recently supported large prairie dog colony complexes, were first extensively stocked with cattle in the late 1600s (Brand 1961)—earlier than any of the regions in the United States other than those along the Rio Grande. Hubbard and Schmitt (1984) found the coincidence between the proliferation of cattle and the expansion of prairie dog populations in Chihuahuan Desert rangelands suggestive of cause-and-effect.

Causal relationships between intensive livestock grazing and range occupancy by prairie dogs are consistent with present-day observations. The largest remaining Chihuahuan Desert colony in New Mexico, southwest of Carrizozo, is adjacent to a long-time livestock water source and holding corrals (J. Truett, unpublished notes), a common cause-effect association in the Great Plains (Knowles 1986). Reintroduced populations of prairie dogs on the Armendaris and Ladder ranches near Truth or Consequences, New Mexico, expanded readily only if sites already were dominated by short-grass species such as burrograss (*Scleropogon brevifolius*) or were burned or mowed (Truett and Savage 1998; Ford et al. 2002). Large proportions of the Janos-Casas Grandes complex in northern Chihuahua have been grazed heavily for a half century (Villa 1955) and probably longer (Brand 1961), some (mainly on ejidos, or community-owned lands) so intensively that few or no perennial grasses remain (List 1997; Desmond 2004).

Prairie Dogs on Desert Range—Prairie dogs, like other grazers such as cattle or bison, consume grasses by preference. But they also can survive on grass-depleted ranges where cattle or bison would starve. Strategies for doing so include (1) routinely going without free water; (2) selectively consuming high-quality fractions of grasses; (3) feeding on parts of plants unavailable to large grazers, e.g., bases and roots; (4) switching to less palatable plants as grasses decline in abundance; and (5) surviving *via* facultative torpor (Lehmer et al. 2001) weeks or even months (J. Truett, unpublished data) with little or no food of any kind. These adaptations allow prairie dogs to impose continuous and often very intensive grazing on the forage base (Whicker and Detling 1988; Detling 1998).

Thus it is no surprise that, over time, the plant dominants inside colonies shift from grazing-sensitive grasses to grazing-resilient ones, and then to unpalatable perennials,

or annuals, or both (Detling 1998). As a result, biomass, production, and cover of palatable vegetation gradually decline, although nutritional quality (e.g., N content) of forage species often increases, offsetting to some extent the decline in forage quantity. Nonetheless, the ability of the vegetation inside colonies to support prairie dogs (or other grazers), i.e., the carrying capacity, trends downward.

In grasslands subject to invasion by mesquite (*Prosopis*) and other woody plants, prairie dogs often suppress such invasions by clipping the seedlings (List 1997; Weltzin et al. 1997). They also may kill larger woody plants under some circumstances. These actions may prevent long-term increases of woody species, which can reduce the productivity potential of grasslands.

Two grassland types commonly support prairie dogs in the northern Chihuahuan Desert. At lower elevations, colonies often cluster (or historically clustered) in swales or in low-lying areas in internally draining basins; such sites commonly receive runoff from surrounding terrain during intensive rainstorms (Oakes 2000). Tobosa (*Hilaria mutica*), alkali sacaton (*Sporobolus aeroides*), burrograss, or a combination of these characteristically dominate such sites. At higher elevations, colonies occupy (or occupied) mesas and plains dominated by blue grama (*Bouteloua gracilis*), other *Bouteloua* species, and sometimes tobosa (List 1997; Oakes 2000).

Given similar grazing intensities, carrying capacity of the forage in desert grasslands may decline more rapidly and to lower levels than that in the more mesic grasslands of the Great Plains, for two main reasons. First, precipitation and the associated water available for plant growth tend to be lower and more temporally variable in desert than in Great Plains environments. Second, the perennial forage grasses in the Chihuahuan Desert seem less resilient to grazing, partly because of water stress but also because of their innate characteristics (Bock and Bock 1993; Navarro et al. 2002).

In the Chihuahuan Desert, tobosa, blue grama, and burrograss tend to be more resilient to grazing than other perennial grasses that may coexist with them, e.g., black grama (*B. eriopoda*), sideoats grama (*B. curtipendula*), hairy grama (*B. hirsuta*), and vine mesquite (*Panicum obtusum*) (Neuenschwander et al. 1975; Bock and Bock 1993; Holechek et al. 1999). But even the resilient species may be more susceptible to grazing damage than their conspecifics in the Great Plains because of the relative dearth of selective pressure by large grazers since the Pleistocene (Mack and Thompson 1982; Bock and Bock 1993). This and the low and erratic rainfall lead one to expect greater long-term loss of grass cover and carrying capacity under prairie dog grazing in the Chihuahuan Desert than in the Great Plains.

Field observations support these expectations. In August 1908, two decades or so

after the 1880s influx of cattle into the American Southwest, Bailey (1931:124) noted of the then extensive prairie dog colonies in southwestern New Mexico's Animas Valley: "In many places where rain had missed a part of the valley the prairie dogs had taken all the season's vegetation and had made barren deserts miles in extent." Present-day observations in large, old prairie dog colonies in Chihuahua indicate that intensive grazing (by both prairie dogs and cattle), coupled with drought, can remove all perennial forage, converting grasslands (originally dominated in this case by blue grama) into a landscape dominated by annuals (List 1997; Desmond 2004). Monitoring of vegetation in prairie dog colonies on the Armendaris Ranch in southern New Mexico showed rapid depletion of perennial grass cover (tobosa, alkali sacaton, burrograss) during drought (J. Northcutt, A. Facka, and B. Duval, New Mexico State University, pers. comm.) (Table 1). Southern Great Plains prairie dog colonies appear to not exhibit such rapid and extreme depletion in vegetative cover (Archer et al. 1987; Weltzin et al. 1997; J. Truett, unpublished observations).

How soon such desert ranges could, in the absence of grazing, recover their former perennial grass cover is not known. New Mexico prairie dog colonies that were eradicated 40 to 80 years ago on the Armendaris and Ladder ranches near Truth or Consequences and on the Jornada Experimental Range north of Las Cruces (Oakes 2000) now support dense stands of tobosa or alkali sacaton, or open stands of burrograss (J. Truett, unpublished observations). Thus recovery is possible. However,

Table 1—Basal cover of perennial grasses (all species) as determined by step-point intercept inside and outside four black-tailed prairie dog colonies on the Armendaris Ranch, Sierra County, New Mexico, 2 October 2004. Percent cover is proportion of 500 points (positioned 1 m apart along five 100-m transects) intercepting grass leaves or bases <2.5 cm above the ground. Differences in cover between inside and outside colonies approximate losses to prairie dog grazing.

Colony name (size in ha)	Date established	Dominant grass	Cover outside colony (%)	Cover inside colony (%)	Cover loss (%)
Red Lake S (11.1)	1998	Alkali sacaton	19.40	7.00	64
S-Curve (10.1)	1999	Alkali sacaton	18.00	5.20	71[a]
Deep Well (4.4)	1999	Alkali sacaton	29.60	0.00	100
Burrograss (6.6)	2000	Burrograss	19.60	6.40	67[b]

[a]B. Duvall (New Mexico State University, unpublished data) estimated 50% cover loss.
[b]B. Duvall estimated 82% cover loss.

with continued occupancy by prairie dogs, some sites seem likely to remain largely free of perennial grasses, in what some managers would call an "altered steady state" (see Westoby et al. 1989; Laycock 1991; Tausch et al. 1993). What are the implications for sustaining prairie dog populations in the Chihuahuan Desert?

Long Term Sustainability—As discussed above, the Chihuahuan Desert may have supported few prairie dogs, at least since the Pleistocene, until the introduction of cattle. By altering the vegetation, cattle expedited the establishment of new prairie dog populations and the expansion of existing ones. As colonies grew, forage production declined. The end result of this process presently is unclear: at what carrying capacity will the vegetation inside colonies reach equilibrium, and how long will that take? Planning the future conservation of prairie dogs calls for a look at the ability of the range to sustain them over the longer term.

Forage production invariably declines as prairie dog colonies age (Archer et al. 1987; Detling 1998). In the Great Plains, production loss may be buffered by the expansion of grazing-resilient grasses such as buffalograss (*Buchloe dactyloides*), blue grama, and tumblegrass (*Schedonnardus paniculatus*) as grazing-sensitive species decline (Bonham and Lerwick 1976; Archer et al. 1987; Weltzin et al. 1997). Under some circumstances, these hardy grasses may persist for many years, perhaps indefinitely. In contrast, Chihuahuan Desert grasses cannot survive the intensities of grazing sustainable in the Great Plains, partly because some dominant species are innately more sensitive to grazing (Bock and Bock 1993; Holecheck et al. 1999; Navarro et al. 2002) and partly because the more xeric climate, especially periodic drought, imposes levels of water stress not encountered in the Great Plains.

A couple of examples can illustrate the magnitude of potential changes:

- In some of the Janos-Casas Grandes prairie dog colonies, the combination of cattle grazing, prairie dog grazing, and drought has in recent years transformed grassland originally dominated by blue grama and some other grazing-resilient species such as tobosa into barren landscapes with few or no perennial grasses (List 1997; Desmond 2004). The more extreme vegetation changes occurred on ejido lands where cattle abundance was high; prairie dogs were present as changes occurred on some such lands, but had been absent for several years on others (R. List, unpublished data).
- On the Armendaris Ranch in the Jornada del Muerto northeast of Truth or Consequences, New Mexico, prairie dog colonies re-established four to six years ago in historic habitat in swales and flats dominated variously by tobosa,

alkali sacaton, and burrograss have lost a high percentage of the original cover of these perennial grasses (Table 1); drought conditions in the last few years undoubtedly exacerbated the losses. Loss of cover in prairie dog colonies took place both with and without livestock (bison) grazing.

As would be expected, prairie dog densities decline with declines in forage availability. In the Janos-Casas Grandes colonies, estimates of density (by visual census) in 1985 on a colony (Loma los Ratones) on private land averaged about 25 animals per hectare (Ceballos et al. 1993) (Table 2). In 2001, after periodic droughts in the 1990s, J. Pacheco (Instituto de Ecologia, UNAM, unpublished data) estimated by visual census that a large colony (El Cuervo) on *ejido* lands in the same area supported a density of 8/ha. In 2004, after three additional years of drought, densities in the El Cuervo colony averaged 1/ha. On the Armendaris Ranch, in three young colonies established in 1998, 1999, and 2000, densities declined from an average 5.7/ha (range =4.4 to 8.2) in 2003 to 1.9/ha (range =0.8 to 2.6) in 2004 (A. Facka, New Mexico State University, unpublished data); the decline accompanied a severe drought during 2003 to early 2004.

Given the depletion over time of the perennial forage base in all these colonies, it seems unlikely that prairie dog densities can rebound to the original levels while colonies still occupy the sites. Rejuvenation of perennial grasses probably would be hindered or prevented by scarcity of propagules and consumption of seedlings by prairie dogs. In new colonies not yet depleted of perennial grasses, prairie dog densities in the future probably will fluctuate around a much lower mean than currently exists.

The densities presented above are, as might have been predicted, generally much lower than densities of the species outside the Chihuahuan Desert, i.e., in the Great Plains (Table 2). In shortgrass steppe on the western (arid) edge of the Great Plains near Raton, New Mexico, on the Vermejo Park Ranch, densities averaged about 25 animals per hectare over five years in a large, old colony, with little variation among years (D. Long, Turner Endangered Species Fund, pers. comm.). Younger colonies had higher densities, one in a particularly productive year about 80/ha. In the more mesic mixed-grass prairie near Pierre, South Dakota, on the Bad River Ranches, densities in variously-aged colonies over two years averaged 64/ha (K. Bly-Honness, Turner Endangered Species Fund, unpublished data). Knowles (2002) summarized densities reported by seven additional investigators in various Great Plains locations; averaging these densities (using means of range extremes where given) yielded an overall mean of 31.2/ha (range =11.6 to 67.2).

TABLE 2—Estimated densities (by visual census) of black-tailed prairie dogs in colonies at selected Chihuahuan Desert and Great Plains (shortgrass steppe, mixed-grass prairie) locations. Multiple years of census under the same location entry and colony type represent the same colonies. Individuals/ha represent means if more than one colony is involved.

Location	Year(s)	Colony Type (n)	Individuals/ha	Data Source
Chihuahuan Desert				
SW of Janos, Chihuahua	1985	Large, old (1)	25	Ceballoa et al. 2003
SW of Janos, Chihuahua	2001	Large, old (1)	8	J. Pacheco, unpublished data
SW of Janos, Chihuahua	2004	Large, old (1)	1	J. Pacheco, unpublished data
NE of T or C, NM	2003	Small, young (3)	6	A. Facka, unpublished data
NE of T or C, NM	2004	Small, young (3)	2	A. Facka, unpublished data
SW of Carrizozo, NM	2004	Large, old (1)	5	M. Hartsough, unpublished data
E of Orogrande, NM	2001	Small, old (8)	7	A. Ernst, unpublished data
E of Orogrande, NM	2002	Small, old (8)	2	A. Ernst, unpublished data
Shortgrass				
SW of Raton, NM	2000 to 2004	Large, old (1)	25	D. Long, unpublished data
SW of Raton, NM	2004	Small, young (1)	80	D. Long, unpublished data
Mixed-grass				
SW of Pierre, SD	2001	Various (5)	71	K. Bly-Honness, unpublished data
SW of Pierre, SD	2004	Various (5)	56	K. Bly-Honness, unpublished data
Short & Mixed				
Great Plains (7 locations)	Various	Various	31	Knowles, 2002

Range scientists and livestock producers have long known that Chihuahuan Desert grasslands cannot sustain the densities of cattle and intensities of their grazing that are possible in the Great Plains (Holecheck and Hawkes 1993; Holecheck et al. 1999). It is little surprise that densities of prairie dogs and their effect on the forage base follow the same pattern.

Prairie Dog Preserves: Mirage in the Desert?—Several questions need addressing to assess whether prairie dog colonies could or should be managed as permanent features in Chihuahuan Desert landscapes. Are they ecologically sustainable, and at what densities? What other species will derive appreciable benefits at the projected densities? Will the decline in vegetation production be economically and socially acceptable? Will plague risks be acceptably low? What will the neighbors think?

The history of prairie dogs in present-day Chihuahuan Desert environments is too clouded to assess with a great deal of confidence the ability of the vegetation to sustain prairie dogs over many decades. However, we believe colonies can persist in favorable locations, although at lower densities than in most other parts of the species' range. Some of the Janos-Casas Grandes colonies may have existed *in situ* for decades, and the more degraded ones still support prairie dogs at densities of 1 to 8/ha. A large (110-ha) colony 15 km southwest of Carrizozo, New Mexico (probably the largest remaining in the Chihuahuan Desert in the state), apparently has persisted for several decades or more and in 2004, after a year of drought, had an average prairie dog density of about 5/ha (M. Hartsough, BAE Systems, White Sands Missile Range, New Mexico, pers. comm.) (Table 2). Eight smaller colonies (1.9 to 7.3 ha) of perhaps similar (though unknown) ages on Otero Mesa 80 to 100 km east of Las Cruces, New Mexico, had an average estimated density (colony densities averaged for 2001 and 2002) of 4.4/ha (range=1.9 to 7.3) (A. E. Ernst, unpublished data). Sustainable densities probably vary greatly among locations and could change if climate changes, but a long-term average of five to ten individuals per hectare in good habitat seems an educated guess at this stage of our knowledge.

Is this density sufficient to benefit other species? The most density-demanding of the species associated with prairie dogs probably is the black-footed ferret. It is too early to know what minimum prairie dog densities ferrets will require in the Chihuahuan Desert, although similarly low densities of white-tailed prairie dogs (*C. leucurus*) in Wyoming appear to be capable of sustaining ferrets (Knowles 2002). The ultimate fate of the ferrets released in the Janos-Casas Grandes prairie dog colonies in 2001 to 2003 (M. Lockhart, U.S. Fish and Wildlife Service, pers. comm.) may begin to answer this question.

Other prairie dog associates tend to be less demanding of high densities of prairie dogs. Burrowing owls can benefit from very low prairie dog densities if suitable burrows are maintained. Berardelli (2003) found approximately one pair of owls nesting per hectare of prairie dog colony area on the Armendaris Ranch in New Mexico; J. McNicholl (New Mexico State University, unpublished data) found that the Janos-Casas Grandes complex holds probably more breeding burrowing owls than any other complex in existence. Numerous species of raptors and predators assemble to feed on prairie dogs at Janos-Casas Grandes (List 1997; Ceballos et al. 1999; Manzano-Fischer et al. 1999). The presence of active colonies, regardless of prairie dog density, seems invariably to attract an array of species and to elevate species diversity (Ceballos et al. 1999; Manzano-Fischer et al. 1999; Desmond 2004).

Without doubt, prairie dog colonies in the Chihuahuan Desert will remove forage that otherwise could be used by livestock. However, livestock growing in such xeric habitats often is economically marginal (Holecheck and Hawkes 1993), usually requiring subsidies to be viable (Donahue 1999). Many such operations must diversify into non-livestock ventures to become profitable in the open market (Holecheck 2001). Properly managed as an ecotourism attraction or scientific study area, or to qualify for conservation funding by agencies, prairie dog colonies could benefit a livestock operation rather than draining it.

What about plague risks? As discussed earlier, it appears likely (though not certain) that prairie dog colonies in the Chihuahuan Desert are less susceptible to plague outbreaks than those in other regions west of the 100th meridian. Furthermore, because a major presumed mode of transmission among colonies closer than about 3 km from each other is from dispersal of infected prairie dogs (Cully and Williams 2001), the natural occurrence of barriers to dispersal in many Chihuahuan Desert areas may further reduce risks from plague. Thus Chihuahuan Desert regions may have greater plague security than many Great Plains regions.

What will the neighbors think? Adjacent landowners often object to prairie dogs nearby because they fear prairie dogs will move onto their property. Many (though not all) circumstances in the Chihuahuan Desert, unlike most in the Great Plains, present formidable barriers to prairie dog dispersal. Suitable prairie dog habitat often exists as rather restricted parcels of land surrounded by expanses of hills, mountains, brushland, or otherwise unsuitable terrain across which prairie dogs would be unlikely to venture and less likely to cross in sufficient numbers to initiate new colonies. This may help allay the neighbors' fear of invasions by prairie dogs.

The other objection neighbors may have is breach of tradition. Those who welcome prairie dogs may be unwelcome by those whose grandparents worked hard to rid the range of prairie dogs. This objection may persist until prairie dogs begin to attract money. We believe that neighbors, over time, can get used to prairie dogs eating grass if they see prairie dog conservation as a profitable enterprise.

Conservation Strategies—The decline in abundance and the ecological importance of prairie dogs have attracted recent attention by conservationists in both México and the United States. Because different sociopolitical regimes exist in the two countries, different administrative approaches to conservation have evolved. However, to be successful, such approaches must consider the ecological needs of the species.

Administrative Approaches and Goals, México—The Janos-Casas Grandes prairie dog complex attracts a variety and abundance of wildlife species, several of international interest (Ceballos et al. 1993; 1999). The biological importance of the area was identified as early as 1937, when the municipalities of Janos and Ascensión were decreed a wildlife refuge, which under Mexican law only bans hunting, without additional restrictions. Today, prairie dogs have been displaced from Ascensión by industrial agriculture, serving as a warning of what could happen in Janos.

Janos is one of the Terrestrial Priority Regions of the Comisión Nacional para el Conocimiento y Uso de la Biodiversidad (Area No. 34 San Luis-Janos; CONABIO, 2000), and an important bird area (AICA de Janos; Manzano-Fischer et al. 2000). The World Wildlife Fund considers the Janos area a priority site for conservation within the Chihuahuan Desert (Ecoregional Plan for the Chihuahuan Desert; Dinerstein et al. 1998). The Wildlands Project and Naturalia include Janos among the most important biological areas in northern México (List et al. 1998; 2000). A recent complimentarity study by the Institute of Ecology of the National University of México (UNAM) to determine the combination of protected areas that would be required to protect 100% of the mammal species in México showed that Janos ranked second in priority in all of México in this regard (only the Reserve of Montes Azules in Chiapas ranked higher) (Ceballos 1999).

A number of non-governmental organizations from México and the United States are cooperating on conservation in the Janos area. Attempts are being made to update the old decree to better conserve resources and benefit local stakeholders. Efforts are under way to buy land and grazing rights to better protect the prairie dog population. Because several human settlements exist in the area and depend economically on

grazing, farming, and other land uses, it will be necessary also to develop economic alternatives for people if conservation plans are to succeed.

Given the importance of the Janos-Casas Grandes complex, it seems reasonable to restore the colony acreage to 1988 levels (55,000 ha). To accomplish this goal, we favor: (1) reestablishment of prairie dogs in areas where they were exterminated in the 1980s and 1990s (at the core of the complex) to form a large colony (>5,000 ha), and (2) increasing the sizes of and connectivity among colonies in areas less threatened by development. Administrative actions needed include legal protection of prairie dogs and the areas they occupy, ecological zoning to regulate agricultural and other developments, purchase of lands and grazing rights to expedite control of land use, and development of economic alternatives to grazing.

Administrative Approaches and Goals, United States—In the United States, black-tailed prairie dog conservation is following a different administrative procedure. States in the species' historic range recently collaborated to develop a conservation strategy (Luce et al. 2001) in response to its potential listing as federally "threatened" (U.S. Fish and Wildlife Service 2000). This multi-state group outlined an approach whereby each state would commit to conserving a minimum acreage of prairie dog colonies, such acreage based in part on estimated area of historical range in the respective states. Despite the recent decision by the U.S. Fish and Wildlife Service not to list the species, most states seem committed to continuing with this strategy.

Conservation plans developed by Arizona (Van Pelt 1999), New Mexico (New Mexico Black-tailed Prairie Dog Working Group 2001), and Texas (Texas Black-tailed Prairie Dog Working Group 2004) set "colony acreage" goals to be met during the next ten years (Table 3). These acreage goals arose from Luce's (2003) recommendations for ten-year acreage goals in "peripheral areas" (which included Chihuahuan Desert regions) equal to at least 0.1% of its historic range, reduced by the proportion of range deemed unsuitable based on a habitat model. New Mexico's plan specifies, in addition, the establishment of at least two viable populations within each county of historical occurrence.

A major conservation challenge appears in Table 3—current acreages in Arizona and New Mexico fall far short of the ten-year goals. Texas' prairie dog colony acreage appears much closer to their ten-year goals than do acreages in Arizona and New Mexico. The acreage data for Texas were based on remote sensing with about 30% of the acreage ground-truthed (Texas Parks and Wildlife Department, Austin, unpubl. data). In New Mexico, we used data from ground-based surveys because remote-sensing

Table 3—Black-tailed prairie dog ten-year conservation goals and currently occupied habitat in the context of the historically suitable habitat in the species' range in Chihuahuan Desert regions of 3 states. Conservation goals were based on an arbitrary 0.1% of suitable historic range as estimated by a habitat model (Luce 2003). Currently occupied habitat was estimated in Arizona and New Mexico on the basis of ground surveys (B. Van Pelt, pers. comm.; G. Schmitt, A. Ernst, and J. Truett, unpublished data) and in Texas by remote sensing coupled with ground truthing of about 30% of the colony acreage (Texas Parks and Wildlife Department, unpublished data).

State	Estimated suitable historic range (ha)	Conservation goal (ha)	Estimated currently occupied habitat (ha)
Arizona	1,858,000	1,858	0.0
New Mexico	6,734,000	6,734	400
Texas	5,780,000	5,780	5,162

inventories of colonies (Johnson et al. 2003) gave results for Chihuahuan Desert areas that were substantially different from our knowledge based on recent ground surveys.

Ecological Considerations—Is a major effort to conserve prairie dogs in a climatically marginal region such as the Chihuahuan Desert justifiable? We think it is, for the following reasons:

- Given the unpredictability of rangewide changes in such factors as climate, land use, and the landscape ecology of plague, it seems prudent to maintain viable populations of prairie dogs in a region sufficiently different from others that it could become a refuge from impacts that occur elsewhere.
- The benefits, both known and potential, of prairie dogs to other Chihuahuan Desert species justifies prairie dog conservation as an endeavor in regional biodiversity conservation.
- Prairie dogs, properly managed, may stand to contribute relatively more to landowner incomes in the Chihuahuan Desert than it could in areas where livestock growing is more profitable, i.e., the Great Plains.

A major ecological issue related to management is that of acreage distribution. Should management for colony establishment and expansion be distributed among many small sites or condensed into a few large ones? We favor focus on a few large sites per state, county, or other jurisdiction, at least for the next ten years. Reasons follow:

- A few large parcels can be more cost-effectively acquired (by fee title or easement) and managed than the same acreage of numerous small sites.

- Large parcels allow for spacing prairie dog colonies farther from neighbors.
- Conservation programs on large parcels gain more public attention and thus are more likely to be copied by others that those on small parcels.
- Prairie dog conservation efforts on large parcels are more likely to attract and support research programs that guide future management than are those on small parcels.
- Large parcels provide adequate space should it turn out that long-term management requires a continually shifting mosaic of colonies to maintain population numbers and protect the forage base, i.e., a slow version of rest-rotation grazing.

Taking Action—We believe nongovernment organizations (NGOs) are best equipped to take the lead in restoring prairie dog populations. Governments (federal, state, local) ideally would sanction projects, remove legal obstacles, and provide permits and approvals where needed. They might be able to provide economic incentives in various ways, as suggested in the state plans referenced earlier. But usually they are not structured to pursue large-scale restoration projects on the ground.

To be cost effective, prairie dog conservation efforts should focus in areas where they are most likely to succeed. We suggest focal areas in each state (Fig. 4) based on historical abundances of prairie dogs and present-day landowner views and management policies that seem inclined toward prairie dog conservation. Locations of these focal areas are generally consistent with present state goals.

How interested organizations should approach prairie dog restoration and conservation in these areas undoubtedly will vary from case to case, but in our experience a stepwise process makes sense, as follows:

- Explore the local ecological needs of prairie dogs, the management and land requirements, the range of potential costs, and the time required to reach the goals envisioned. Visits to ongoing projects are recommended at this stage.
- Insure a reliable source of funding for land acquisition, conservation easements, equipment and supplies, management personnel, and the like.
- Survey the options available for long-term control of suitable landscapes. Outright purchase or conservation easements may be options for parties that initially do not have suitable land holdings.
- Visit potential purchase or easement options, or survey lands already available, with a view to assessing terrain suitability for prairie dogs, resilience of the forage base to grazing, need for and availability of large grazers to expedite habitat

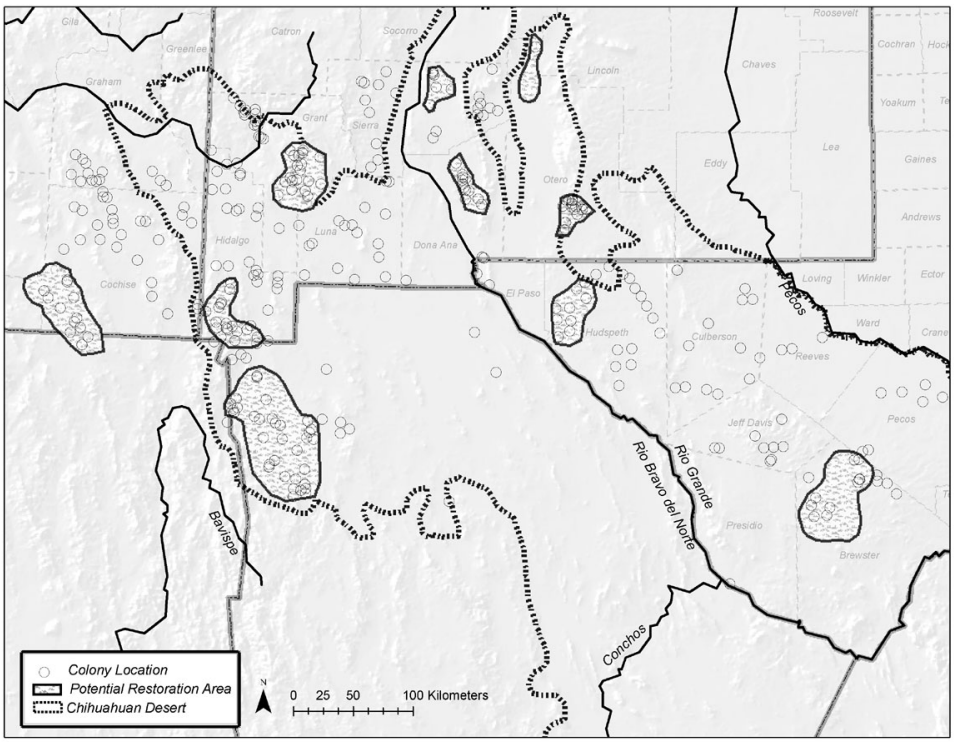

Fig. 4—Suggested focus areas for restoration of black-tailed prairie dogs (*Cynomys ludovicianus*) in and near the Chihuahuan Desert. Delineation of focus areas was based on historical occurrences of prairie dogs (circles) (Schmidly 1977; Ceballos et al. 1993; Knyazhnitskiy et al. 1999; Oakes 2000), current patterns of land ownership and management, and general goals of the respective states.

management, presence and nature of barriers to prairie dog movement, and views of neighbors toward prairie dogs. Advice from appropriately experienced individuals will help at this stage.

- Assume that, despite what others have found, you will encounter surprises and can adjust. Management of prairie dogs is not yet, and may never be, a prescriptive science with highly predictable outcomes.
- Assess the probable long-term support of agencies that regulate prairie dogs. Imposition of new regulations limiting management options could impede progress.

We believe the future of prairie dog conservation lies with such efforts by motivated individuals and organizations. Early endeavors by those willing and able to engage in such conservation will help pave the way for those who follow. Indeed, some already

have begun conservation efforts, both in the United States and México. The black-tailed prairie dog will not be called a pest forever, and those "running" prairie dogs on their holdings may someday be asked to join those crowding the coffee tables at restaurants on the main streets of small towns in and near the Chihuahuan Desert grasslands.

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Literature Cited

Agenbroad, L.D., and C.V. Haynes. 1975. *Bison bison* remains at Murray Springs, Arizona. *Kiva* 40(4):309–313.

Akins, N.J. 1984. Temporal variation in faunal assemblages from Chaco Canyon. In: W.J. Judge and J.D. Schelberg, editors. *Recent Research on Chaco Prehistory*. U.S. National Park Service, Albuquerque, New Mexico. Pages 225–240.

Anderson, E., S.C. Forrest, T.W. Clark, and L. Richardson. 1986. Paleobiology, biogeography, and systematics of the black-footed ferret, *Mustela nigripes* (Audubon and Bachman), 1851. *Great Basin Naturalist Memoirs* 8:11–62.

Anyon, R., and S.A. LeBlanc. 1984. *The Galaz Ruin: A Prehistoric Mimbres Village in Southwestern New Mexico*. Maxwell Museum of Anthropology and University of New Mexico Press, Albuquerque.

Archer, S., M.G. Garrett, and J.K. Detling. 1987. Rates of vegetation change associated with prairie dog (*Cynomys ludovicianus*) grazing in North American mixed-grass prairie. *Vegetatio* 72:159–166.

Bailey, R.G., P.E. Avers, T. King, and W.H. McNab, editors. 1994. *Ecoregions and Subecoregions of the United States*. U. S. Forest Service, Washington, D.C.

Bailey, V. 1905. Biological survey of Texas. *North American Fauna* 25:1–222.

Bailey, V. 1906. New Mexico: Cliff: Mammals. Nov. 6–9, 1906. Smithsonian Institution Archives, Record Unit 7176, U.S. Fish and Wildlife Service, 1860–1961, Field Reports. Washington, D.C.

Bailey, V. 1931. Mammals of New Mexico. *North American Fauna* 53:1–412. Republished in 1971 by Dover Publications, New York, New York.

Bailey, V. 1932. Corralitos and Sierra Madre, Chihuahua, Mexico. Smithsonian Institution Archives, Record Unit 7176, U.S. Fish and Wildlife Service, 1860–1961, Field Reports.

Bak, J.M., K.G. Boykin, B.C. Thompson, and D.L. Daniel. 2001. Distribution of wintering ferruginous hawks (*Buteo regalis*) in relation to black-tailed prairie dog (*Cynomys ludovicianus*) colonies in southern New Mexico and northern Chihuahua. *Journal of Raptor Research* 35:124–129.

Barnes, A.M. 1993. A review of plague and its relevance to prairie dog populations and the black-footed ferret. In: J.L. Oldemeyer, D. E. Biggins, B. J. Miller, and R. Crete, editors. *Management of Prairie Dog Complexes for the Reintroduction of the Black-footed Ferret*. U.S. Fish and Wildlife Service Biological Report 13, Washington, D.C. Pages 28–37.

Berardelli, D. 2003. A comparative study of burrowing owl (*Athene cunicularia*) nest success and factors that influence nest success between urban and grassland habitat. Unpublished M.S. thesis, New Mexico State University, Las Cruces.

Bock, C.E., and J.H. Bock. 1993. Cover of perennial grasses in southeastern Arizona in relation to livestock grazing. *Conservation Biology* 7:371–377.

Bonham, C.D., and A. Lerwick. 1976. Vegetation changes induced by prairie dogs on shortgrass range. *Journal of Range Management* 29:221–225.

Brand, C.J. 2002. Landscape ecology of plague in the American Southwest. Proceedings of an American Southwest workshop. *U.S. Geological Survey Information and Technology Report 2002-0001*.

Brand, D.D. 1961. The early history of the range cattle industry in northern Mexico. *Agricultural History* 35:132–139.

Bryson, R.A. 1974. A perspective on climate change. *Science* 184(4138):753–760.

Ceballos, G. 1999. Conservación de los mamíferos de México. *Biodiversitas* (*Boletín de la Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, CONABIO*) 27:1–8

Ceballos, G., E. Mellink, and L.R. Hanebury. 1993. Distribution and conservation status of prairie dogs *Cynomys mexicanus* and *Cynomys ludovicianus* in Mexico. *Biological Conservation* 63:105–112.

Ceballos, G., J. Pacheco, and R. List. 1999. Influence of prairie dogs (*Cynomys ludovicianus*) on habitat heterogeneity and mammalian diversity in Mexico. *Journal of Arid Environments* 41:161–172.

Cincotta, R.P., D.W. Uresk, and R.M. Hansen. 1988. A statistical model of expansion in a colony of black-tailed prairie dogs. In: D.W. Uresk, G.L. Schenbeck, and R. Cefkin, technical coordinators. *Proceedings Eighth: Great Plains Wildlife Damage Control Workshop*. U.S. Forest Service General Technical Report RM-154. Pages 30–33.

CONABIO. 2000. *Regiones Prioritarias Terrestres de México*. CONABIO, Mexico D.F.

Cook, R.R., J.E. Cartron, and P.L. Polechla, Jr. 2003. The importance of prairie dogs to nesting ferruginous hawks in grassland ecosystems. *Wildlife Society Bulletin* 31:1073–1082.

Cottam, L., and M. Caroline. 1965. The black-tailed prairie dog in Texas. *Texas Journal of Science* 17:294–302.

Cully, J.F., Jr., and E.S. Williams. 2001. Interspecific comparisons of sylvatic plague in prairie dogs. *Journal of Mammalogy* 82:894–905.

Desmond, M. 2004. Effects of grazing practices and fossorial rodents on a winter avian community in Chihuahua, Mexico. *Biological Conservation* 116:235–242.

Desmond, M.J., J.A. Savidge, and K.M. Eskridge. 2000. Correlations between burrowing owl and black-tailed prairie dog declines: a 7-year analysis. *Journal of Wildlife Management* 64:1067–1075.

Detling, J.K. 1998. Mammalian herbivores: ecosystem-level effects in two grassland national parks. *Wildlife Society Bulletin* 26:438–448.

Dick-Peddie, W.A. 1993. *New Mexico Vegetation: Past, Present, and Future*. University of New Mexico Press, Albuquerque.

Dinerstein, E., D. Olson, J. Atchley, C. Loucks, S. Contreras-Balderas, R. Abell, E. Eñigo, E. Enkerlin, C.E. Williams, and G. Castilleja. 1998. *Ecoregional-based Conservation in the Chihuahuan Desert: a Biological Assessment and Biodiversity Vision*. World Wildlife Fund, Washington, D.C.

DiPeso, C.C., J.B. Rinaldo, and G.J. Fenner. 1974. *Casas Grandes: A Fallen Trading Center of the Gran Chicimeca*. Volume 8. Amerind Foundation, Dragoon, Arizona, and Northland Press, Flagstaff, Arizona.

Dobie, J.F. 1953. Bison in Mexico. *Journal of Mammalogy* 34:150–151.

Donahue, D.L. 1999. *The Western Range Revisited: Removing Livestock From Public Lands to Conserve Native Biodiversity*. University of Oklahoma Press, Norman.

Escudero, J.A. 1834. *Noticias Estadísticas del Estado de Chihuahua*. Reimpresión por orden del supremo gobierno.

Ford, P.L., E.L. Fredrickson, M.L. Anderson, and J.C. Truett. 2002. Fire as a management tool to facilitate expansion of reintroduced black-tailed prairie dog colonies in Chihuahuan Desert grasslands. Society for Conservation Biology 16th annual meeting, Canterbury, England.

Goodwin, H.T. 1995. Pliocene-Pleistocene biogeographic history of prairie dogs, genus *Cynomys* (Sciuridae). *Journal of Mammalogy* 76:100–122.

Graham, R.W., and E.L. Lundelius, Jr. 1984. Coevolutionary disequilibrium and Pleistocene extinctions. In: P.S. Martin and R.G. Klein, editors. *Quaternary Extinctions: A Prehistoric Revolution*. University of Arizona Press, Tucson. Pages 223–249.

Hall, E. 1981. *The Mammals of North America*. Volume 1. John Wiley and Sons, New York, New York.

Haskett, B. 1935. Early history of the cattle industry in Arizona. *Arizona Historical Review* 6(4):2–42.

Hilliard, G. 1996. *A Hundred Years of Horse Tracks: The Story of the Gray Ranch*. High-Lonesome Books, Silver City, New Mexico.

Holecheck, J.L. 2001. Western ranching at the crossroads. *Rangelands* 23(1):17–21.

Holecheck, J.L., and J. Hawkes. 1993. Desert and prairie ranching profitability. *Rangelands* 15(3):104–109.

Holecheck, J.L., M. Thomas, F. Molinar, and D. Galt. 1999. Stocking desert rangelands: what we've learned. *Rangelands* 21(6):8–12.

Hoogland, J.L. 1981. The evolution of coloniality in white-tailed and black-tailed prairie dogs (Sciuridae: *Cynomys leucurus* and *C. ludovicianus)*. *Ecology* 62:252–272.

Hubbard, J., and C. Schmitt. 1984. The black-footed ferret in New Mexico. Report to U.S. Bureau of Land Management, Santa Fe, New Mexico, from New Mexico Department of Game and Fish, Santa Fe.

Johnson, K., T. Neville, and L. Pierce. 2003. *Remote Sensing Survey of Black-tailed Prairie Dog Towns in the Historical New Mexico Range*. University of New Mexico, New Mexico Natural Heritage Program, Publication No. 03-GTR-248, Albuquerque.

Knowles, C.J. 1982. Habitat affinity, populations, and control of black-tailed prairie dogs on the Charles M. Russell National Wildlife Refuge. Unpublished Ph.D. dissertation, University of Montana, Missoula.

Knowles, C.J. 1986. Some relationships of black-tailed prairie dogs to livestock grazing. *Great Plains Naturalist* 46:198–203.

Knowles, C.J. 2002. *Status of White-tailed and Gunnison's Prairie Dogs*. National Wildlife Federation, Missoula, Montana, and Environmental Defense, Washington, D. C.

Knyazhnitskiy, O.V., R.R. Monk, N.C. Parker, and R.J. Baker. 2000. *Assignment of Global Information Systems Coordinates to Classical Museum Localities for Relational Database Analysis*. Occasional Papers, Museum of Texas Tech University No. 199, Lubbock.

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

Krieger, A.D. 2002. *We Came Naked and Barefoot: The Journey of Cabeza de Vaca across North America*. University of Texas Press, Austin.

Lauenroth, W.K., I.C. Burke, and M.P. Gutman. 1999. The structure and function of ecosystems in the central North American grassland region. *Great Plains Research* 9:223–259.

Laycock, W.A. 1991. Stable states and thresholds of range condition on North American rangelands: A viewpoint. *Journal of Range Management* 44:427–433.

Lehmer, E.M., B. Van Horne, B. Kulbartz, and G.L. Florant. 2001. Facultative torpor in free-ranging black-tailed prairie dogs (*Cynomys ludovicianus*). *Journal of Mammalogy* 82:551–557.

List, R. 1997. Ecology of kit fox (*Vulpes macrotis*) and coyote (*Canis latrans*) and the conservation of the prairie dog ecosystem in northern Mexico. Unpublished Ph.D. dissertation, University of Oxford, U.K.

List, R., and D.W. Macdonald. 2003. Home range and habitat use of the kit fox (*Vulpes macrotis*) in a prairie dog (*Cynomys ludovicianus*) complex. *Journal of Zoology* 259:1–5.

List, R., P. Manzano-Fischer, and D. W. Macdonald. 2003. Coyote and kit fox diets in a prairie dog complex in Mexico. In: M. Sovada and L. Carbyn, editors. *The Swift Fox: Ecology and Conservation of Swift Foxes in a Changing World*. Canadian Plains Research Center, University of Regina, Saskatchewan, Canada.

List, R., O. Moctezuma, and C. Martínez del Rio. 2000. Cooperative conservation: Wildland Project efforts in the Sierra Madre. *Wild Earth* 10:51–54.

List, R., O. Moctezuma, and M. Miller. 1998. What to protect in Chihuahua and Sonora. In: *Proceedings of the 9th U.S./Mexico Border States Conference on Recreation, Parks, and Wildlife*. Tucson, Arizona, 3 to 6 June 1998. U.S. Department of Agriculture.

Luce, R.J. 2003. A multi-state conservation plan for the black-tailed prairie dog, *Cynomys ludovicianus*, in the United States: An addendum to the Black-tailed Prairie Dog Conservation Assessment and Strategy, November 3, 1999. Prairie Dog Conservation Team, Sierra Vista, AZ.

Luce, R.J., P. Gober, B. Van Pelt, and S. Grassel. 2001. A multi-state, range-wide approach to black-tailed prairie dog conservation and management. *Transactions of the North American Wildlife and Natural Resources Conference* 66:464–479.

Mack, R.N., and J.N. Thompson. 1982. Evolution in steppe with few large, hoofed mammals. *American Naturalist* 119:757–773.

Manzano-Fischer, P., G. Ceballos, R. List, O. Moctezuma, and J. Pacheco. 2000. Janos-Nuevo Casas Grandes. In: C. Arismendi and L. Márquez Valdemar, editors. *Áreas de Importancia Para la Conservación de las Aves en México*. CONABIO, México, D.F.

Manzano-Fischer, P., R. List, and G. Ceballos. 1999. Grassland birds in prairie-dog towns in northwestern Chihuahua, Mexico. *Studies in Avian Biology* 19:263–271.

Marcé, S.E. 2001. Distribución y fragmentación de las colonias de perros llaneros de cola negra (*Cynomys ludovicianus*) en el noroeste de Chihuahua, México. B.S. thesis, Universidad Nacional Autonoma de México, Mexico.

McClaran, M.P. 1995. Desert grasslands and grasses. In: M.P. McClaran and T. R. Van Devender, editors. *The Desert Grassland*. University of Arizona Press, Tucson. Pages 1–30.

Mearns, E. 1907. *Mammals of the Mexican Boundary of the United States*. Smithsonian Institution, United States National Museum Bulletin 56. U.S. Government Printing Office, Washington, D.C.

Merriam, C.H. 1902. The prairie dog of the Great Plains. In: *Yearbook of the United States Department of Agriculture, 1901*. Government Printing Office, Washington, D.C. Pages 257–270.

Messing, J.H. 1986. A late Pleistocene-Holocene fauna from Chihuahua, Mexico. *Southwestern Naturalist* 31:277–288.

Navarro, J.M., D. Galt, J. Holecheck, J. McCormick, and F. Molinar. 2002. Long-term impacts of livestock grazing on Chihuahuan Desert rangelands. *Journal of Range Management* 55:400–405.

Neuenschwander, L.F., S.H. Sharrow, and H.A. Wright. 1975. Review of tobosa grass (*Hilaria mutica*). *Southwestern Naturalist* 20:255–263.

New Mexico Black-tailed Prairie Dog Working Group. 2001. Interagency conservation and management working plan for black-tailed prairie dogs in New Mexico. Sixth draft. Unpublished report, New Mexico Game and Fish Department, Santa Fe.

Oakes, C.L. 2000. History and consequences of keystone mammal eradication in the desert grasslands: the Arizona black-tailed prairie dog (*Cynomys ludovicianus arizonensis*). Unpublished Ph.D. dissertation, University of Texas, Austin.

Osborn, B., and P.F. Allan. 1949. Vegetation of an abandoned prairie-dog town in tallgrass prairie. *Ecology* 30:322–332.

Parmenter, R.R., E.P. Yadav, C.A. Parmenter, P. Ettestad, and K.A. Gage. 1999. Incidence of plague associated with increased winter-spring precipitation in New Mexico. *American Journal of Tropical Medicine and Hygiene* 61:814–821.

Reed, E.K. 1955. Bison beyond the Pecos. *Texas Journal of Science* 7:132–134.

Roe, F.G. 1970. *The North American Buffalo: A Critical Study of the Species in its Wild State*. Second edition. University of Toronto Press, Ontario, Canada.

Schmidly, D.J. 1977. *The Mammals of Trans-Pecos Texas*. Texas A&M University Press, College Station.

Schmidt, R.H., Jr. 1979. A climatic delineation of the "real" Chihuahuan Desert. *Journal of Arid Environments* 2:243–250.

Shaffer, B.S. 1991. The economic importance of vertebrate faunal remains from the Nan ruin (LA 15049), a Classic Mimbres site, Grant County, New Mexico. Unpublished M.A. thesis, Texas A&M University, College Station.

Smith, R.E. 1967. *Natural History of the Prairie Dog in Kansas*. University of Kansas Museum of Natural History and State Biological Survey Miscellaneous Publication No. 49.

Snell, G.P., and B.D. Hlavachick. 1980. Control of prairie dogs—the easy way. *Rangelands* 2(6):239–240.

Tausch, R.J., P.E. Wigand, and J.W. Burkhardt. 1993. Viewpoint: Plant community thresholds, multiple steady states, and multiple successional pathways: legacy of the Quaternary? *Journal of Range Management* 46:439–447.

Texas Black-tailed Prairie Dog Working Group. 2004. Texas black-tailed prairie dog conservation and management plan. Draft. Unpublished report. Texas Parks and Wildlife Department, Lubbock.

Tinker, B. 1978. *Mexican Wilderness and Wildlife*. University of Texas Press, Austin

Truett, J.C. 1996. Bison and elk in the American Southwest: in search of the pristine. *Environmental Management* 20:195–206.

Truett, J.C. 2003. Migrations of grasslands communities and grazing philosophies in the Great Plains: a review and implications for management. *Great Plains Research* 13:3–26.

Truett, J.C., K. Bly-Honness, D.H. Long, and M.K. Phillips. 2006. Habitat restoration and management. In: J.E. Roelle, B.J. Miller, J.L. Godbey, and D.E. Biggins, editors. *Recovery of the Black-Footed Ferret: Progress and Continuing Challenges*. Scientific Investigations Report 2005-5293. Fort Collins Science Center, Fort Collins, CO: U.S. Geological Survey. Pages 97–110.

Truett, J.C., and T. Savage. 1998. Reintroducing prairie dogs into desert grasslands. *Restoration and Management Notes* 16:189–195.

U.S. Fish and Wildlife Service. 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(24):5476–5488.

Van Devender, T.R. 1986. Pleistocene climates and endemism in the Chihuahuan Desert flora. In: J.C. Barlow, A.M. Powell, and B.N. Timmermann, editors. *Second Symposium on Resources of the Chihuahuan Desert Region*. Chihuahuan Desert Research Institute, Alpine, Texas. Pages 1–19.

Van Devender, T.R. 1990. Late Quaternary vegetation and climate of the Chihuahuan Desert, United States and Mexico. In: J.L. Betancourt, T.R. Van Devender, and P.S. Martin, editors. *Packrat Middens: The Last 40,000 Years of Biotic Change*. University of Arizona Press, Tucson. Pages 104–133.

Van Devender, T.R. 1995. Desert grassland history: changing climates, evolution, biogeography, and community dynamics. In: M. McClaran, and T. Van Devender, editors. *The Desert Grassland*. University of Arizona Press, Tucson. Pages 68–99.

Van Devender, T.R., G.L. Bradley, and A.H. Harris. 1987. Late Quaternary mammals from the Hueco Mountains, El Paso and Hudspeth counties, Texas. *Southwestern Naturalist* 32:179–195.

VAN PELT, W.E. 1999. *The Black-tailed Prairie Dog Conservation Assessment and Strategy.* Nongame and Endangered Wildlife Program Technical Report 159. Arizona Game and Fish Department, Phoenix.

VILLA, R.B. 1955. Observaciones acerca de la última manada berrendos (*Antilocapra americana*) en el Estado de Chihuahua, México. *Anales del Instituto de Biología* 26:229–236.

WALLACE, L. 1866. A buffalo hunt in northern Mexico. In: N.B. Carmony and D.E. Brown (editors) 1971. *Mexican Game Trails: Americans Afield in Old Mexico, 1866-1940*. University of Oklahoma Press, Norman.

WELTZIN, J.F., S.L. DOWHOWER, AND R.K. HEITSCHMIDT. 1997. Prairie dog effects on plant community structure in southern mixed-grass prairie. *Southwestern Naturalist* 42:251–258.

WESTOBY, M., B. WALKER, AND I. NOY-MEIR. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266–274.

WHICKER, A.D., AND J.K. DETLING. 1988. Ecological consequences of prairie dog disturbances. *BioScience* 38:778–785.

WOOSLEY, A.I., AND A.J. MCINTYRE. 1996. *Mimbres Mogollon Archaeology: Charles C. DiPeso's Excavations at Wind Mountain*. Amerind Foundation, Dragoon, Arizona, and University of New Mexico Press, Albuquerque.

WORLD WILDLIFE FUND. 2000. *World Wildlife Fund Ecoregions.* Environmental Systems Research Institute, Inc., Redlands, California.