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CURRENT STATUS, DISTRIBUTION, AND CONSERVATION OF THE BURROWING OWL IN OKLAHOMA

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ABSTRACT.—In Oklahoma, the Burrowing Owl (*Athene cunicularia*) historically inhabited much of the western half of the state. Over the last century, habitat destruction and alteration, including destruction of prairie dog (*Cynomys* spp.) colonies, have taken a toll on the remaining Burrowing Owls in Oklahoma. Currently, owls occupy only a relatively small portion of their historical range in the state. A recent survey indicated that total colony area in the state continues to decline, decreasing 4–7% over the past 10 yr. As prairie dogs continue to be eradicated by humans and impacted by plague over significant areas of Oklahoma, it is not surprising that Burrowing Owls continue to decline. Currently, there are an estimated 800–1000 Burrowing Owls breeding in Oklahoma, and most of these occur in the three panhandle counties (Cimarron, Texas, and Beaver). Breeding Bird Survey data showed that the Burrowing Owl population has significantly declined (12.3%/yr) in the state. Christmas Bird Count data, although limited, also suggest decreasing numbers of wintering Burrowing Owls in the state. These findings are a cause of great concern for the Burrowing Owl in Oklahoma. Major cooperative efforts are needed to ensure that viable populations of Burrowing Owls continue to exist throughout the species' range in Oklahoma.

KEY WORDS: *Burrowing Owl;* Athene cunicularia; *status; distribution; conservation; black-tailed prairie dog;* Cynomys ludovicianus; *Oklahoma.*

Estado actual, distribución, y conservación del Búho Cavador en Oklahoma

RESUMEN.—En Oklahoma, el Búho Cavador (*Athene cunicularia*) históricamente ha habitado la mayor parte del lado oeste del estado. En el ultimo siglo, la destrucción del hábitat y su alteración, incluyendo la destrucción de las colonias de perros de la pradera (*Cynomys* spp.) ha tomado un numero de bajas en los restantes Búhos Cavadores de Oklahoma. Actualmente los búhos ocupan solamente una porción relativamente pequeña de su rango histórico en el estado. Un estudio reciente indicó que el área total de las colonias de los perros de la pradera continua disminuyendo abruptamente, decreciendo 4–7% en los últimos 10 años. Como los perros de las praderas están siendo erradicados por los humanos y devastados por la peste sobre áreas significativas de Oklahoma, no es sorprendente que el numero de Búhos Cavadores continúe decayendo. En la actualidad, hay un estimado de 800–1000 Búhos Cavadores reproduciéndose en Oklahoma, y la mayoría de estas ocurren en los tres condados de la región "manija" (Cimarron, Texas, y Beaver). Los datos del Estudio de Aves en Reproducción muestran que las poblaciones de búho cavador han decrecido significativamente (12.3%/año) en el estado. La continuación de estas tendencias resultará probablemente en la necesidad de protección legal bajo la ley estatal de especies en peligro. Se necesitan esfuerzos cooperativos mas grandes para asegurar que poblaciones viables de Búhos Cavadores continúen existiendo a lo largo y ancho de su rango en Oklahoma.

[Traducción de Victor Vanegas y César Márquez]

Historically, the Burrowing Owl (*Athene cunicularia*) inhabited the western one-half of Oklahoma (Baumgartner and Baumgartner 1992, Haug et al. 1993). Prior to settlement of the Oklahoma Territory in the 1880s, Burrowing Owls were locally common summer residents in grasslands of central and western Oklahoma, but they were largely ex-

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tirpated by 1930 (Baumgartner and Baumgartner 1992). They were commonly found in shortgrass prairie habitats and were closely associated with black-tailed prairie dogs (*Cynomys ludovicianus*). Currently, they are a rare and local summer resident, mainly in the Oklahoma panhandle and other western counties (Baumgartner and Baumgartner 1992). Modern development and agriculture have resulted in large-scale destruction and alteration of Burrowing Owl habitat in Oklahoma and other Great Plains states. In addition, sylvatic plague (*Yersinia pestis*), shooting, and poisoning have greatly reduced prairie dog populations, resulting in population numbers that are only a fraction of what they were historically. Burrowing Owls today occupy only a relatively small portion of their historical range in Oklahoma, and numbers are greatly reduced from historical estimates. The largest populations are found in Cimarron County in the panhandle (Baumgartner and Baumgartner 1992). Currently, the Burrowing Owl is classified as a Species of Special Concern in Oklahoma (Oklahoma Department of Wildlife Conservation publ. comm.). It is also a Species of Special Concern in the neighboring state of Kansas, but has no official listing in either Texas or New Mexico (Sheffield 1997a). The black-tailed prairie dog, a species that is ecologically linked to the Burrowing Owl in the Great Plains, is also classified as a Species of Special Concern in Oklahoma (Oklahoma Department of Wildlife Conservation publ. comm.).

To date, there has been no systematic survey of Burrowing Owls in Oklahoma. In the summer of 1970, Butts (1971) studied the ecology of Burrowing Owls in Beaver and eastern Texas counties. This is the most complete estimate of population density of Burrowing Owls in Oklahoma, and there has not been a similar survey since. In 1970, the total area covered by prairie dog colonies in Oklahoma was less than half of the area it was in 1960 (Butts 1971). Burrowing Owl populations are small or nonexistent in areas of central and western Oklahoma where prairie dogs have been eradicated (Butts and Lewis 1982). The Oklahoma panhandle is still largely undeveloped, and is characterized mainly by cattle ranching, agriculture, and open prairie. In this area, prairie dog colonies are still relatively large and numerous. As you move east from the panhandle, development is more prevalent, prairie dog colonies are less frequent and more fragmented, and there are fewer Burrowing Owls (Tyler 1968, Butts and Lewis 1982, J. Shackford, J. Tyler, and L. Choate unpubl. data).

SUMMER RECORDS

The current summer (breeding) range of the Burrowing Owl in Oklahoma was derived from BBS data (1966–99), other breeding records, and personal observations. Burrowing Owl family groups have been documented during the summer months in the prairie dog colonies of 13 western counties (Fig. 1). It is likely that Burrowing Owls also nest in or around several prairie dog colonies in Cotton and Custer counties, but there are no confirmed records or sightings. Based on Tyler's (1968) data and our subjective assessment of changes since that survey, we estimated that there is a current summer population of 800–1000 Burrowing Owls in Oklahoma, with most owls occurring in the three panhandle counties (Cimarron, Texas, and Beaver; Fig. 1).

Tyler (1968) surveyed black-tailed prairie dog colonies in Oklahoma, recording a total of 788 Burrowing Owls, and derived a state population estimate of 900–1000 individuals. In his survey in 1970, Butts (1971) found a total of 543 Burrowing Owls, and estimated an overall density of nesting Burrowing Owls of approximately 0.12 owls/km^2 He also found that 66% of the nests occurred in black-tailed prairie dog colonies, although those colonies made up <20% of the total landscape surveyed. Burrowing Owl densities varied greatly between those owls occupying black-tailed prairie dog colonies (38.1 owls/km^2) and those at least 1.6 km from black-tailed prairie dog colonies (0.04 owls/km^2). All Burrowing Owl nests were found in vegetation that was <10 cm in height (Butts 1971).

According to the Oklahoma Breeding Bird Atlas (OBBA) conducted through the 2001 field season, Burrowing Owls were recorded in 32 of the 42 OBBA blocks (1.86 × 2.17 km) surveyed in the Oklahoma panhandle that also had at least one prairie dog colony (D. Reinking pers. comm.). This included 9 of 11 blocks for Beaver County, 11 of 16 for Texas County, and 12 of 15 for Cimarron County. In addition to the above, nesting records exist for Grant, Cleveland, Oklahoma, Canadian, Custer, Blaine, Woods, and Alfalfa counties. The latter records, however, ranged in date from 1909–65, and it is not clear how many of these represent annual nesting attempts by established populations opposed to accidental or occasional nesting attempts. Baumgartner and Baumgartner (1992) in-

Figure 1. Breeding range (shown in gray) of the Burrowing Owl in Oklahoma, as determined by Breeding Bird Survey data (1966–99), other breeding records, and personal observations. Gray areas denote regular breeding range.

dicated that the Burrowing Owl was not a regular breeding species in central Oklahoma prior to European settlement.

Breeding Bird Survey (BBS) data indicate that Burrowing Owls occur in many of the western counties in Oklahoma (Sauer et al. 2000). The BBS data indicate that relative abundance of Burrowing Owls is low (range 0.13–1.95) for all four physiographic regions of the state. Analysis of these data demonstrate that Burrowing Owl numbers in Oklahoma declined by 12.3% per yr during the 34-yr period from 1966–99. BBS data quality for Burrowing Owls, although less than optimal due to the relatively small number of BBS routes in the state, is nonetheless the most useful data available for determining population trends of this species in Oklahoma.

WINTERING RECORDS

The current wintering range of the Burrowing Owl is restricted to western Oklahoma (Fig. 2), based on Christmas Bird Count (CBC) data, other wintering records, and personal observations (1930–99). Most Burrowing Owls migrate south from Oklahoma in the fall (usually October) and some winter as far south as central Mexico (Butts 1976, G. Holroyd pers. comm.). Therefore, Burrowing Owls are considered either rare winter residents or are very secretive in the panhandle and the northern tier of counties in Oklahoma (Butts 1976). The winter can be relatively severe in northern Oklahoma, and Burrowing Owls facing these conditions generally migrate south for the winter. In the southwestern counties of Oklahoma, owls are considered occasional winter residents (Baumgartner and Baumgartner 1992). The survey by Butts (1976) allowed a comparison of summer and winter Burrowing Owl numbers. He surveyed an area of 4367 km^2 in the eastern panhandle and found 543 adult owls during the 1970 breeding season and 527 adult owls during the 1971 breeding season. However, he located only six owls in the same area during the 1970–71 winter (ca. 1% of the summer population).

Burrowing Owls have been recorded on CBCs at Kenton (Black Mesa), Cimarron County, Arnett (Ellis County), Oklahoma City, Oklahoma County, and Norman (Cleveland County). There have never been more than a few individuals reported from any count. In addition to winter records in the western counties, there are winter records of Burrowing Owls for a number of scattered counties in other areas of Oklahoma, including Oklahoma, Muskogee, Garvin, Tulsa, Pawnee, Payne, and Washington counties (Baumgartner and Baumgartner 1992, Sauer et al. 1996). The winter distribution of Burrowing Owls is broader than their breeding distribution in Oklahoma (Figs. 1, 2) and may be due, at least in part, to stopover of migrants

Figure 2. Non-breeding range of the Burrowing Owl in Oklahoma, as determined by Christmas Bird Count data (1930–99), other wintering records, and personal observations. Dark gray area denotes regular winter range, light gray areas denote extra-limital winter records.

from more northern parts of the range. A similar pattern of winter distribution in Texas and Mexico offers some evidence for this idea (G. Holroyd pers. comm.).

STATUS OF PRAIRIE DOGS IN OKLAHOMA

In Oklahoma, black-tailed prairie dog colonies once covered approximately 400 000 ha, but now exist only in scattered, disjunct populations (U.S. Fish and Wildlife Service 2000). Tyler (1968) reported that millions of hectares of prairie dog colonies were found historically in Oklahoma, but that by 1968, the total area of colonies had been reduced to 3856 ha. Historically, black-tailed prairie dogs were locally common and widespread in the western-most counties, including Cimarron, Texas, Beaver, Harper, and Ellis counties, but became less common eastward into the mixed-grass prairie. Most of the decline of black-tailed prairie dogs (and presumably Burrowing Owls) occurred between 1885–1925. In recent years, populations of black-tailed prairie dogs in the Oklahoma panhandle have been unstable due to sylvatic plague and active eradication programs (U.S. Fish and Wildlife Service 2000, S. Sheffield pers. observ.).

A survey of prairie dog colonies was conducted in Oklahoma for the Oklahoma Department of Wildlife Conservation (ODWC) in 1988–89 (J. Shackford, J. Tyler, and L. Choate unpubl. data). More recently, ODWC game wardens conducted a follow-up survey in the fall of 1998. Of the 399 prairie dog colonies recorded by J. Shackford and colleagues, 313 of these were revisited. At least 110 previous unrecorded prairie dog colonies were found incidentally while trying to verify the locations of the previous survey. These new colonies probably are a combination of newly colonized sites, colonies that were small 10 yr ago, colonies missed by the 1988–89 survey, and colonies for which the legal description was incorrectly recorded in 1989 so that the colony was recorded as absent in 1998 and a "new" colony was found nearby. The minimum number of colonies present in 1998 was 302, though the actual number was probably closer to 380. Population sizes in colonies were not estimated in the 1998 survey, so trends cannot be determined.

In the main part of the state, the total number of prairie dog colonies appears to have declined by about 7% (ODWC unpubl. data). In Cimarron County, the number of prairie dog colonies is estimated to have declined by 34%. This may have been due, at least in part, to the plague outbreak that was documented there in 1991–92. However, the number of prairie dog colonies in the two other panhandle counties (Texas and Beaver) seems to have increased by 19%. In central Oklahoma, black-tailed prairie dog colonies apparently were rare but some were very large.

ASSOCIATION BETWEEN BURROWING OWLS AND BLACK-TAILED PRAIRIE DOGS IN OKLAHOMA

Tyler (1968) found 280 black-tailed prairie dog colonies in his Oklahoma survey, and found Burrowing Owls inhabiting 40% of the prairie dog colonies checked. The largest number of owls in a single dog colony was 30 individuals. Butts and Lewis (1982) found that, within prairie dog colonies, Burrowing Owls aggregated their nests into clusters and often concentrated nests at edges of black-tailed prairie dog colonies. Prairie dog colonies appeared to be the only habitat with sufficient densities of burrows to provide both nesting and satellite burrows. There may be a certain minimum area of prairie dog colony(ies) required for Burrowing Owls to nest, but this threshold is not known. J. Shackford (unpubl. data) found owls in regions of the state where there were at least seven individual prairie dog colonies or at least 162 ha of prairie dog colonies in close proximity. Black-tailed prairie dog colonies in Oklahoma became unsuitable for Burrowing Owls 1–3 yr after abandonment by black-tailed prairie dogs (Butts and Lewis 1982). They suggested that Burrowing Owls nesting outside of prairie dog colonies in Oklahoma were utilizing marginal habitat and may represent individuals forced out of preferred prairie dog colony habitat (Butts and Lewis 1982).

Barko et al. (1999) found that Burrowing Owl abundance was significantly higher on sites with black-tailed prairie dog colonies than at uncolonized sites in Oklahoma during the spring and summer. They recorded Burrowing Owls on prairie dog-colonized sites of 3–302 ha ($N = 5$). Desmond et al. (2000) found strong correlations between Burrowing Owl and black-tailed prairie dog declines and provided evidence of a time lag in Burrowing Owl population response to changes in active burrow densities of prairie dogs in Nebraska between 1990–96.

In Oklahoma, there has been great variation in Burrowing Owl occupation of large versus small prairie dog colonies. Butts (1971) found a large range in the density of nesting Burrowing Owls in prairie dog colonies. He found that large colonies (>40.5 ha) in Beaver County did not have Burrowing Owls, but 19 of 21 colonies that were <4 ha in size supported Burrowing Owls. Tyler (1968) found a 1.2 ha prairie dog colony in Jackson County with 30 Burrowing Owls. These data indicate that Burrowing Owls will utilize small colonies. Therefore, assumption that larger prairie dog colonies are more likely to contain Burrowing Owls does not appear to be valid in all cases. There is some evidence that Burrowing Owls are easier to detect in smaller prairie dog colonies or colonies with fewer prairie dogs (M. Desmond and M. Restani pers. comm.).

Burrowing Owls have coevolved with prairie dogs and other colonial sciurids in the prairie grassland ecosystem in North America. They have been found to be tightly associated with prairie dog colonies in Oklahoma (Tyler 1968), Nebraska (Desmond and Savidge 1996), South Dakota (Sharps and Uresk 1990), and Wyoming (Campbell and Clark 1981). In addition, Clark et al. (1982) found a strong correlation between increased vertebrate abundance and increased colony size ($r = 0.81$). Prairie dog colonies provide heterogeneous plant cover, high densities of prey species, high seed production, low vegetation height, and good visibility of prey and predators (Clark et al. 1982). One main benefit of this close association for both owls and prairie dogs appears to be increased protection from predation (Desmond et al. 2000).

Clearly, black-tailed prairie dog colonies are critically important to Burrowing Owls in Oklahoma, as well as in much of the rest of midwestern North America (Butts and Lewis 1982). However, Burrowing Owl populations have suffered in Oklahoma because of their close ecological association with black-tailed prairie dogs. Although both black-tailed prairie dogs and Burrowing Owls were considered locally common in the state prior to European settlement, both species were virtually wiped out by a statewide poisoning campaign in 1922 (Baumgartner and Baumgartner 1992).

OUTLOOK FOR BURROWING OWLS IN OKLAHOMA

Burrowing Owls should be able to persist in the panhandle and in other western counties of Oklahoma, where there is relatively little development and where habitat has not been greatly altered. However, one problem area is Cimarron County, where the major loss of prairie dog colonies is cause for concern. Prairie dog colonies in Oklahoma should be monitored closely at least every 2–4 yr, including monitoring of both Burrowing Owls and prairie dogs. If the focus of conservation efforts is on the prairie dog/grassland ecosystem, then there is a good chance that the Burrowing Owl also will be protected in

Oklahoma. Major cooperative efforts are needed to ensure that viable populations of both species continue to exist throughout their ranges in Oklahoma so that they do not continue to decline toward endangered status.

Most of the nearly 400 prairie dog colonies in Oklahoma occur on private lands. This is of concern because there is a greater likelihood of habitat alteration and less ability to enact conservation actions on private lands. State-sponsored initiatives to conserve prairie dog colonies on private lands would address this situation.

In 2000, the ODWC began aerial transect surveys of prairie dog colonies in Cimarron, Texas, Beaver, Harper, and Ellis counties, and in 2002 will attempt to ground-truth colonies that were identified during the aerial survey. Burrowing Owls will be monitored during this effort.

Finally, Burrowing Owl mortality factors, such as pesticide poisoning, can be significant in some areas of Oklahoma, particularly in agricultural and rangeland areas where pesticides are applied, and both direct and secondary poisoning can occur (Sheffield 1997b). Conservation and management measures, education, and changes in both public attitudes and policies are necessary for the continued existence of viable populations of Burrowing Owls and grassland sciurids in Oklahoma and in North America in general (Holroyd et al. 2001).

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Current Status, Distribution, and Conservation of the Burrowing Owl (*Speotyto cunicularia*) in Midwestern and Western North America

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Abstract.—The Burrowing Owl (*Speotyto cunicularia*) inhabits open prairie grassland habitat in the midwestern and western US and Canada. For several years now, numbers of this species in North America have been declining at an alarming rate. Currently, Burrowing Owls are listed as endangered in Canada and threatened in Mexico. In the United States, the Burrowing Owl was listed as a Candidate 2 species by the USFWS until 1996, but currently is not formally a listed species. However, Burrowing Owls are listed as either endangered, threatened, or a species of special concern in virtually every state/province in which it occurs in midwestern and western North America. Habitat destruction/alteration, with a subsequent increase in mammalian predation has played a major role in the decline of populations. Exposure to large amounts of pesticides and other human-related disturbances have also played a role in their decline. Burrowing Owls rely on colonial sciurid towns as an integral part of their preferred habitat, but black-tailed prairie dog (*Cynomys ludovicianus*) populations have been reduced over 98 percent since 1900. These important components of the North American prairie ecosystem are significant and highly coevolved systems where resident species such as Burrowing Owls rely to a significant extent on the other species in the system. I suggest that Burrowing Owls serve as a model sentinel species of the health of the midwestern and western grassland ecosystems and that proactive conservation measures and changes in policy are necessary for the continued existence of populations of Burrowing Owls.

The Burrowing Owl (*Speotyto cunicularia*) is an inhabitant of the prairie grassland ecosystem of midwestern and western North America. This particular ecosystem is considered by many to be at greatest risk of human perturbation. This species has experienced both local and regional population declines and as a result it is listed in virtually all states and provinces in which it occurs. Specifically, the subspecies *S. c. hypugea*, the western Burrowing Owl, is the taxon of Burrowing Owl listed in midwestern and western North America.

The objectives of this paper are to present the current population status, distribution, and conservation status of the Burrowing Owl in midwestern and western North America. In addition, a further objective is to review current conservation measures taken for Burrowing Owls and to suggest future research and conservation needs for this species.

Populational trends presented here are derived from 30 years of Breeding Bird Count (BBS) data (Sauer *et al.* 1996a) and Christmas Bird Count (CBC) data (Sauer *et al.* 1996b). BBS data are from 1966-1994 and CBC data are from 1959-1988. Avian population counts such as the BBS and CBC generally are now acknowledged to be useful indicators of patterns of avian biogeography and population trends. The BBS and CBC data allow analysis of distribution and abundance of avian species during the breeding season (late spring) and during early winter, respectively. In addition, these long-term databases probably are more reliable for the highly diurnal and relatively

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easy to count Burrowing Owl than for most other raptor species. Although these databases are invaluable as tools to estimate population numbers and trends, there are certain pitfalls associated with their use (see Butcher 1990 and Droege 1990 for details on uses of BBS and CBC data, respectively).

POPULATION STATUS/DISTRIBUTION

The Burrowing Owl occurs from the southern portions of western Canada through the western United States and Mexico through Central America and into South America south to southern Argentina (Haug *et al.* 1993). Disjunct populations occur in Florida and adjacent Caribbean Islands. In Canada, Burrowing Owls occur in Manitoba, Saskatchewan, Alberta, and British Columbia (fig. 1). In the United States, Burrowing Owls occur from western Minnesota and Iowa to south to Texas and west from Washington through California (fig. 1).

Maps of average count and percent change/year for Burrowing Owls from BBS data are shown in figure 2. The BBS data indicate that there has been an overall decrease of 0.6 percent/year in Burrowing Owl numbers in North America and 0.5 percent/year in the US (table 1). For both North America and the US, however, the trends from 1966-1979 were a 1.6 percent and 1.8 percent increase in numbers and the trend from 1980-1994 was a 2.1 percent and 2.0 percent increase in numbers, respectively. In the Central Region of North America, there was a 2.8 percent/year decrease overall, a 2.3 percent/year increase from 1966-1979 and 0.5 percent/year decrease from 1980-1994 (table 1). In this region, significant recent (from 1966-1979 to 1980-1994) declines were seen in North Dakota, New Mexico, Nebraska, and Texas (table 1). Significant declines over shorter periods of time have been seen in west-central Kansas, adjacent portions of Oklahoma and Nebraska, western portions of the Texas panhandle, the Trans-Pecos region of Texas, and southern New Mexico (Haug *et al.* 1993). Significant increases were seen in Colorado and South Dakota. In the Western Region of North America, there was a 4.6 percent/year increase overall, a 1.3 percent

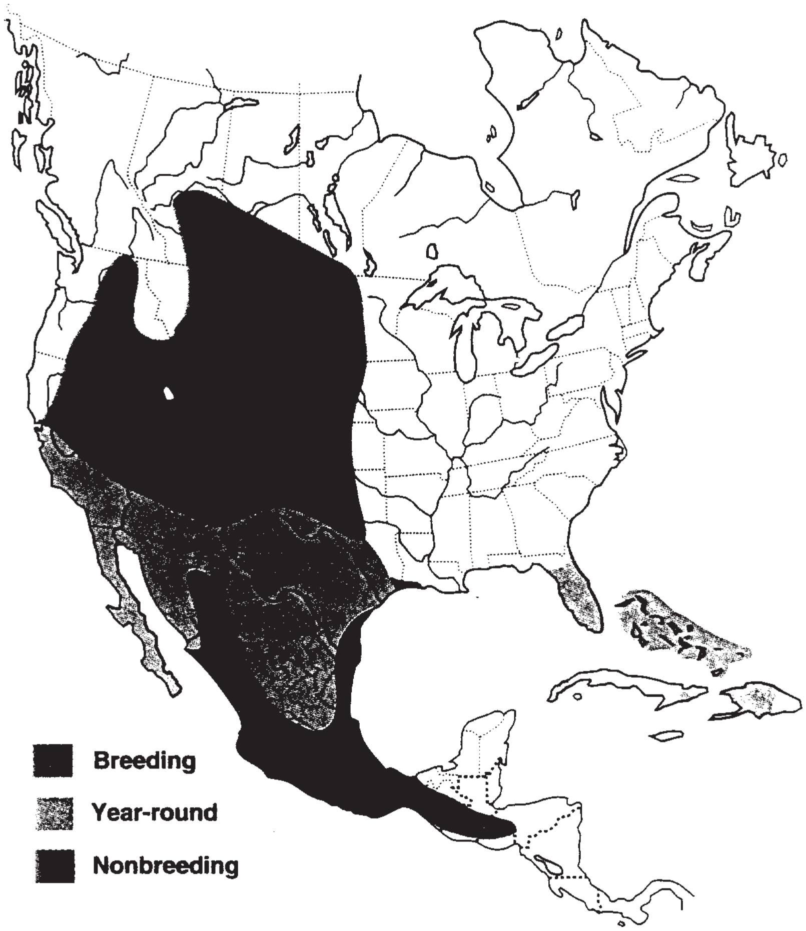

Figure 1.—*Range map of the Burrowing Owl (*Speotyto cunicularia*) in North America (map from Haug* et al. *1993).*

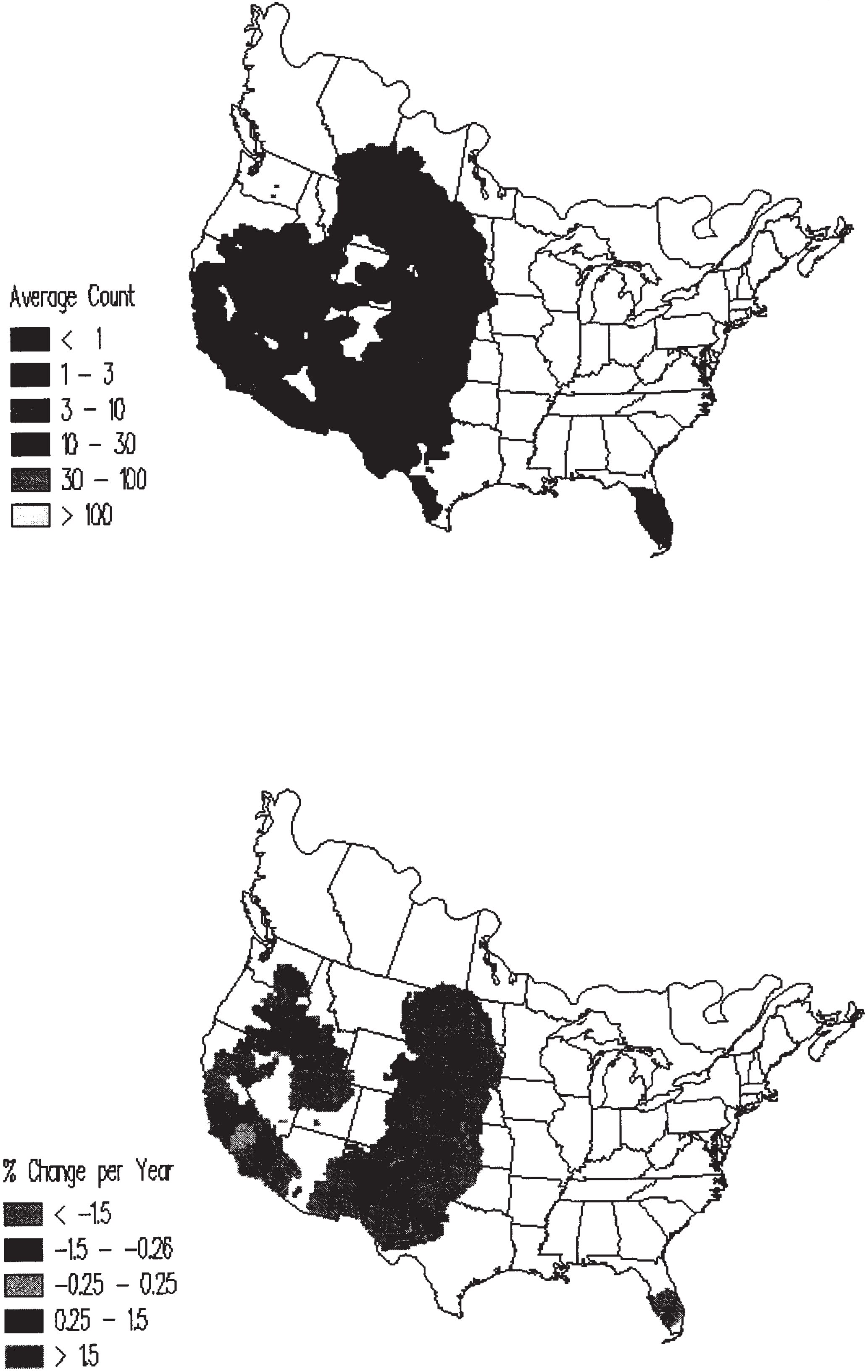

Figure 2.—*Maps of average count and percent change per year for Burrowing Owls (*Speotyto cunicularia*) from Breeding Bird Survey data (1966-1994; from Sauer* et al. *1996a).*

Table 1.—*Population trend (percent change/year) based on breeding bird survey data for the Burrowing Owl (*Speotyto cunicularia*) in North America (1966-1994) (Sauer* et al. *1996a).*

Area	**Population trend (N)**		
	(1966-1994)	(1966-1979)	(1980-1994)
North America	-0.6 (245)	+1.6 (121)	+2.1 (175)
United States	-0.5 (238)	+1.8 (116)	+2.0 (173)
Central Region	-2.8 (128)	+2.3 (66)	-0.5 (96)
Western Region	+4.6 (109)*	+1.3 (51)	+4.2 (74)*
California	+5.3 (32)*	-2.3 (20)	+6.3 (22)*
Colorado	-3.8 (25)	-7.1 (9)	+4.7 (23)
Nebraska	+6.0 (15)	+25.5 (8)*	-2.0 (10)
New Mexico	-0.6 (22)	-4.1 (6)*	-1.6 (18)
North Dakota	+4.2 (16)	+11.2 (8)	-9.9 (13)*
South Dakota	-5.8 (19)	+5.6 (15)	+10.1 (9)
Texas	-1.4 (22)	+18.9 (14)	-8.0 (17)

* = significant population trend

increase from 1966-1979 and a 4.2 percent increase from 1980-1994 (table 1). However, data from this region is less complete than that from the Central Region and is made up mainly from California. In this region, significant increases were seen in California. However, it is known that Burrowing Owls were extirpated from British Columbia by 1980 (Haug *et al.* 1993). In California, a survey by DeSante and Ruhlen (1995) has shown that there has been approximately a 50 percent decline in numbers in the State over the last 10 years. However, significant increases over shorter periods of time have been seen in the lower Sonoran Desert, lower Colorado River Valley in western Arizona and adjacent California, and the interior valley of California (Haug *et al.* 1993).

The CBC data are more limited for Burrowing Owls since northern populations move south for the winter. Burrowing Owls are known to winter primarily in California, Arizona, New Mexico, Texas, Louisiana, and Florida (fig. 3). Overall, available data indicate a significant decrease of about 0.6 percent/year (table 2). California showed a significant decreasing trend (1.2 percent/year), while Arizona and Texas showed slight increasing trends (table 2). However, overall CBC data for Burrowing Owls suggest a decline in numbers since the mid-1970's. A similar analysis of Burrowing Owl wintering numbers using CBC data found comparable overall trends in numbers in the United States, although analysis including Florida resulted in a slightly positive overall trend and analysis of the limited CBC data from Mexico indicated that Mexican populations were decreasing slightly as well (James and Ethier 1989).

REASONS FOR DECLINE

It is clear that the number one reason for the overall decline of Burrowing Owls is the destruction and alteration of their habitat. This has come about largely due to development of grasslands into agricultural croplands and through destruction of prairie dog towns. As long ago as the 1930's, it was recognized that intensive cultivation of grasslands and native prairies was the major factor in declining Burrowing Owl populations (Bent 1938). Burrowing Owls strongly prefer open grassland habitat with colonial sciurid populations, and since 1900, black-tailed prairie dog (*Cynomys ludovicianus*) populations have been reduced more than 98 percent. In addition to direct destruction of prairie dog towns, the shooting of prairie dogs and sylvatic plague have decimated prairie dog populations in many areas. The remaining prairie dog towns are generally highly fragmented and suboptimal nesting and foraging habitat. This has led to a scarcity of suitable nesting burrows for Burrowing Owls in many locations, and may reduce chances that unpaired owls will be able to find mates. Habitat destruction and alteration has also led to indirect negative impacts on Burrowing Owls, including an increased frequency of mammalian predators (White 1994). Such mammalian species as coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), gray foxes (*Urocyon*

Figure 3.—*Map of winter distribution of Burrowing Owls (*Speotyto cunicularia*) from Christmas Bird Count data (1959-1988; from Sauer* et al. *1996b).*

Table 2.—*Population trend and abundance based on Christmas bird count data for the Burrowing Owl (*Speotyto cunicularia*) in North America (1959-1988; from Sauer* et al. *1996b).*

Area	Population trend (N)	Relative abundance
North America	-0.6 (213)*	0.12
Arizona	+0.2 (16)	0.10
California	-1.2 (97)*	0.29
Texas	+1.2 (52)	0.23

* = significant population trend

cinereoargenteus), and badgers (*Taxidea taxus*) have increased in numbers in many grassland habitats due to the widespread habitat alteration that has tended to modify habitats into early successional stages.

In addition to habitat destruction and alteration, direct mortality due to vehicle collisions and shootings have been important in population declines in some areas (Haug *et al.* 1993). In western Oklahoma, shooting was responsible for 66 percent of the known mortality (Butts 1973). Exposure to environmental contaminants such as anti-cholinesterase (anti-ChE) insecticides has proven to negatively impact Burrowing Owl populations. For example, the carbamate insecticide carbofuran was found to result in severe reproductive effects in exposed Canadian Burrowing Owls (Fox *et al.* 1989). Anti-coagulant rodenticides (e.g., brodifacoum and other second generation (or super warfarin) compounds) and other types of rodenticides (e.g., strychnine) have been shown to cause mortality in many different owl species, even through the ingestion of as few as one poisoned prey item (Sheffield 1997). Burrowing Owls located in proximity to strychnine-coated grain used to control Richardson's ground squirrels (*Spermophilus richardsonii*) were found to have significantly decreased adult body mass and slightly decreased breeding success as compared to control owls (James *et al.* 1990). Burrowing Owls are known to scavenge dead rodents and other prey items, making them highly susceptible to secondary poisoning by insecticides and rodenticides.

At least two life history traits of the Burrowing Owl act to restrict rapid population recovery following mortalities. Due to their small body size and ground nesting habits, Burrowing

Owls are vulnerable to a large number of mammalian, avian, and reptilian predators. Also, they only produce one brood per year, and will renest only if the first nest is destroyed early in breeding (Haug *et al.* 1993).

CONSERVATION STATUS

Since 1972, the Burrowing Owl has been included on the Blue List, a list intended to provide an early warning of North American bird species undergoing population or range reductions. During the past decade, the Burrowing Owl has been listed as declining (Blue List; Tate 1986), vulnerable (Jeopardy List; USDI 1991), sensitive (Sensitive List; USDI 1992), federal threatened (Canada, COSEWIC, 1979, 1991), federal candidate 2 species (USFWS), and declining (White 1994). The federal candidate 2 species category was officially dropped by the USFWS in late 1996 (published in the 5 December 1996 Federal Register). Currently, the Burrowing Owl has no formal federal listing in the US, but is included on an informal internal list of former C2 candidate species known as "Species of Concern." Burrowing Owls are listed as federally endangered in Canada (COSEWIC 1995), and are listed as endangered in the provinces of Manitoba, Saskatchewan, Alberta, and British Columbia in Canada (table 3). Burrowing Owls are listed as a "Species of Special Concern" in almost all of the midwestern and western states of the United States (table 3). In Mexico, Burrowing Owls were listed as a federally threatened (amenazada) species in 1994 (Secretaria de Desarollo Social de Mexico, 1994). In addition, Burrowing Owls are a CITES Appendix 2 species, which makes it illegal to transport or trade this species (or body parts) across international borders without an appropriate convention export permit.

Table 3.—*Conservation status of the Burrowing Owl (*Speotyto cunicularia*) in North America by country and state/province.*

State/Province	Listing
CANADA	ENDANGERED
Alberta	Red List (Endangered)
British Columbia	Red List (Endangered)
Manitoba	Endangered
Saskatchewan	Red List (Endangered)
UNITED STATES	NO LISTING[1]
Arizona	No listing
California	Species of Special Concern
Colorado	Undetermined
Idaho	Species of Special Concern
Iowa	Endangered
Kansas	Species of Special Concern
Minnesota	Endangered
Montana	Species of Special Concern
Nebraska	Species of Special Concern
New Mexico	No listing[2]
North Dakota	Watch (Species of Special Concern)
Oklahoma	Species of Special Concern
Oregon	Species of Special Concern
South Dakota	Species of Special Concern
Texas	No listing
Utah	Species of Special Concern
Washington	Species of Special Concern
Wyoming	Candidate 2 Species
MEXICO	THREATENED

[1] Included on informal federal list of "Species of Concern"
[2] Included on informal state list of "Species of Special Concern"

CONSERVATION MEASURES

Several innovative approaches have been taken in order to conserve Burrowing Owl populations in the United States and Canada. The use of artificial burrows has allowed the establishment of small Burrowing Owl colonies and allows close study of nest success. Artificial perches have also been used to provide increased hunting and predator observation sites. Pesticide label restrictions now exist for carbofuran use in and around Burrowing Owl nesting areas in Canada. More drastic conservation efforts such as reintroduction programs have been attempted with mixed results in British Columbia, Manitoba, and Minnesota. In Canada, a Burrowing Owl recovery plan and a Canadian Burrowing Owl Recovery Team are in place. In the provinces of Manitoba, Saskatchewan, and Alberta, programs to protect private lands from cultivation and reseeding practices through lease agreements (both voluntary and monetary) have been initiated. Another important conservation effort for the Burrowing Owl is mandatory mitigation of developmental impacts in and around its colonies. Relocations of Burrowing Owls have been attempted in California and Saskatchewan. Finally, public education efforts have been underway in many areas throughout the range of the Burrowing Owl. For example, Operation Burrowing Owl in

Saskatchewan has over 500 members and has acted to protect over 40,000 acres of Burrowing Owl habitat (Haug *et al.* 1993).

CONSERVATION RECOMMENDATIONS

The Burrowing Owl will require human assistance if it is to continue to have healthy populations in North America. Among the conservation needs of this species are the following:

1. A change of philosophy is required towards prairie dog and ground squirrel towns and grasslands in general—they should not be looked at as easily developed, weedy or problem areas but should be actively conserved as an integral part of the prairie grassland ecosystem.

2. Tighter controls should exist over grassland development and disturbances, and mitigation of impacts (direct or indirect) should be mandatory. Protection of prairie dog, ground squirrel, and selected other burrowing mammal populations and their towns as habitat should be an integral part of grassland conservation actions.

3. Continued efforts to control prairie dog and ground squirrel populations in midwestern and western North America are detrimental to Burrowing Owl populations. Pesticide use in these systems should never occur in the vicinity of active Burrowing Owl nests and all pesticide use should be closely monitored for negative impacts on Burrowing Owls.

4. The Burrowing Owl should be included as a formal candidate species in the United States. Further, adding candidate species to the list of species receiving recovery plans and active protection (including protection of habitat) should be part of the Endangered Species Act reauthorization bill in the U.S.

5. The passage of a strong, proactive Endangered Species Act reauthorization bill in the U.S. and a Canadian Endangered Species Act are crucial to Burrowing Owl conservation. In addition, affording legal protection to Burrowing Owls in Mexico is of great importance, and efforts should be made to coordinate Burrowing Owl conservation among North American countries.

6. Further research and population monitoring is necessary, including the following areas:
   a. Continued monitoring of population numbers and trends is critically important. Volunteer data is highly valuable to this effort.
   b. The efficacies of conservation measures currently in use require study to determine what works and what does not work. Currently, there is little quantitative information available on the success of various management strategies.
   c. Further development of effective survey techniques.
   d. Further analysis of migration and fate of migratory individuals is badly needed. In particular, it is not known with any certainty where Burrowing Owls winter in Mexico, Central America, or South America. We need to ascertain whether or not there are environmental problems existing in areas occupied by wintering Burrowing Owls.
   e. Continued monitoring and assessment of the hazard of secondary poisoning from pesticides (insecticides and rodenticides) is necessary.
   f. The impact of increased mammalian predators on nesting success of Burrowing Owls needs to be determined.

CONCLUSIONS

Although listed throughout most of their range in North America, Burrowing Owls continue to undergo mild to relatively severe local and regional population declines. The BBS data indicate an overall decreasing trend in North American Burrowing Owls, whereas the CBC data indicate a slight overall increasing trend in North America, although a significant decrease was seen in California, by far the largest wintering population of Burrowing Owls. Virtually all of the reasons for declines in Burrowing Owl populations still occur throughout most of their range. Habitat destruction and alteration probably account for much of the population decline occurring. Prairie dogs and ground squirrels continue to be actively exterminated in many areas of North America, and prairie grasslands continue to be converted for agriculture and other uses. Habitat alteration may indirectly affect Burrowing Owls through the increase in mammalian nest predators. Vehicle collisions, shooting, and exposure to environmental contaminants may be significant sources of Burrowing Owl mortality in some areas. Many different conservation measures have been attempted in recent years in order to conserve Burrowing Owl populations in North America. Burrowing Owls serve as ideal sentinels of the health of the midwestern and western grassland ecosystem. Proactive conservation measures and changes in land use philosophy and policy are necessary for the continued existence of healthy populations of this species in the grasslands of North America.

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CHAPTER 15

Role of Federal Lands in the Conservation of Prairie Dogs

John G. Sidle, Gregory L. Schenbeck, Eric A. Lawton, and Daniel S. Licht

As populations of black-tailed prairie dogs (hereafter, simply "prairie dogs") continue to decline (Chapter 16), attention is shifting to federal lands and how they might contribute to conservation. As on private lands, prairie dogs on federal lands sometimes have been targets of recreational shooting, poisoning, and loss of habitat (Chapters 8, 10, and 16). Despite such persecution, some of today's largest colonies and complexes of prairie dogs are on federal lands, such as the Charles M. Russell National Wildlife Refuge in Montana, the Thunder Basin National Grassland in Wyoming, and the Buffalo Gap National Grassland in South Dakota.

Ranchers frequently purchase permits so that their livestock can graze on federal lands, especially on lands administered by the United States Bureau of Land Management (BLM) and the United States Forest Service (USFS). Consequently, in addition to favoring the elimination of prairie dogs on their private lands (Chapters 5, 7, and 16), ranchers commonly favor the reduction of prairie dog populations on federal lands as well. Grazing by livestock on federal lands thus complicates the conservation of prairie dogs.

In this chapter we document the areas inhabited by prairie dogs on federal lands under the authority of BLM, National Park Service (NPS), United States Fish and Wildlife Service (USFWS), and USFS. We then explain the policies of these federal agencies before and after the prairie dog became a candidate species in 2000 for the Federal List of Endangered and Threatened Wildlife and

Plants (FLETWP) (USFWS 2000a, Chapter 12). Finally, we discuss the role of federal lands in the conservation of prairie dogs, and how the removal of the prairie dog from the candidate list in 2004 might affect this role.

Federal Lands That Contain Prairie Dogs

As outlined below, prairie dogs currently inhabit 55,100 hectares (136,200 acres) of federal lands managed by four agencies (Figure 15.1) (Table 15.1).

Bureau of Land Management (BLM)

BLM lands include about four million hectares (ten million acres) within the former geographic range of the prairie dog. When managing these lands, BLM must consider numerous factors, including development of sources for minerals and energy; conservation of habitat for fish, burros, wild horses, and other wildlife; grazing by domestic livestock; and numerous federal statutes such as the Federal Land Policy and Management Act (1976). In addition to thousands of other hectares that are probably suitable for colonization, BLM lands include 19,800 hectares (49,000 acres) currently inhabited by prairie dogs (Table 15.2).

National Park Service (NPS)

Most NPS units in the Great Plains were established for reasons other than conservation of wildlife. Fort Larned National Historic Site, for example, was established for cultural resources, Devils Tower National Monument for geologic features, and Badlands National Park for paleontologic treasures. Nevertheless, prairie dogs currently inhabit a cumulative area of about 2,800 hectares (6,900 acres) in three national parks (Badlands, Theodore Roosevelt, and Wind Cave), and small areas (less than 40 hectares [99 acres]) in four other NPS units (Table 15.3). Much of the habitat within NPS units is unsuitable for colonization, but prairie dogs nonetheless inhabit 2% of the total area of the seven units with colonies. Except for the small colony at Bent's Old Fort National Historic Site in Colorado, all colonies within NPS units are in areas with no history of plague (Chapter 11).

United States Fish and Wildlife Service (USFWS)

USFWS manages the National Wildlife Refuge System, for which the conservation of biological diversity is a priority. Prairie dogs currently inhabit about

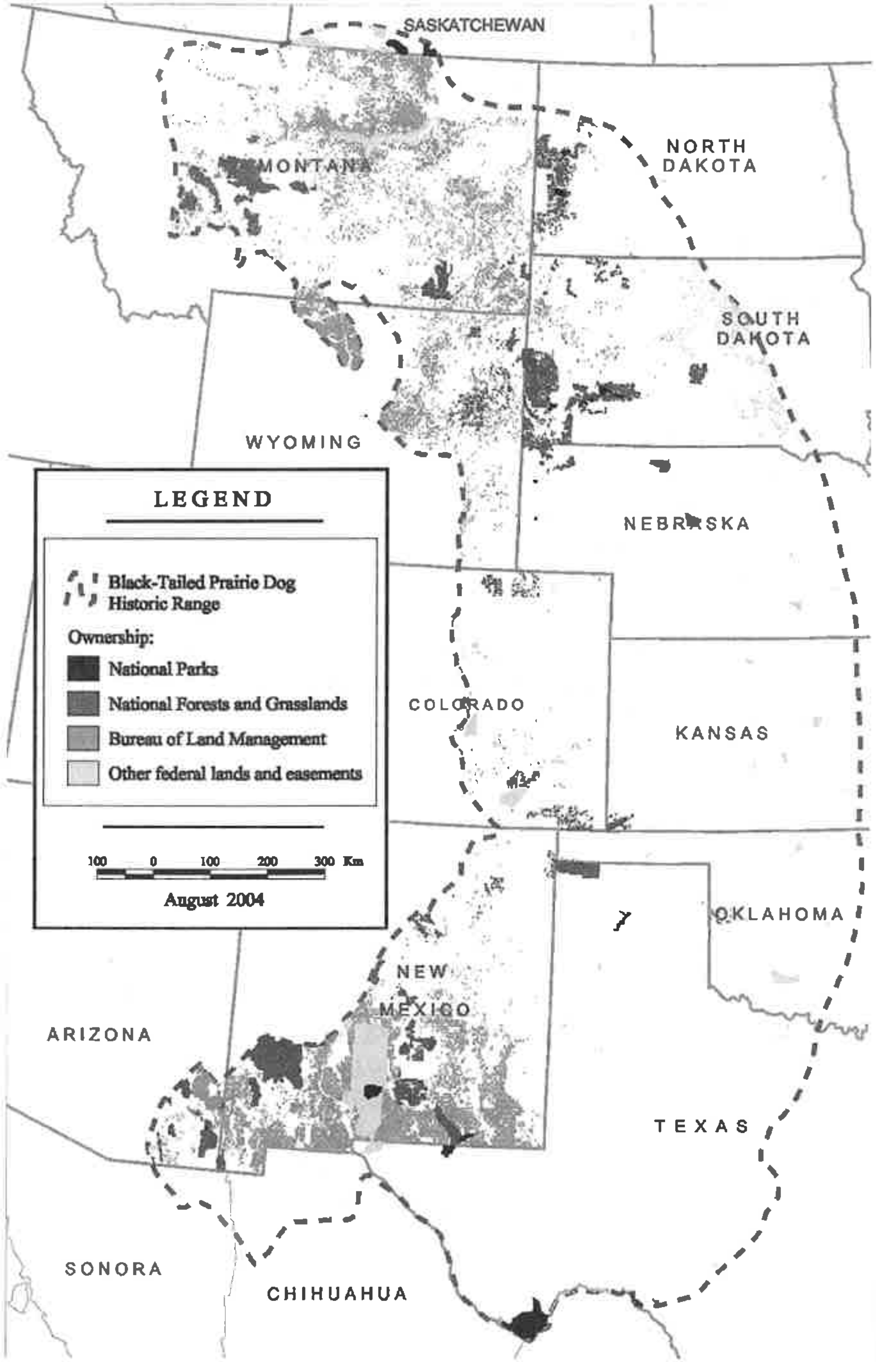

Figure 15.1. Location of principal federal lands administered by BLM, NPS, USFWS, and USFS in the geographic range of the prairie dog.

Table 15.1. Area currently inhabited by prairie dogs on federal lands. Estimates for BLM, NPS, and USFWS are from 2002; estimates for USFS are from 2004.

	Area currently inhabited by prairie dogs on federal lands (hectares)
Bureau of Land Management (BLM)	19,800
National Park Service (NPS)	2,800
United States Fish and Wildlife Service (USFWS)	3,700
United States Forest Service (USFS)	28,800
TOTAL	55,100

Table 15.2. Area inhabited by prairie dogs on BLM lands in 2002.

BLM unit	*Area inhabited in 2002 (hectares)*
Royal Gorge, Colorado	No data
Northeast, Colorado	No data
Billings, Montana	2,260
Big Dry, Montana	2,185
Powder River, Montana	1,457
Lewistown, Montana	318
Lewistown West Hi-Line, Montana	48
West Hi-Line, Montana	1,609
Headwaters, Montana	0.4
Malta, Montana	3,253
Glasgow, Montana	212
White Sands, New Mexico	87
Roswell, New Mexico	236
Carlsbad, New Mexico	4
North Dakota	81
South Dakota	85
Cody, Wyoming	56
Casper, Wyoming	2,023
Buffalo, Wyoming	4,505
Newcastle, Wyoming	1,356
TOTAL	19,775

Table 15.3. Area inhabited by prairie dogs in NPS units in 2004.

NPS unit	*Area inhabited in 2004 (hectares)*	*Nearest colony*	*Issues of management for prairie dogs*	*Future plans for prairie dogs*
Badlands National Park, South Dakota	2,544	Large complexes adjacent to park	Occasional non-lethal control for "good neighbor" purposes, or for protection of park facilities. Park has black-footed ferrets.	Writing new plan for conservation.
Bent's Old Ft. National Historic Site, Colorado	20	About 8 kilometers	None reported.	Writing new plan for conservation.
Chiricahua National Monument, Arizona	0	Unknown	None reported.	None.
Coronado National Memorial, Arizona	0	About 6 kilometers (in Mexico)	None reported.	Some initial efforts at reintroduction of prairie dogs.
Devils Tower National Monument, Wyoming	16	No colonies nearby	Occasional encroachment into campground and visitor areas. Neighbors want control.	Writing new plan for conservation.
Fort Bowie National Historic Site, Arizona	0	120–160 kilometers	None reported.	Reintroduction of prairie dogs under consideration.
Fort Larned National Historic Site, Kansas	13	About 16 kilometers	Burrowing occurs in historic trail ruts.	Maintain current area inhabited by prairie dogs.
Guadalupe Mountains National Park, Texas	0	Unknown	None reported.	Has unsuccessfully attempted to restore prairie dogs. Might try again.
Scotts Bluff National Monument, Nebraska	37	No colonies nearby	Colony has increased from about 2 hectares to 14 hectares in last few years.	None.
Theodore Roosevelt National Park, North Dakota	343	Colonies on national grasslands adjacent to park	Might initiate control for "good neighbor" policy. Moved a picnic area in response to encroachment.	Writing new plan for conservation.
Wind Cave National Park, South Dakota	809	Colonies on state and private lands adjacent to park	Might initiate control near campground and for "good neighbor" purposes. Home for current research on genetics and habitat requirements for prairie dogs.	Writing new plan for conservation. Possible reintroduction of black-footed ferrets.

Table 15.4. Area inhabited by prairie dogs on national wildlife refuge units in 2000, 2001, or 2002.

National Wildlife Refuge System unit	*Area inhabited in 2000, 2001 or 2002 (hectares)*
Big Sag Waterfowl Production Area, Montana	2
Bitter Lake National Wildlife Refuge, New Mexico	2
Buffalo Lake National Wildlife Refuge, Texas	67
Charles M. Russell National Wildlife Refuge, Montana	1,254
Fort Niobrara National Wildlife Refuge, Nebraska	40
Hailstone National Wildlife Refuge, Montana	51
Halfbreed National Wildlife Refuge, Montana	23
Hewitt Lake National Wildlife Refuge, Montana	6
Kingsbury Lake Waterfowl Production Area, Montana	30
Kirwin National Wildlife Refuge, Kansas	24
LaCreek National Wildlife Refuge, South Dakota	121
Lake Mason National Wildlife Refuge, Montana	193
Maxwell National Wildlife Refuge, New Mexico	53
Muleshoe National Wildlife Refuge, Texas	16
Quivira National Wildlife Refuge, Kansas	2
Rainwater Basin Wetland Management District, Nebraska	16
Rocky Mountain Arsenal National Wildlife Refuge, Colorado	127
Sullys Hill National Game Preserve, North Dakota	2
UL Bend National Wildlife Refuge, Montana	1,347
Wichita Mountains National Wildlife Refuge, Oklahoma	38
Willow Creek National Wildlife Refuge, Montana	190
Yellow Water National Wildlife Refuge, Montana	88
TOTAL	3,692

2,600 hectares (6,400 acres) within Montana's UL Bend and Charles M. Russell National Wildlife Refuges, and about 1,100 hectares (2,700 acres) scattered among 20 other national wildlife refuges (Table 15.4). Several refuges contain additional habitat that is probably suitable for colonization by prairie dogs.

United States Forest Service (USFS)

The federal government purchased 65-hectare (160-acre) plots of land from destitute farmers and ranchers in the 1930s and 1940s. These plots originally were given to citizens in the late 1800s via the Homestead Act. The plots are not always contiguous, but rather are intermingled with private lands (Figure 15.2). In 1960, these new federal lands collectively assumed the name of "national grasslands," under the management of USFS. A primary objective within

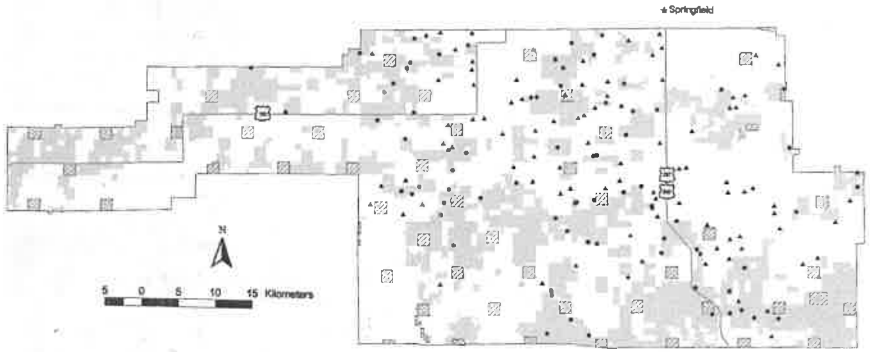

Figure 15.2. The distribution of prairie dog colonies within and near Comanche National Grassland (CNG) in Colorado. As illustrated here, national grasslands are often fragmented and intermingled with private lands. Circles indicate colonies on federal lands, and triangles indicate colonies on state and private lands; white indicates private lands, gray indicates national grasslands, and hatched indicates state lands. Large prairie dog complexes that include both CNG lands and private lands can promote the conservation of the prairie dog and its grassland ecosystem.

Over 75% of the habitat within national grasslands probably is suitable for colonization, but prairie dogs currently inhabit less than 2% (USFS 2001). Specifically, prairie dogs currently occupy about 28,800 hectares (71,200 acres) within national grasslands (Table 15.5).

Policies of Federal Agencies Before the Prairie Dog Became a Candidate Species for FLETWP in 2000

Bureau of Land Management (BLM)

Before 2000, BLM encouraged recreational shooting to reduce prairie dog numbers. BLM also cooperated with Animal and Plant Health Inspection Service (APHIS) of the United States Department of Agriculture (USDA) to poison prairie dogs (Chapter 8).

In the late 1980s, BLM in Montana began to more actively conserve prairie dogs (Flath and Clark 1989). BLM identified an area called the 40 Complex near the Charles M. Russell National Wildlife Refuge, for example, as a sanctuary for prairie dogs and black-footed ferrets.

National Park Service (NPS)

NPS has a rich history of research with prairie dogs. A 15-year study of the behavioral ecology of prairie dogs occurred at Wind Cave National Park

Table 15.5. Area inhabited by prairie dogs on USFS lands in 1980, 2002, and 2004. References: Schenbeck1981; USFWS 2002; unpublished reports.

USFS unit	*Area inhabited in 1980 (hectares)*	*Area inhabited in 2002 (hectares)*	*Area inhabited in 2004 (hectares)*
Black Kettle National Grassland, Oklahoma	0	0	0
Buffalo Gap National Grassland, South Dakota	17,240	7,327	10,620
Cimarron National Grassland, Kansas	20	1,344	2,280
Comanche National Grassland, Colorado	730	2,497	4,906
Fort Pierre National Grassland, South Dakota	380	260	535
Grand River National Grassland, South Dakota	610	723	817
Little Missouri National Grassland, North Dakota	550	1,680	1,680
Oglala National Grassland, Nebraska	120	516	909
Pawnee National Grassland, Colorado	180	729	1,158
Kiowa/Rita Blanca National Grassland, Oklahoma and Texas	420	2,185	1,665
Thunder Basin National Grassland, Wyoming	2,550	1,750	3,864
Black Hills National Forest, South Dakota	No data	89	111
Custer National Forest, Montana	No data	218	218
Nebraska National Forest (Bessey), Nebraska	57	26	36
Samuel R. McKelvie National Forest, Nebraska	0	0	0
TOTAL	22,800	19,344	28,799

example (Hoogland 1995). Other notable studies of prairie dogs at Wind Cave have investigated social behavior and population dynamics (King 1955); effects on aboveground biomass and nutrient dynamics (Coppock et al. 1983a, 1983b; Krueger 1986; Detling 1998); nonlethal methods for reducing colony size (Garrett and Franklin 1983); spatial distribution and use of habitat (Wydeven and Dahlgren 1985); dispersal (Garrett and Franklin 1988); influence on the grassland ecosystem (Whicker and Detling 1993); ontogeny of behaviors (Loughry and Lazari 1994); foraging and vigilance (Kildaw 1995); and population genetics (Dobson et al. 1998). Further, several NPS units have in-field displays about the ecology and social behavior of prairie dogs (e.g., Badlands, Wind Cave, and Theodore Roosevelt National Parks, and Devils Tower National Monument). Prairie dog colonies are feature attractions at NPS units where they occur (Figure 15.3). At Devils Tower National Monument, for example, the prairie dog is second only to the tower itself at charming visitors.

Figure 15.3. Children watching prairie dog. Tourists frequently stop to observe the antics of prairie dogs at Badlands, Wind Cave, and Theodore Roosevelt national parks, and at Devils Tower National Monument. Photo by Daniel S. Licht.

Despite mandates and policies that promote natural processes, NPS sometimes reduces wildlife populations for political or other reasons (Sellars 1997). At Wind Cave National Park in the early 1980s, for example, both poisoning (Fisher 1982) and shooting (J. L. Hoogland, personal communication, 2004) of prairie dogs occurred. Park administrators argued that the killings were necessary to conserve the park's biological diversity, and that reduction of the area inhabited by prairie dogs from 728 hectares (1,800 acres) to 283 hectares (700 acres) still would provide sufficient habitat for black-footed ferrets. Poisoning of prairie dogs also occurred in other NPS units prior to 2000, commonly as a "good-neighbor" policy—that is, in response to complaints by neighboring landowners who worried that prairie dogs from the NPS unit would disperse to their private lands (Wilkinson 1994; Roemer and Forrest 1996).

United States Fish and Wildlife Service (USFWS)

Like NPS, USFWS sometimes has struggled with the conservation of prairie dogs. Within national wildlife refuges prior to 2000, for example, USFWS authorized occasional poisoning of prairie dogs. In the late 1990s, however, USFWS made two important changes. First, in 1994, USFWS agreed to prohibit poisoning and to allow reintroductions of black-footed ferrets at prairie dog colony-sites at the UL Bend National Wildlife Refuge in Montana. Second, in 1997, USFWS initiated translocations of prairie dogs into the Charles M. Russell National Wildlife Refuge in Montana.

United States Forest Service (USFS)

Prior to 1972, USFS commonly poisoned prairie dogs on national grasslands and encouraged recreational shooting. Use of nonselective poisons such as Compound-1080 became illegal on federal lands in 1972, however, and prairie dog populations consequently increased on national grasslands in the mid- and late 1970s. Ranchers with permits to allow their livestock to graze on national grasslands protested the expansion of prairie dog colonies, as did neighboring landowners. When a more selective rodenticide (zinc phosphide) became available, poisoning of prairie dogs resumed on the Buffalo Gap National Grassland in 1978 (USFS 1978), and soon on other national grasslands as well.

Policies of Federal Agencies After the Prairie Dog Became a Candidate Species in 2000

Bureau of Land Management (BLM)

In 2000, BLM directed all field offices to improve conservation of prairie dogs, and to ensure that actions authorized, funded, or carried out by BLM do not contribute to possible listing (i.e., addition to FLETWP). Further, BLM initiated several new policies to enhance conservation, including the following: mapping and tracking of all known colony-sites on BLM lands; participation in formulation of "A multi-state conservation plan [MSCP] for the black-tailed prairie dog, *Cynomys ludovicianus*, in the United States" (Luce 2003; Chapter 14); notification of the general public, including ranchers, that unauthorized poisoning of prairie dogs on BLM lands is a violation of BLM policy; consideration for the conservation of prairie dogs in the evaluations of BLM lands for activities such as grazing by livestock, finding and development of oil and gas reserves, granting rights-of-way, and organized recreational events; evaluation of the need to reduce or prohibit recreational shooting of prairie dogs on some BLM lands; and distribution of questionnaires, and sponsoring of workshops and meetings, regarding the importance of conserving prairie dogs.

National Park Service (NPS)

After USFWS's designation of the prairie dog as a candidate species in 2000, NPS improved conservation in several ways. NPS acknowledged in internal memoranda that the prairie dog is a keystone species worth saving, for example, and transferred authority regarding conservation of prairie dogs from its Integrated Pest Management Program to the Natural Resource Stewardship and Science Division.

Park superintendents are responsible for control of prairie dogs within NPS units. Current NPS policy permits control under three circumstances: when prairie dogs threaten human health (e.g., when infected with plague; see Chapter 11); when they jeopardize cultural resources or park objectives; or when their colonies abut private land. Control of prairie dogs since 2000 has involved occasional nonlethal measures, such as barriers that deter expansion of colonies into campgrounds and administrative areas. Control also has involved limited livetrapping either for translocations (Chapter 13) or to provide prey for captive black-footed ferrets. No poisoning has occurred within NPS units since 2000.

Several NPS units are considering actions to promote expansion of prairie dog colonies. Wind Cave National Park, for example, is assessing the feasibility of increasing the number and size of prairie dog colonies to accommodate black-footed ferrets.

United States Fish and Wildlife Service (USFWS)

In 2000, USFWS directed the National Wildlife Refuge System to improve the conservation of prairie dogs. Neither poisoning nor recreational shooting of prairie dogs is currently permitted. Wildlife managers at several refuges (e.g., Rocky Mountain Arsenal National Wildlife Refuge in Colorado and Charles M. Russell National Wildlife Refuge in Montana) have translocated prairie dogs from local private lands into refuges to initiate new colonies, or to reestablish former colonies that disappeared because of plague. Written guidelines for refuge managers regarding the conservation of prairie dogs are now complete (USFWS 2003).

United States Forest Service (USFS)

In 2001, new plans regarding conservation of prairie dogs emerged for national grasslands in Nebraska, North Dakota, South Dakota, and Wyoming (USFS 2001). The new plans deviated sharply from the old plans (USFS 1984). Specifically, the new plans identified habitat components required by prairie dogs, and, with only a few exceptions, prohibited poisoning. Consequently, the cumulative area inhabited by prairie dogs on national grasslands probably would have increased over the next ten years (Table 15.6). In 2005, however, USFS's policies changed prairie dogs on USFS lands probably will increase (USFS 2005). The predicted increase of cumulative area inhabited by prairie dogs over all national grasslands (Table 15.6) now seems unlikely.

Prairie dog colonies on federal lands in general, and on national grasslands in particular, are fragmented (Figure 15.2), and thus more prone to extinction (Chapter 2). If prairie dogs can survive on private lands adjacent to federal lands, then fragmentation will decrease and large complexes will result—so that extinction of colonies will be less common, and recolonization of deserted colony-sites will be more common (Chapter 16). Private landowners near federal lands thus can play a key role in the conservation of prairie dogs via voluntary cooperation or financial incentives (Chapter 14).

Role of Federal Lands in the Conservation of Prairie Dogs

Federal lands offer enormous potential for the conservation of prairie dogs (Wuerthner 1997; Chapter 16). Changes in policies after the prairie dog became a candidate species for FLETWP in 2000 indicated that BLM, NPS, USFWS, and USFS all would help to promote conservation. But USFWS concluded in 2004 that the prairie dog is no longer a candidate species (Chapter 12). And in 2005, USFS rescinded many of its earlier restrictions (USFS 2001) on the poisoning of prairie dogs. Consequently, in response to increasing prairie dog populations and pleas for presidential intervention, poisoning of prairie dogs has resumed at USFS's Conata Basin (Buffalo Gap National Grasslands, South Dakota) (Chapters 12 and 18), where black-footed ferrets also live. As for USFWS and USFS, will policies for BLM and NPS soon become less favorable for prairie dogs? The answer to this question will determine the role of federal lands in the conservation of the prairie dog and its grassland ecosystem.

Summary

- Prairie dogs currently inhabit 55,100 hectares (136,200 acres) of federal lands managed by BLM, NPS, USFWS, and USFS.
- Prior to the designation of the prairie dog as a candidate species in 2000, BLM, NPS, USFWS, and USFS all authorized occasional or frequent poisoning of prairie dogs, and BLM encouraged recreational shooting as well.
- After the designation of the prairie dog as a candidate species in 2000, policies of BLM, NPS, USFWS, and USFS became more favorable to prairie dogs.
- The role of federal lands in the conservation of the prairie dog and its grassland ecosystem will depend on how BLM, NPS, USFWS, and USFS respond to the recent removal of the prairie dog from the list of candidate species for FLETWP.

Table 15.6. Prairie dogs in the national grasslands and national forests in the northern Great Plains in 1998. Predicted areas of occupancy for prairie dog colony-sites under new management derive from a colony expansion model (USFS 2001). The lower end of the range is expected if normal or above-normal precipitation occurs over the next ten years. The upper end of the range is expected if below-normal precipitation occurs . USFS (2005) recently has rescinded many of its earlier restrictions on the poisoning of prairie dogs, so predictions for certain national grasslands will change.

National grassland or forest	*Total area of national grassland or national forest (hectares)*	*Number of prairie dog colonies*	*Cumulative area inhabited by prairie dogs (hectares)*	*Number of colonies in 1998 that inhabited colony-sites of the following areas (hectares)*				*Predicted cumulative area inhabited by prairie dogs in ten years (hectares)*
				0.4–9.7	*10.1–19.8*	*20.2–40*	*>40.4*	
Little Missouri, North Dakota	462,705	149	1,157	113	18	9	9	2,185–3,804
Grand River, South Dakota	62,717	37	615	9	5	0	5	1,052–1,659
Fort Pierre, South Dakota	46,941	42	291	33	6	1	2	485–769
Buffalo Gap, South Dakota	241,666	296	5,374	133	44	27	28	9,307–14,973
Oglala, Nebraska	38,234	9	300	4	1	2	2	485–769
Nebraska, Nebraska	36,488	8	28	8	0	0	0	Unknown
Thunder Basin, Wyoming	226,688	146	7,421	47	17	26	34	12,545–20,234

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Semantic information distinguishing individual predators in the alarm calls of Gunnison's prairie dogs

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Abstract. Gunnison's prairie dogs, *Cynomys gunnisoni*, are colonial social rodents that give alarm calls upon the approach of a predator. Field experiments at two natural colonies showed that the prairie dogs are able to encode information into their alarm calls about the colour of clothes and general shape of individual humans eliciting alarm calls. This shows that the prairie dogs are able to incorporate information about the characteristic features of individuals within a given predator category.

An increasing body of evidence suggests that the alarm calls of some animals contain semantic information, with non-iconic calls that apparently designate particular external referents (Altmann 1967; Lyons 1977; Green & Marler 1979). Semantic information in predator-specific calls has been found in the alarm calls of some ground squirrels, *Spermophilus beecheyi* (Leger & Owings 1978; Owings & Virginia 1978), vervet monkeys, *Cercopithecus aethiops* (Seyfarth et al. 1980; Seyfarth & Cheney 1986), and domestic fowl, *Gallus domesticus* (Gyger et al. 1987). Owings & Leger (1980) and Leger et al. (1980) have identified calls of the California ground squirrel for several specific predators, although a related ground squirrel, *Spermophilus beldingi*, seems to lack such predator-specific calls (Leger et al. 1984). Seyfarth et al. (1980) found that vervet monkeys give acoustically different alarm calls in response to different predators, particularly the leopard, *Panthera pardus*, martial eagle, *Polemaetus bellicosus*, python, *Python sebae*, and baboon, *Papio cynocephalus*. These researchers found that vervet monkeys appear to process information contained in the calls at a semantic level, not just according to acoustic similarity (Cheney & Seyfarth 1988).

Semantic processing of information is not limited to alarm calls. Domestic chickens can communicate semantic information about the quality of food that is available to them (Marler et al. 1986a, b) and rhesus monkeys *Macaca mulatta*, can communicate semantic information about their roles in agonistic interactions (Gouzoules et al. 1984). However, alarm calls have some advantages for studying semantic content experimentally: because alarm calls are made in response to predators, the external referent is usually present, and the context of the call can be determined easily.

Previous work with Gunnison's prairie dogs, *Cynomys gunnisoni*, has shown that these animals have distinct calls for different categories of predators (e.g. humans; domestic dogs, *Canis familiaris*) and that, in an experimental laboratory setting, the animals have distinct calls for different individuals within a predator category (Slobodchikoff et al. 1986). In this paper, we report the results of field experiments with a naturally occurring colony of Gunnison's prairie dogs, in which prairie dog individuals call in response to several humans that differ in size, shape and colour of clothes.

Humans are frequent predators of prairie dogs, and elicit alarm calls when they appear within sight of a prairie dog colony. Undoubtedly, native Americans have hunted prairie dogs for thousands of years, though their use of this animal as a food source is more a matter of tradition than written record. Both the Hopi and Navajo Indian tribes have recipes for the culinary preparation of baked prairie dogs (Gorman 1981). White settlers considered the prairie dog a pest that threatened livestock and crops; a program of eradication of this species, both by hunting and by poisoning, has been ongoing for at least 150 years (McNulty 1971). The mean generation time for Gunnison's prairie dogs is 1·5 years (Rayor 1985; Slobodchikoff, unpublished data). Thus, at least 100 generations of prairie dogs have had contact with settlers who kill

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them, and many more generations have undoubtedly been hunted by native Americans. Although it is not clear whether the alarm calls of prairie dogs are genetically determined or learned, there has been ample time for a human alarm call to evolve if it is genetically based (Wright 1978).

METHODS

Field research was conducted in two natural colonies of Gunnison's prairie dogs. One colony (HS) was located in an undeveloped area of Flagstaff, Arizona. The colony was 2·5 ha in size, and situated in an alpine meadow at an elevation of 2250 m, away from human habitation. The colony had a mean density of 85 animals per ha. The other colony (PL) was located 30 km north of Flagstaff, in an alpine meadow at 2580 m, and had a mean density of 20 animals per ha. A variety of natural predators were observed hunting at both colonies: golden eagles, *Aquila chrysaetos*; red-tailed hawks, *Buteo jamaicensis*; coyotes, *Canis latrans*; humans; and domestic dogs. Intermittent observations of ferruginous hawks, *Buteo regalis*, rough-legged hawks, *Buteo lagopus*, harriers, *Circus cyaneus*, badgers, *Taxidea taxus*, and feral cats, *Felis sylvestris*, were also noted. Humans in the Flagstaff area also hunt prairie dogs intensively.

Prairie dogs were live-trapped weekly from March to October 1988 using Tomahawk squirrel-sized traps. Each animal was ear-tagged (Monel no. 1 tags) and marked with a Nyanzol dye code that allowed identification from a distance. During each trapping session, captured prairie dogs were weighed and checked for reproductive condition.

This study encompassed three field experiments, all of which involved humans acting as test stimuli presented to wild prairie dog colonies. A prescribed route along a square 100 m on a side was selected through the colonies. During each trial, one person walked along this route at a relaxed, steady pace, while another researcher sitting in a car parked outside the colony recorded any alarm calls given by the prairie dogs. Recordings were made with a Sennheiser directional microphone (ME-88) and a Uher cassette tape recorder (Model 160). Recording distances between vocalizing prairie dogs and the microphone were in the range of 50–150 m. All trials were conducted during the prairie dogs' reproductive season, in June and July 1988. This time of year is a period of intense alarm calling, because the pups have just been weaned and are out foraging by themselves for the first time, and are at a stage of maximum vulnerability to predators.

The recordings were then reviewed in the laboratory. Because the researcher recording each trial was able to note when calls were given from different animals (either from direct observation of the caller, or from noting calls given from different areas of the colony), it was possible to identify a calling 'bout' from each calling animal. Calls were isolated to call elements (a single call within a calling 'bout') and studied using a Unigon II Real Time Analyzer (Multigon Industries).

For each call element, we measured a total of 12 variables (Fig. 1). For each experiment, these variables were then subjected to a discriminant function analysis (DFA), a test that examines all variables for all calls and assigns the most similar calls to groups (Nie et al. 1975).

In the first experiment ('white laboratory coat'), four adult humans, two males (C.S. and E.C.) and two females (C.F. and J.K.) walked individually through the HS colony on 3 separate days, and wore sunglasses and the same white laboratory coat over jeans. The second experiment ('four-person coloured shirt') involved the same four people, all wearing jeans, but instead of the laboratory coat, each person wore a tee-shirt of a different colour: C.S., blue; E.C., grey; C.F., orange; and J.K., green. This experiment was replicated at the HS and PL colonies. The third experiment ('two-person same shirt') involved one male, E.C., and one female, C.F. Each walked through the HS colony 10 times. In one-half of the trials, C.F. walked through the colony wearing a yellow tee-shirt, and for the other trials, she wore a white tee-shirt. E.C. wore the same white and yellow shirts for his walk-throughs. Our aim in this test was to determine whether the prairie dogs could distinguish between these two people (who were approximately the same height) even when they wore the same clothing. This experiment also tested whether the prairie dogs could identify C.F. and E.C. respectively, even though they wore different colours on different occasions. All tests were carried out in mornings or late afternoons; within this framework, the actual time of testing was randomized.

RESULTS

White Laboratory Coat

In the first experiment, the discriminate function analysis (DFA) of alarm calls indicated that the

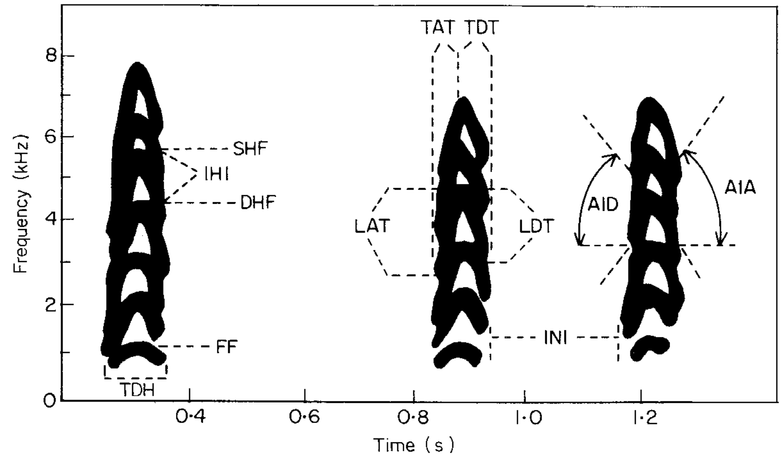

Figure 1. Sonagram of alarm calls given by a Gunnison's prairie dog in response to a human approaching the prairie dog colony. Shown here is a calling bout containing three call elements, i.e. three individual alarm calls, all given by the same animal. All measurements of call structure were performed on a single call element, but are shown here over three call elements for illustrative purposes. Call structure characteristics that were measured are as follows: FF, fundamental frequency; DHF, dominant harmonic frequency; SHF, supradominant harmonic frequency; IHI, interharmonic interval (Hz) between DHF and SHF; TDH, time of dominant harmonic; TAT, time of ascending tail of dominant harmonic; TDT, time of descending tail of dominant harmonic; LAT, length (mm) of ascending tail of dominant harmonic; LDT, length (mm) of descending tail of dominant harmonic; AIA, angle (degrees) of ascent of dominant harmonic; AID, angle (degrees) of descent of dominant harmonic; INI, interval (s) between two adjacent call elements in a calling bout.

Table I. F-statistics and significances between pairs of groups in white laboratory coat experiment

	C.S.	J.K.	E.C.
J.K.	2·00 $P=0{\cdot}16$		
E.C.	2·28 $P=0{\cdot}12$	4·40 $P=0{\cdot}02$	
C.F.	4·17 $P=0{\cdot}03$	3·84 $P=0{\cdot}03$	12·1 $P=0{\cdot}004$

$df=3,14$.

prairie dogs' abilities to distinguish between the four people was mixed (Table I): calls for C.S. were confused with those for E.C. and J.K. (NS); J.K. and E.C. were differentiated a significant percentage of the time ($P=0{\cdot}02$); and all the calls given for C.F. were properly grouped ($P=0{\cdot}03$ for C.F. compared with C.S. and J.K., $P=0{\cdot}004$ for C.F. compared with E.C.; see Table I). This last result shows that the prairie dogs consistently identified C.F. correctly and confused her with no one else. Overall, the DFA was able to classify 70% of the calls to their appropriate group (Table II).

Four-person Coloured Shirt

In this experiment, the prairie dogs' discriminatory ability increased notably. Calls given at colony HS for each person were correctly classified into their proper groups a significant portion of the time (P-values ranging from 0·003 to $<0{\cdot}001$, Table III). While some mistakes were made in identifying each person, overall discriminatory accuracy (as defined by the total number of calls the DFA classified into their proper groups), was 79·1% (Table IV). Plotting the groups along three discriminant function axes (Fig. 2) showed that the placement of calls for each person and the colour of shirt that they wore corresponded closely to the order of colours in the spectrum of light visible to the prairie dogs. Calls given at colony PL also were correctly classified into their proper groups ($P<0{\cdot}001$ for all groups). Overall discriminatory accuracy was 85·6% (Table V).

We further analysed the data from colony PL by using a small subset of the variables used in the above DFA. Three variables were selected: DHF, dominant harmonic frequency; SHF, supradominant harmonic frequency; and LAT, length of ascending tail of dominant harmonic (see Fig. 1). These variables were selected because each had a

Table II. Classification table for results of white laboratory coat experiment; percentages along each horizontal line indicate the percentage of cases from a group that are classified into each predicted group

		Predicted group			
Group	N	C.S.	J.K.	E.C.	C.F.
C.S.	5	2 (40%)	2 (40%)	1 (20%)	0 (0%)
J.K.	5	1 (20%)	4 (80%)	0 (0%)	0 (0%)
E.C.	5	1 (20%)	1 (20%)	3 (60%)	0 (0%)
C.F.	5	0 (0%)	0 (0%)	0 (0%)	5 (100%)

Percentage of cases correctly classified to proper group: 70%.

Table III. F-statistics and significances between pairs of groups in the four-person coloured shirt experiment

	C.S.–BL	J.K.–GR	E.C.–GY
J.K.–GR	3·18 $P=0{\cdot}003$		
E.C.–GY	3·86 $P=0{\cdot}001$	3·56 $P=0{\cdot}002$	
C.F.–OR	8·71 $P<0{\cdot}001$	7·94 $P<0{\cdot}001$	9·93 $P<0{\cdot}001$

$df=9,55$.

significant univariate F-ratio, and in the step-wise DFA reported above, SHF was the variable entered in the first step (out of eight steps), with a high F-to-remove (51·1), LAT was the variable entered in the second step with a much lower F-to-remove (6·9), and DHF was not included in the analysis. Three variables were used so that the number of variables would be less than the number of groups (Nie et al. 1975). The results of this analysis showed that the calls for each person were still classified into their proper groups a significant percentage of time ($P<0{\cdot}001$ for all groups). However, overall discriminatory accuracy decreased to 64·4%.

Two-person Same Shirt

In this last experiment, discriminatory ability reached its highest level ($P<0{\cdot}001$ for all comparisons; Table VI). When each person wore a yellow shirt, C.F. and E.C. were correctly identified in most of the trials, and they were seldom mistaken for each other (Table VII). Overall accuracy for this series was 94·4%. A plot of the four DFA groupings (Fig. 3) shows two distinct placements of E.C. along one axis and C.F. along the other.

DISCUSSION

The results of these experiments suggest that prairie dogs can distinguish between individual predators and can incorporate information about the physical features of individual predators into alarm calls.

Table IV. Classification table for results of the four-person coloured shirt experiment at colony HS

		Predicted group			
Group	N	C.S.–BL	J.K.–GR	E.C.–GY	C.F.–OR
C.S.–BL	11	8 (73%)	2 (18%)	0 (0%)	1 (9%)
J.K.–GR	15	2 (13%)	11 (73%)	2 (13%)	0 (0%)
E.C.–GY	21	2 (10%)	3 (14%)	15 (71%)	1 (5%)
C.F.–OR	20	0 (0%)	0 (0%)	1 (5%)	19 (95%)

Percentage of cases correctly classified to proper group: 79·1%.

Table V. Classification table for results of the four-person coloured shirt experiment at colony PL

		Predicted group			
Group	*N*	C.S.–BL	J.K.–GR	E.C.–GR	C.F.–OR
C.S.–BL	25	22 (88%)	0 (0%)	0 (0%)	3 (12%)
J.K.–GR	17	0 (0%)	14 (82%)	0 (0%)	3 (18%)
E.C.–GY	25	3 (12%)	0 (0%)	22 (88%)	0 (0%)
C.F.–OR	23	2 (9%)	0 (0%)	2 (9%)	19 (83%)

Percentage of cases correctly classified into proper group: 85·6%.

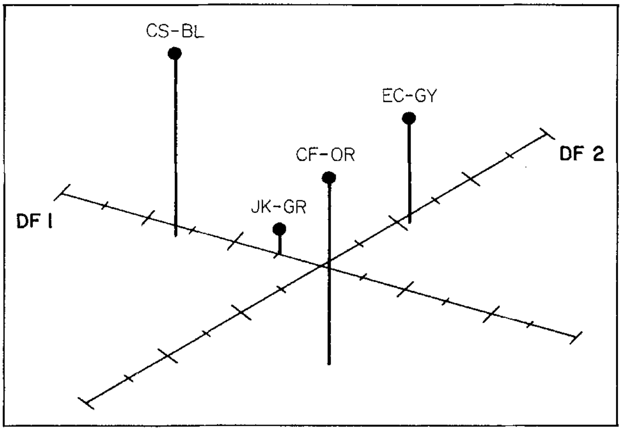

Figure 2. Group centroids for calls elicited by different human subjects in the four-person coloured shirt experiment. Positions of group centroids are shown in three-dimensional space, with the horizontal dimensions corresponding to discriminant functions 1 and 2, and the vertical dimension corresponding to discriminant function 3 in DFA. CS-BL is human subject C.S. wearing a blue shirt, JK-GR is subject J.K. wearing a green shirt, EC-GY is subject E.C. wearing a grey shirt, and CF-OR is subject C.F. wearing an orange shirt.

Table VI. *F*-statistics and significances for the two-person same shirt experiment

	Group		
	C.F.–Y	C.F.–W	E.C.–Y
C.F.–W	14·6 P<0·001		
E.C.–Y	8·68 P<0·001	23·9 P<0·001	
E.C.–W	10·3 P<0·001	8·50 P<0·001	10·5 P<0·001

df=8,29.

The physical features seem to include colour: prairie dogs are known to have dichromatic colour vision (Jacobs & Pulliam 1973). They also seem to include aspects of shape: the white laboratory coat obscured not only colour but to some extent the shape of the individual human wearing it, and the prairie dogs had the most difficulty in distinguishing between individual humans under this experimental régime. When both colour and shape were available to the prairie dogs, in the second experiment, the animals showed a remarkable ability to incorporate this information into their calls. That the colour component is distinct from the other, shape-related, component is seen in the results of the third experiment, where the group centroids for C.F. and E.C. have the same position along discriminant function 1 for yellow and the same position for white (Fig. 3).

In these experiments, humans were used for convenience, in that human subjects are more responsive than other species in following directions about

Table VII. Classification table of results of the two-person same shirt experiment

		Predicted group			
Group	*N*	C.F.-Y	C.F.-W	E.C.-Y	E.C.-W
C.F.-Y	5	5 (100%)	0 (0%)	0 (0%)	0 (0%)
C.F.-W	10	0 (0%)	9 (90%)	0 (0%)	1 (10%)
E.C.-Y	10	0 (0%)	0 (0%)	10 (100%)	0 (0%)
E.C.-W	11	0 (0%)	0 (0%)	1 (9%)	10 (91%)

Percentage of cases correctly classified to proper group: 94·4%.

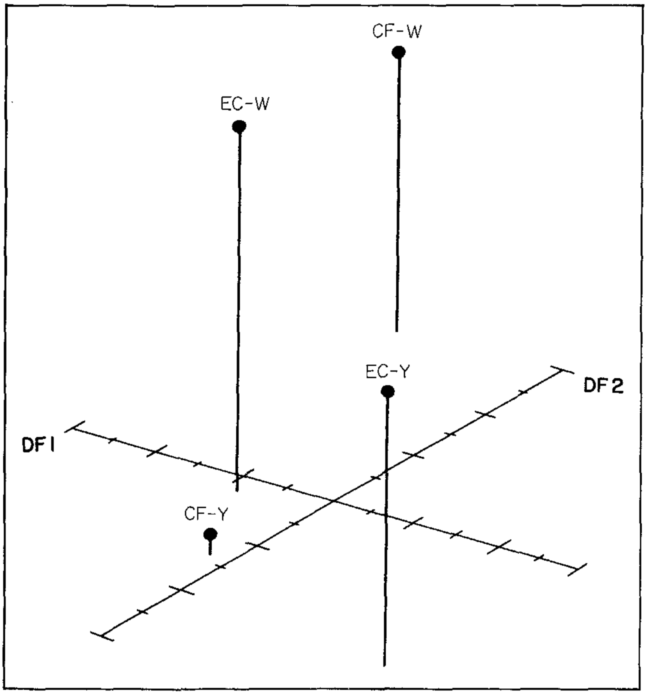

Figure 3. Group centroids for calls elicited by two human subjects, E.C. and C.F., each wearing either the same white (W) or the same yellow (Y) shirt. Axes are the same as in Fig. 2.

speed of walking and maintaining a fixed path through the colony. However, humans have been predators of prairie dogs for at least 150 years.

The selective advantage of being able to distinguish between individuals within a particular category of predator may be related to individual variation in hunting behaviour. Hunting skills may vary between individual predators, with older animals having more experience and more success than younger ones. Thus, there might exist some assessment by the prairie dogs of 'dangerousness level' that is associated with each individual within a predator category. Also, since a prairie dog colony is spatially fixed to a particular location, the home ranges of several individuals within a predator species might overlap either part or all of the colony. Animals who hunt regularly on a colony might have a fairly regular path and type of approach, as well as an individual hunting style. It thus would be to the prairie dogs' advantage to recognize and differentiate any such individual differences on the part of their predators.

Although we show here that prairie dogs are able to incorporate information about individual difference of predators into the alarm calls, there is still no evidence that this information is actually communicated to prairie dogs that hear the alarm calls. While we presume that information that is encoded into an alarm call can be understood by a recipient prairie dog, this still remains to be tested.

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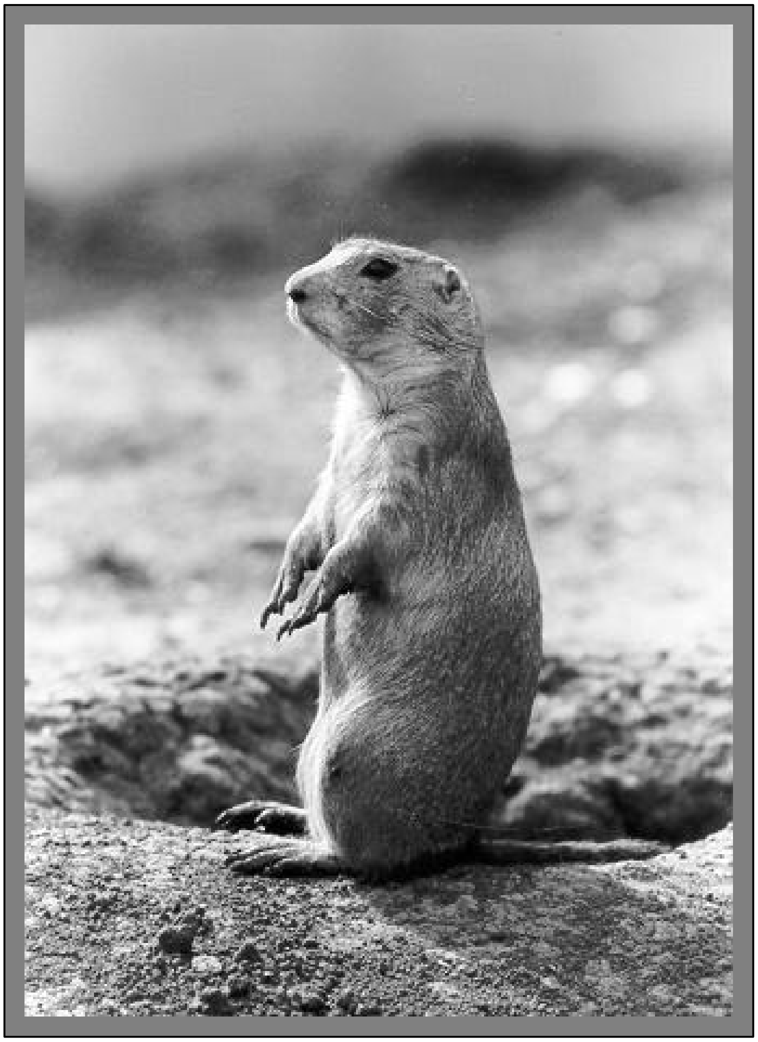
SOUTH DAKOTA BLACK-TAILED PRAIRIE DOG

MANAGEMENT PLAN



DRAFT 2 -- October 2001

South Dakota Prairie Dog Work Group

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I. Introduction

I-A. Background events:

On July 31, 1998 the National Wildlife Federation (Federation) submitted a "Petition for Rule Listing the Black-tailed Prairie Dog (*Cynomys ludovicianus*) as Threatened Throughout its Range." The petitioner further asked the Secretary of Interior to use emergency powers to list the species, because of the fear that poisoning of prairie dog colonies would increase because of the threat of federal listing. The Biodiversity Legal Foundation and Predator Project (now known as the Predator Conservation Alliance) submitted a second petition, which the U. S. Fish and Wildlife Service treated as supplemental to that of the Federation. The U.S. Fish and Wildlife Service (Service) denied the emergency listing request of the Federation.

On March 2, 1999 the Service published a positive 90-Day Finding on the Federation's petition (U. S. Fish and Wildlife Service 1999). The Service concluded that the petition presented sufficient information to indicate that federal listing may be warranted. Following publication of the finding, the Service began a status review for the black-tailed prairie dog to gather information needed to determine whether federal listing was warranted. This status review included published requests for information and specific requests of state, federal, and tribal wildlife entities for information to assist the Service in its decision-making.

On February 4, 2000 the Service published a positive 12-Month Finding on the Federation's petition (U. S. Fish and Wildlife Service 2000). The Service announced that listing of the black-tailed prairie dog was warranted but precluded by higher listing priorities, an action that designated this species as a federal candidate species for listing. The Service's action was based on their interpretation of the significance of threats, including sylvatic plague, inadequate regulatory mechanisms, and general population declines since 1980. The Service assigned a listing priority of 8, based on a moderate overall magnitude of threats and an imminent overall immediacy of threats.

In response to the threat of removal of state authority for the black-tailed prairie dog, state wildlife and agriculture agencies began coordination activities following receipt of the Federation's petition in 1998. South Dakota began its participation in multi-state activities in November 1998 with a meeting with representatives from the state wildlife and agriculture departments in Wyoming and Montana. The major initial focuses were to discuss current prairie dog legal and population statuses and to develop strategies to avoid federal listing of the species.

This multi-state, multi-agency cooperative effort expanded in 1999 with a meeting in Colorado to discuss rangewide conservation planning for the black-tailed prairie dog. Meeting participants committed themselves to the development of a conservation agreement to "manage, maintain, and enhance habitat and populations of black-tailed prairie dogs across its historic range and reduce the number of threats impacting their viability through the cooperation of private, tribal, federal, and state landowners." (Van Pelt 1999).

"The Black-tailed Prairie Dog Conservation Assessment and Strategy" (Van Pelt 1999) summarizes the current status of the species and includes goals, objectives, and strategies designed to provide for long-term viability and, as a result of commitment to completion of these activities, avoid the need for federal listing. The conservation strategy portion of the document includes a tiered approach with opportunities for involvement of states, federal agencies, tribes, and private entities. The South Dakota Department of Game, Fish and Parks (SDGFP) has participated in development of the conservation assessment and strategy document and will integrate its prairie dog management activities with this national planning effort as closely as possible.

I-B. Management plan scope and goals:

This plan is written in the format of a strategic plan, with an overall goal, objectives designed to support achievement of the goal, and strategies associated with each objective. Operational plans will follow, which will describe annual activities designed to help fulfill commitments contained in this strategic plan.

The scope of South Dakota's prairie dog management plan is limited by land ownership and prairie dog distribution patterns in the state. Approximately 20% of South Dakota's 49,310,000 acres are in federal, state, or tribal ownership or trust (Table 1). The State of South Dakota recognizes tribal sovereignty and the respective directives of federal land management agencies. Although exact prairie dog acreages are not available for much of South Dakota, general estimates indicate that the majority of remaining prairie dog acreage is found on federal and tribal lands (Tschetter 1988, SDGFP 1996). In light of the state's land ownership and prairie dog distribution patterns, the State of South Dakota is interested in working cooperatively with interested land managers, whether private, federal, tribal, or state-affiliated.

The primary goal of the South Dakota Black-tailed Prairie Dog Management Plan is to manage for long-term, self-sustaining prairie dog populations in South Dakota while avoiding negative impacts to landowners that do not wish to accommodate prairie dogs on their properties. An associated benefit of the Plan is the assurance of the long-term viability of species closely dependent on the prairie dog ecosystem.

Table 1. Land acreages of South Dakota public and tribal land ownership[1]

U.S. Forest Service	2,400,000
U.S. Army Corps of Engineers	520,000
U.S. Bureau of Land Management[2]	275,000
U.S. Fish and Wildlife Service	
Waterfowl Production Areas	156,087
National Wildlife Refuges	44,251
National Park Service[3]	139,000
U.S. Bureau of Reclamation	24,000
Federal lands subtotal	*3,558,338*
Tribal and tribal trust lands	*4,867,438*
S.D. Office of School and Public Lands	807,000
S.D. Department of Transportation[4]	142,000
Meandered lakes[5]	166,800
SDGFP Game Production Areas	163,000
SDGFP other lands	104,949
Other state lands	46,000
State lands subtotal	*1,429,749*
Total tribal, federal, and state lands	**9,855,525**

[1] Unless otherwise noted, source: Dave McGuigan, SDGFP, Pierre
[2] Source: Chuck Berdan, BLM, South Dakota
[3] Does not include South Unit of Badlands National Park (133,000 acres), which lies within Pine Ridge Indian Reservation and is managed cooperatively by Oglala Sioux Tribe and Badlands National Park.
[4] Based on average road right-of-way distance of 150 feet
[5] Source: Lynn Beck, SD Department of Environment and Natural Resource, Pierre

II. Historical Background

II-A. South Dakota historical prairie dog acreage:

Estimated historical prairie dog acreage has been compared to current estimated acreage in supporting conclusions that the black-tailed prairie dog presently occupies only a small fraction of its former range (USFWS 1999, USFWS 2000). The historical range of the black-tailed prairie dog is often represented in a format similar to the distribution map found in Hall (1981), although this portrayal was apparently derived from connecting the outermost collection sites for the species. In fulfilling a portion of its commitments under the Endangered Species Act, the U.S. Fish and Wildlife Service (Service) is required to base its decisions on the best available information. The Service's approach to describing historical occupied habitat was to apply a uniform standard across the range, arriving at a conclusion that, at a given time, approximately 20% of potential habitat was inhabited by prairie dogs (P. Gober, pers. comm.) In its 12-Month Finding for a Petition to List the Black-tailed Prairie Dog as Threatened, the Service reported historical estimates for South Dakota as ranging from 33,000 acres to 1,757,000 acres (USFWS 2000).

No statewide prairie dog inventory has been conducted in South Dakota. Statewide acreage estimates to date are largely derived from results of surveys or questionnaires circulated to land management agencies and county or state weed and pest control personnel. Tschetter (1988) circulated letters and county maps to SDGFP conservation officers and extension trappers and local weed and pest supervisors in 1987 requesting estimates of prairie dog town sizes and locations. Results of this survey indicated that the 1987 statewide prairie dog estimate was 184,186 acres distributed as follows: 139,600 acres (75.8%) on tribal lands, 9,927 acres (5.4%) on public lands, and 34,659 acres (18.8%) on private lands. These figures do not include prairie dog towns less than 10 acres in size.

SDGFP (1996) circulated a questionnaire to a total of 84 entities involved in prairie dog control or management. The distribution included 66 county weed and pest supervisors, 4 state land management agencies, 8 federal land management agencies, and 6 Native American tribes. SDGFP requested information on prairie dog estimated acreage and survey operations. Highest estimated prairie dog acreages were reported by Rosebud Agency (75,000 acres), Ziebach County Weed and Pest Board (40,000 acres, which included Cheyenne River Reservation), Dewey County Weed and Pest Board (36,000 acres, which included Dewey and Ziebach counties), Pine Ridge Agency (30,000 acres), Standing Rock Agency (14,000 acres), and Wall Ranger District of Nebraska National Forest (10,400 acres). The total statewide acreage estimate was 264,709 acres distributed as follows: 122,800 acres (46.4%) on tribal lands, 29,099 acres (11%) on public lands, and 112,810 acres (42.6%) on private lands.

This questionnaire (SDGFP 1996) also revealed that 28 responding entities conducted prairie dog surveys. The most common reasons for conducting prairie dog surveys were to determine prairie dog control or management needs; to collect information to develop prairie dog management plans for a county or land unit; to assess long-term prairie dog population trends; to collect information related to livestock stocking rates; to determine abundance to meet recreational needs; to attain block clearance from black-footed ferret survey requirements; to determine abundance to meet threatened and endangered species needs; and to assess disease impacts. Approximately one-third of respondents conducted prairie dog surveys at least annually, and approximately one-third conducted prairie dog surveys at intervals ranging from 2-10 years. Survey techniques varied from a crude visual assessment from a moving vehicle to more sophisticated methods used by several federal land management or natural resource agencies. For entities conducting frequent surveys with specific techniques, survey completeness ranged from 50-100%.

The South Dakota Department of Agriculture (SDDA) estimated statewide acreage for 1996-1997 at 240,287 acres, based on information contained in the 1997 South Dakota Weed and Pest Annual Report (G. Williams, pers. comm.). This estimate did not include Bennett, Harding, or Lawrence counties or many counties east of the Missouri River that did not report prairie dog acreage estimates. Highest acreage estimates were reported by weed and pest representatives from the following counties: Shannon (50,000 acres), Todd (40,000 acres), Dewey (39,500 acres), Mellette (30,000 acres), Jackson (27,000 acres), and Pennington (12,000 acres).

Statewide estimates of prairie dog acreage are collected annually by the South Dakota Weed and Pest Program, Division of Agricultural Services, SDDA, by surveying county weed and pest supervisors. The most recent results, from 1999, indicated a statewide estimate of 135,455 acres (SD Dept. of Agriculture 1999).

Ground-truthing of acreage or density of reported prairie dog colonies using the previously described survey or questionnaire technique was either limited or not conducted.

II-B. Statewide prairie dog control efforts:

Several entities have had statewide influence or authority for prairie dog control in South Dakota. Federal prairie dog control or technical assistance has been provided by the Bureau of Biological Survey, U.S. Department of Agriculture (USDA); the U.S. Fish and Wildlife (USFWS), U.S Department of Interior; and the Animal and Plant Health Inspection Service (APHIS) – Wildlife Services, USDA. The Bureau of Biological Survey was transferred from the U.S. Department of Agriculture to the U.S. Department of Interior in 1940 to become the USFWS. The USFWS delegated its animal damage control authority in South Dakota to the SDGFP in 1974 under a Grant-in-Aid Agreement. In 1985, federal animal damage management responsibilities were transferred from the U.S. Fish and Wildlife Service to the U.S. Department of Agriculture, under a program called Animal Damage Control, which was eventually renamed Wildlife Services.

The SDGFP and the South Dakota Department of Agriculture (SDDA) have provided statewide prairie dog control or technical assistance, in cooperation with state or county weed and pest control entities. In addition, various public, tribal, and private landowners have conducted prairie dog control for many years.

Hansen (1988) presented a summary of historical events related to prairie dog control in South Dakota. According to Hansen, a rodent control law was passed by the South Dakota legislature in 1919. Nearly 400,000 acres were treated in 1920 in nine counties west of the Missouri River. By 1930, prairie dogs were reduced to small, scattered colonies. Acreage increased during the drought years of the 1930s, although federal emergency work programs focused on prairie dog control and reduced prairie dogs to possibly the lowest levels in recent history. Hansen estimated that 20,000-50,000 acres were treated annually from the 1940s to the mid-1950s. In 1972, President Nixon's Executive Order 11643 prohibited toxicant use on federal lands or with federal funds, halting affected prairie dog control through 1975. Beginning in 1976, zinc phosphide became the standard prairie dog control tool. From 1980-1984, nearly 1 million acres were baited for subsequent control in the state, including 464,000 acres on the Pine Ridge Indian Reservation. During 1985-1986, 329,000 acres were baited, including 240,000 acres on Pine Ridge Indian Reservation, with control work on Pine Ridge costing an estimated $7.88 per acre. Hansen concluded that, during the period 1920-1980, South Dakota's prairie dog population appeared to peak approximately every 15 years. APHIS-Wildlife Services has not conducted direct prairie dog control in South Dakota since the mid-1980s (T. Pugh, pers. comm.).

The South Dakota Department of Agriculture annually surveys county weed and pest officials regarding "infested" acres of animal pests and noxious weeds. Among the survey questions is a request for information on the number of acres controlled for each weed or pest. For example, in the most recent report available, respondents reported that 40,040 acres of prairie dogs were controlled in 1999 (SD Dept. of Agriculture 1999).

SDGFP has two main roles in prairie dog control in South Dakota (Appendix 1). SDGFP provides direct control of prairie dogs that have moved from adjacent public lands onto private lands, as per SDCL 34A-8-7. SDGFP policy is to provide direct control at no initial cost to the landowners with prairie dogs that have moved from adjacent, previously uncontrolled public lands. Upon completion of control on both private and public lands, the landowner assumes maintenance responsibility for prairie dog control. During the years 1996-1999, SDGFP provided direct control for a total of 1,165 acres (R. Sieg, pers. comm.).

SDGFP also provides technical assistance to landowners for control of colonies 160 acres or larger. SDGFP field personnel provide equipment and time to supervise pre-baiting and bait application. Landowners are responsible for the cost of bait material, for applying the bait, and for follow-up treatment and continued maintenance. During the years 1996-1999, SDGFP provided technical assistance for prairie dog control on a total of 2,920 acres (R. Sieg, pers. comm.).

Following designation of the black-tailed prairie dog as a federal candidate species, the U.S. Forest Service and Bureau of Land Management modified policies for prairie dog control on their lands. The candidate species designation has not stopped control on these lands. The U.S. Forest Service made an internal decision to limit control to situations of human health and black-footed ferret recovery. For example, a prairie dog colony encroaching on a residence would be cause for control (J. Sidle, pers. comm.).

III. Current Situation

III-A. Relevant state statutes and administrative rules:

This section is not inclusive of every statute or rule dealing with prairie dogs in South Dakota's state laws and administrative rules. The most relevant statutes and rules are described.

The black-tailed prairie dog has state designations under several legal authorities. The species is a game species and a predator/varmint species, regulated by the SDGFP (South Dakota Codified Laws {SDCL} 41-1-1.21). Among other relevant statutes are SDCL 34A-8-7, which states that "The Secretary of Agriculture and the Secretary of Game, Fish and Parks shall establish programs, with legislative approval and may enter into cooperative agreements with federal and state agencies or with private persons as deemed necessary for the management of nongame, endangered or threatened species. The secretaries shall establish and conduct control programs at state expense on private lands that are encroached upon by prairie dogs from contiguous public lands."

SDCL 40-36-1 states that: "The Department of Game, Fish and Parks shall cooperate and enter into cooperative agreements with the United States Fish and Wildlife Service or any other agency in the control and disposition of coyotes, feral dogs, fox, prairie dogs, and other wild animals in this state that are injurious to livestock, poultry, game, land, and the public health." SDCL 36-3 states that "The Department of Agriculture may enter into cooperative agreements with other governmental agencies, counties, associations, corporation or individuals if such cooperation is necessary to promote the control and disposition of animals pursuant to § 40-36-1." SDCL 36-3.1 states that "The Secretary of Game, Fish and Parks shall establish a program to continue prairie dog control on private lands at the written request and with the cooperation of the participating landowner. The program is to be funded from revenues in the state animal damage control fund."

SDCL 41-11-15 tied prairie dog management to state participation in black-footed ferret reintroduction with the following conditions: The Department of Game, Fish and Parks and the Department of Agriculture may participate in programs to reintroduce the black-footed ferret if the following conditions are being met:

(1) Areas containing prairie dogs but not having the potential to support black-footed ferrets shall be identified, evaluated and declared ferret-free;
(2) The existing United States Forest Service Prairie Dog Management Plan for the Conata Basin, Buffalo Gap National Grasslands shall be strictly adhered to, and if future increases in prairie dog acres are needed, a funding mechanism shall be established to provide financial compensation to landowners suffering lost income;
(3) No additional land may be acquired for ferrets through condemnation, and the multiple use concept of the United States Forest Service shall be continued;
(4) The initial ferret reintroduction efforts shall be concentrated within the boundaries of Badlands National Park, and once release techniques are refined, the

prairie dog management plan on the Buffalo Gap National Grasslands is functioning and local citizens have had the opportunity to view the progress, then reintroduction efforts may be expanded to the grasslands; and
(5) The United States Fish and Wildlife Service shall attempt to provide for the continued meeting on a regular basis during and after the ferret reintroduction of the local level committee consisting of representatives of the United States Forest Service, Pine Ridge Indian Reservation, United States National Parks Service, United States Fish and Wildlife Service, affected state agencies, private organizations and local landowners.

NOTE: The following discussion of pest statutes is included for historical background. Senate Bill 64, passed during the 66th Session of the South Dakota Legislature, created a new "species of management concern" category. The black-tailed prairie dog has been placed in this category, an action that removed the species from the state list of declared pests.

The State Weed and Pest Control Commission designated the black-tailed prairie dog as a statewide declared pest soon after state weed and pest statutes were enacted in 1983 (Clarke 1988). As a statewide declared pest, this species is covered under Administrative Rules (Article 12:62) and statutes (Chapter 38-22 of South Dakota Codified Laws) governing weed and pest control.

Article 12:62:02:01.2 defines a declared pest as follows: "a pest which the commission has designated as sufficiently detrimental to the state to warrant enforcement of control measures." Characteristics of a declared pest are contained in Article 12:62:03:01.01 and are as follows: "(1) The pest is capable of spreading rapidly by natural means in a previously uninfested area; (2) The pest is not controllable without special preventive, chemical, biological, and cultural practices; (3) The pest is capable of materially reducing the production of crops and livestock."

The declaration of the prairie dog as a statewide declared pest is included in Article 12:62:03:01.05. Procedures for additions to or deletions from the lists of noxious weeds and declared pests are contained in Article 12:62:03:06 and are as follows: "The commission shall evaluate additions and deletions to the noxious weed and declared pest lists at its annual meeting. Commissioners shall consider all requests for changes to the noxious weed and declared pest lists."

SDCL Chapter 38-22 contains statutes relating to weed and pest control. Much of this chapter pertains to administrative operations and regulatory powers of the State Weed and Pest Control Commission. Relevant components include SDCL 38-22-16: "If any owner of weed or pest infested land fails to rid the land of such infestation and the Secretary of Agriculture finds that such infestation is a menace to neighboring lands or to the state or its people he may declare such infested land to constitute a public nuisance and may enter such infested areas and perform such protective operations as may be necessary." SDCL 38-22-16.1 state that: "The existence of weeds or pests in any amount or quantity upon land is sufficient to determine that such land is infested."

The relationship between state weed and pest authorities and federal lands is discussed in SDCL 38-22-17.2: "If any agency of the United States fails or refuses to suppress weeds or pests on any land owned or controlled by such agency after receiving notice of such infestation by the county weed and pest board pursuant to this chapter, the South Dakota Weed and Pest Control Commission, at the request of the county board, shall intervene on its behalf. The Attorney General shall provide such legal counsel as the South Dakota Weed and Pest Control Commission may require to resolve any such dispute."

The South Dakota Prairie Dog Working Group addressed the federal listing criteria of overutilization for commercial, recreation, scientific, or educational purposes (ex: prairie dog shooting) and inadequacy of existing regulatory mechanisms (ex: prairie dog control) by discussing alternatives to unregulated prairie dog shooting and statewide animal pest designation. The South Dakota Department of Game, Fish and Parks' Commission passed a regulation on January 11, 2001 to establish a regulated prairie dog shooting season (Appendix 2).

The second action item resulting from Working Group recommendations was a bill to create a new category (species of management concern) for wildlife species with both negative and positive aspects associated with their presence on private lands (Appendices 3-5). Working Group discussions on these topics emphasized that individual action items are not as critical to demonstrating commitment to long-term prairie dog management as is the complete management package.

III-B. Description of current prairie dog management plans and inventory efforts:

1. South Dakota Department of Game, Fish and Parks

SDGFP lands currently support a few, small, scattered prairie dog colonies, although total acreage is minimal. SDGFP has attempted to encourage prairie dogs on its lands with the use of mowing, with generally poor results. Because of the absence of livestock grazing on SDGFP lands, these lands are not likely to provide extensive prairie dog habitat. Prairie dogs occurring on SDGFP lands are, by policy, not poisoned (D. McGuigan, pers. comm.)

As part of its Strategic Approach to Management planning effort, SDGFP released a strategic plan for the black-tailed prairie dog in March 1994 (SDGFP 1994). The goal of the prairie dog strategic plan was:

> "To achieve and maintain populations of prairie dogs that will preserve this unique ecosystem, help buffer predatory losses to livestock and provide increased recreational opportunity consistent with economic, ecological, social, and aesthetic values for the people of South Dakota and its visitors."

The authors estimated that prairie dogs occupied 200,000-250,000 acres in South Dakota at the time of publication of the plan, based on federal, state, tribal, and county sources.

Eight objectives with respective strategies were included in the strategic plan. The objectives were as follows:

1. Determine future management of prairie dogs by 1996.
2. Determine statewide density and distribution of prairie dog colonies.
3. Assist with threatened and endangered species recovery programs.
4. Research prairie dog ecosystems and develop/utilize criteria to preserve and enhance.
5. Evaluate prairie dog control programs and activities.
6. Determine the positive and negative impacts of prairie dogs.
7. Improve access to prairie dog towns on private lands.
8. Develop/apply mechanisms for conservation easements, covenants and other appropriate means to provide landowners financial incentives to protect prairie dog colonies/complexes selected from those colonies identified as having: (1) sufficient potential to support existing BFF populations and requiring searches; (2) those that have potential as candidate BFF reintroduction sites; and (3) those that exhibit unique/high quality ecosystem values.

Aside from participation in activities related to black-footed ferret reintroduction in South Dakota, SDGFP has made little progress in achieving the outlined objectives and strategies.

In an earlier document (SDGFP 1978), SDGFP's goals for prairie dog management were to:

> "Monitor supply and demand for prairie dogs to forever perpetuate recreational value of prairie dog shooting and to promote public access to prairie dog towns for nonconsumptive users."

Strategies to attain these general goals included studies of prairie dog density and distribution, coordination with tribal and other entities in research and management activities, and maintenance of a portion of the prairie dog range in South Dakota for black-footed ferret populations.

2. South Dakota Office of School and Public Lands

The South Dakota Office of School and Public Lands manages approximately 807,000 acres. The Office is currently updating estimates of prairie dog acreage on their properties, with an estimate to be available in December 2001 (B. Jennings, pers. comm.). The Office has not set a prairie dog acreage goal for its properties. A related land management goal is to exchange prairie dog-occupied lands with federal agencies due to better expertise and funding for management within federal land management agencies and the Office's constitutional mandate to generate optimal income from managed lands for the permanent school trust fund (B. Jennings, pers. comm.).

The Office is presently involved in a cooperative prairie dog survey and inventory project, in cooperation with the Bureau of Land Management and funded by the National Fish and Wildlife Foundation. The results of this project will help direct future prairie dog management planning for the Office. Current survey techniques include the use of global positioning system (GPS) equipment and geographic information systems (GIS) mapping. Prairie dog management planning will help the Office develop and implement a consistent survey and inventory procedure to accurately assess acreages and habitat types, to identify and map public access roads to occupied prairie dog towns, to assess habitat diversity and quality, and to organize prairie dog data into a land management database.

3. Bureau of Land Management

Bureau of Land Management (BLM) lands in South Dakota occupy approximately 275,000 acres and presently have an estimated 500 acres of prairie dogs, based on field surveys using GPS equipment. BLM is presently conducting a prairie dog mapping project in cooperation with the South Dakota Office of School and Public Lands (see previous description for project goals). In addition to above-stated goals, this mapping project will provide BLM with prairie dog distribution data for Harding and Butte counties. A management concern for South Dakota BLM lands supporting prairie dogs is the potential for conflicts with adjoining private landowners, due to the fractured land ownership patterns. Specific future prairie dog acreage goals have not been established for lands owned by BLM in South Dakota (C. Berdan, pers. comm.).

4. Badlands National Park

Badlands National Park occupies 107,000 acres within the North Unit and 133,000 acres within the South Unit. The South Unit is contained within the boundaries of Pine Ridge Indian Reservation and is managed cooperatively by Badlands National Park and the Oglala Sioux Tribe. Badlands National Park currently has 3,050 acres of prairie dogs in the North Unit, and 1,408 acres of prairie dogs in the South Unit, based on GPS mapping conducted during the spring of 2001, producing an estimated total of 4,458 acres within the North and South Units of Badlands National Park (D. Albertson, pers. comm.). Badlands National Park does not currently have a specific prairie dog management plan (D. Albertson, pers. comm.).

Prairie dog inventories have been conducted with GPS mapping following the active burrow line and the vegetation clip line. Prairie dog density estimates are derived from two published techniques, Biggins et al. (1993) for burrow line transects and Severson and Plumb’s (1998) visual count model. Badlands National Park’s prairie dog management direction allows for natural population expansion or contraction within the park’s interior, with a prairie dog objective of 4,000-5,000 acres. Prairie dogs have been live-trapped for use as food for black-footed ferrets on park boundaries adjacent to private lands. Future resolution of this potential conflict will involve live-trapping and translocation to the park’s interior. Current prairie dog research activities include the efficacy of trapping and translocation to control migration onto adjoining private lands, ungulate-prairie dog-plant interactions in Badlands National Park, and the study of dispersal rates and distances of individual prairie dogs from coteries in relation to disease events (D. Albertson, pers. comm.).

5. Wind Cave National Park

Wind Cave National Park occupies 28,295 acres, with an estimated current prairie dog acreage of 1,580 acres and a tentative prairie dog acreage goal of 1,500-2,000 acres (B. Muenchau, pers. comm). Previous estimates included 1,216 acres in 1994 based on GPS mapping and 1,296 acres in 1995 based on photointerpretation of infrared photography. All towns were GPS-mapped during 2000 based on vegetation clip lines and presence of active prairie dog burrows. Wind Cave's most recent Prairie Dog Management Plan (WICA-N-0001) is outdated, and staff are developing a revised plan that will incorporate the concept of expansion of prairie dogs within the interior of Wind Cave.

An upcoming research project will be conducted by Lisa Savage of Colorado State University on "The Effects of Fragmentation on the Population Genetics of Black-tailed Prairie Dogs." Primary research objectives include delineation of the relationship between the factors of genetic variability, degree of isolation of a given colony, colony size, and extinction risk in prairie dog metapopulations. Savage will be examining prairie dog populations in fragmented vs. unfragmented colonies in plague-free and plague-affected areas and will include study sites at Wind Cave National Park, an additional South Dakota area, and two areas in Colorado (B. Muenchau, pers. comm.).

Wind Cave will comply with a National Park Service goal of maintaining and restoring black-tailed prairie dog populations. Wind Cave will control prairie dogs in specific situations, such as sites with potential human health hazards and areas where prairie dogs conflict with other park management objectives. Wind Cave will continue to practice its Good Neighbor Policy in considering prairie dog control when prairie dogs expand onto adjoining private lands. Wind Cave personnel suggest that these adjoining private lands be considered for financial incentive payments or prairie dog easements, if such programs are instituted, to enhance existing, contiguous colonies (B. Muenchau, pers. comm).

6. Bureau of Reclamation

Bureau of Reclamation lands in South Dakota presently have an estimated 65 acres of prairie dogs. These lands are managed in cooperation with SDGFP (K. Parr, pers. comm.)

7. Nebraska National Forest

Nebraska National Forest lands include 590,000 acres on Buffalo Gap National Grassland and 116,000 acres on Fort Pierre National Grassland. Current prairie dog acreage estimates are 625 acres on Fort Pierre, based on on-the-ground mapping and digitizing in 1999 and 15,000 acres on Buffalo Gap, based on GPS mapping in 1998 and 1999. The previous prairie dog management direction (USDA-Forest Service 1988) has been revisited, and a new prairie dog management decision is forthcoming. The final environmental impact statement for revised national grassland management plans anticipates that with very limited prairie dog control, prairie dog colonies will expand on Buffalo Gap to 22,000-36,000 acres and on Fort Pierre to 1,200-1,900 acres during the next ten years (J. Sidle, pers. comm.)

Prairie dog management scenarios recommended for consideration by Nebraska National Forest staff include establishment of regulated shooting and control guidelines to protect prairie dog ecosystem-dependent species, potential use of Sikes Act management areas for shooting to generate funding for conservation easements, easement or walk-in shooting areas on private lands adjacent to public lands, and coordination with USDA APHIS – Wildlife Services for prairie dog control on private lands adjacent to public lands (B. Perry, pers. comm.)

Sidle et al. (in press) described results of an aerial survey to estimate the extent of black-tailed prairie dog colonies in the Northern Great Plains using a stratified aerial line intercept technique. The study area included portions of Nebraska, South Dakota, North Dakota, and Wyoming between 98°09’W and 107°22’W longitude. Their method was similar to techniques used to estimate vegetative canopy cover. Sidle flew along transect lines, using a GPS receiver to record intersections with prairie dog colony boundaries. Transects were stratified into high- and low-density strata. High-density strata were based on areas with known prairie dog colonies. Low-density areas contained no known prairie dog colonies. High density transects covered a stratum area of 10,712 km^2 and were flown at 0.86 km intervals. Low-density transects covered a stratum area of 358,199 km^2 area and were flown at 13.85 km intervals. For the area sampled, South Dakota prairie dog acreage coverage was estimated at 576 km^2 (222.3 mi^2) of active colonies and 152.9 km^2 (61.2 mi^2) of inactive colonies. Sidle estimated South Dakota’s prairie dog acreage at 142,300 acres, with a standard error of 7% (J. Sidle, pers. comm.).

8. Grand River National Grassland

Grand River National Grassland covers approximately 154,200 acres in Perkins and Corson counties. Current prairie dog acreage is approximately 1,600 acres; an estimate derived from the grassland's draft Land Management Plan. Inventory methods include colony identification from the air and on-the-ground knowledge of town locations, followed by mapping with GPS units. The current Forest Plan describes an acceptable prairie dog acreage for Grand River National Grassland as 1,000 acres at a time when known acreage was 2,107 (Forest Service 1986). The draft revised plan contains no maximum acreage objectives. The preferred alternative contains a prediction of 1,500-3,700 prairie dog acres in 10 years. Grand River National Grassland has applied for a grant to research water quality, which will include an examination of sheet erosion from active prairie dog towns. The grassland plans to complete a site-specific prairie dog management plan in the next two years. The plan will address buffers, shooting restrictions, conservation easements, and habitat management within a landscape context. The south half of Grand River National Grassland will receive increased management attention for expanding black-tailed prairie dogs (D. Svingen, pers. comm.)

9. The Nature Conservancy

The Nature Conservancy (TNC) is a private, non-profit organization dedicated to the conservation of worldwide biological diversity. This mission is achieved with land acquisition and management, through various cooperative endeavors with land managers and landowners, and with a variety of stewardship and data collection efforts. TNC owns or has primary management responsibility for approximately 15,710 acres in South Dakota. The largest property within the range of the black-tailed prairie dog in South Dakota is the Whitney Preserve, currently 4,601 acres in size (B. Paulson, pers. comm.).

TNC recently completed an ecoregional conservation planning effort for the Northern Great Plains Steppe Ecosystem. This planning effort was not intended to be a land acquisition blueprint, but rather a tool for a variety of innovative conservation tools. The Northern Great Plains Steppe Ecosystem includes the majority of western South Dakota outside of the Black Hills and a portion of northcentral South Dakota east of the Missouri River. The planning effort included identification of "primary conservation target species." The black-tailed prairie dog was one of six mammal species identified as target species. This species is an important component of the following "ecologically significant areas" in South Dakota described in this plan: Grand River National Grassland, Harding County – Slim Buttes, Bad River Prairie, Badlands National Park Complex, Cheyenne River – Cherry Creek, White River, and Thunder Basin – Cheyenne River. Future management planning efforts at these sites will incorporate the needs of the black-tailed prairie dog ecosystem (Martin 1999).

10. Bad River Ranches

The Bad River Ranches, owned by R. E. Turner, occupy an estimated 140,000 acres in portions of Jones and Stanley counties. Prairie dogs currently occupy 854 acres; an estimate based on a 1999 aerial survey and annual GPS mapping (K. Bly Honness, pers. comm.). Inventory methods include visual counts described Severson and Plumb (1998) to determine minimum population densities of prairie dogs. The average density of prairie dogs in colonies on the Bad River Ranches in 2000 was ~28 per acre. Restoration work carried out by the Turner Endangered Species Fund involves establishing a prairie dog complex, through translocations, suitable for a future black-footed ferret reintroduction. In the future, 10% or more of the Bad River Ranches could support prairie dogs based in part on a GIS prairie dog habitat suitability model of the ranch (M. Phillips, pers. comm.). Management principles and planned actions for prairie dog restoration on Turner properties are included in a ten-year draft management plan (Truett 2000).

11. Yankton Agency

The Yankton Agency, Bureau of Indian Affairs, occupies 36,000 acres, including one 20-acre prairie dog town. Prairie dog management is not addressed in land management plans, but limited shooting is allowed on this town (L. Thompson, pers. comm.).

12. Other tribal and trust lands in South Dakota

In an attempt to assemble a description of the current status of prairie dog management planning and acreage estimates within South Dakota's boundaries, SDGFP contacted Native American tribes in central and western South Dakota in February 2000. The information from the Yankton Agency is the only acreage information received from South Dakota tribes. The Crow Creek Sioux Tribe and the Lower Brule Sioux Tribe responded to SDGFP with similar messages; i.e., these tribes will not share prairie dog acreage data with the State of South Dakota, they do not wish to be involved in the statewide prairie dog planning effort, and they will be working with the Service in developing individual Candidate Conservation Agreements with Assurances. A similar message was shared at a July 14, 2000 meeting of the South Dakota Prairie Dog Working Group by representatives of Cheyenne River Sioux Tribe's Prairie Management Program and the Rosebud Sioux Tribe (H. Dikeman, pers. comm., B. Whiting, pers. comm.). The Lower Brule Sioux Tribe has subsequently provided information on prairie dog acreage and specific planning activities.

Because of the intermingling of private and tribal lands within reservation boundaries and the need for meaningful ecosystem planning, the State of South Dakota is hopeful that cooperative prairie dog management planning with Native American tribes will occur. The State of South Dakota will encourage the Service to serve in its capacity as an intermediary between the State and the South Dakota tribes.

IV. Conservation Strategies

IV-A Prairie dog acreage goal

Objective 1: Determine a statewide population goal and identify prairie dog focus areas by June 2002.

Strategy 1.1: Review scientific and popular literature for historical prairie dog acreage.
Strategy 1.2: Determine current prairie dog acreage in South Dakota.
Strategy 1.3: Investigate potential existing data sources for use in setting prairie dog acreage goals.
Strategy 1.4: Coordinate state population goals with standards established by Interstate Black-tailed Prairie Dog Conservation Team.
Strategy 1.5: Coordinate with federal, state, and tribal land managers in establishing acreage goals and focus areas.
Strategy 1.6: Establish focus area management goals, monitoring schedules, and management strategies.
Strategy 1.7: Complete necessary formal agreements associated with focus area management.
Strategy 1.8: Implement legal measures to assist in meeting and maintaining statewide population goal.

IV-B Population monitoring

Objective 2. Determine an effective population monitoring tool by June 2002.

Strategy 2.1: Evaluate existing data sources for their usefulness in monitoring prairie dog populations.
Strategy 2.2: Evaluate supplemental data sources for their usefulness in monitoring prairie dog populations.
Strategy 2.3: Implement selected monitoring tool to estimate South Dakota’s prairie dog populations at three-year intervals.
Strategy 2.4: Evaluate effectiveness of selected monitoring tool by comparison with other data sources.

IV-C Disease monitoring and contingency plan

Objective 3. Develop a disease monitoring protocol by January 2002 for detecting sylvatic plague and other diseases detectable on prairie dog colonies, to include a contingency plan in case sylvatic plague is detected in South Dakota.

Strategy 3.1: Review existing information on plague occurrence in South Dakota.
Strategy 3.2: Survey other wildlife agencies for input on protocol development.

Strategy 3.3: Contact wildlife disease experts for input on protocol development.
Strategy 3.4: Contact state human health officials for input on protocol development.
Strategy 3.5: Contact SDGFP Wildlife Damage Management staff and APHIS-Wildlife Services staff for input on incorporating protocol into existing activities.
Strategy 3.6: Develop plague contingency plan, to include consideration of prairie dog colony dusting, quarantine procedures, follow-up surveillance strategies, public awareness strategies, and interagency coordination, particularly with agricultural interests.
Strategy 3.7: Participate in national plague reporting system established by Interstate BTPD Conservation Team.

IV-D Landowner incentive program

Objective 4. Develop a private landowner incentive program by June 2002 to further statewide prairie dog management goals (implementation goal – October 2002).

Strategy 4.1. Determine landowner attitudes about prairie dogs and acceptance conditions.
Strategy 4.2. Build coalition of landowners and other affected parties to support legislative efforts to establish private landowner incentive program.
Strategy 4.3. Review existing and potential revenue sources to determine funding level for private landowner incentive program.
Strategy 4.4. Develop priorities for apportioning available funding for private landowner incentive program.
Strategy 4.5: Design and implement specifics of private landowner incentive program, if funded, to include eligibility requirements, deadlines, and contact information.
Strategy 4.6: Evaluate effectiveness of private landowner incentive program following completion of first major sign-up increment; i.e., five- or ten-year easement period.

IV-E Public outreach

Objective 5. Increase public awareness of positive and negative impacts of prairie dog ecosystem (timeframe – ongoing).

Strategy 5.1. Establish a South Dakota Prairie Dog Working Group.
Strategy 5.2. Develop priorities for enhancing public awareness.
Strategy 5.3: Implement public awareness activities of highest priority and those most easily incorporated into existing information outlets.
Strategy 5.4. Develop public involvement plan to target landowners and managers in and near prairie dog focus areas
Strategy 5.5: Evaluate effectiveness of public outreach efforts.

IV-F Research needs

Objective 6. Identify and prioritize research needs in South Dakota for consideration by state, tribal, and federal agencies and private entities interested in prairie dog management (timeframe – ongoing).

Strategy 6.1. Summarize results of relevant studies conducted in South Dakota.
Strategy 6.2. Determine perceived research priorities among a group of interested and informed participants.
Strategy 6.3. Seek additional, specific input on research priorities from wildlife and range science researchers.
Strategy 6.4. Make research priority lists available to individuals, agencies, and universities.
Strategy 6.5: Prepare pre-proposals for highest priority topics to make use of available research funding sources.
Strategy 6.6: Investigate opportunities for multi-state or multi-agency research projects.

IV-G Wildlife components of prairie dog ecosystem

Objective 7. Determine and attempt to accommodate conservation needs of species dependent on prairie dog ecosystem (timeframe – ongoing).

Strategy 7.1. Review available information on state status of species dependent on prairie dog ecosystem.
Strategy 7.2. Determine inventory needs for species dependent on prairie dog ecosystem.
Strategy 7.3. Incorporate conservation needs of dependent species into prairie dog management opportunities.
Strategy 7.4. Investigate opportunities for cooperative conservation activities.

IV-H Evaluation of planning effort

Objective 8. Use adaptive management method to evaluate progress of prairie dog planning effort and adjust as needed to accomplish program goals.

Strategy 8.1. Formulate interagency team to review progress toward meeting objectives at three-year intervals to coincide with population monitoring intervals.

IV-I Relevance of conservation strategies in addressing federal listing factors

IV. Conservation Strategies

IV-A. Prairie dog acreage goal

Objective 1: Determine a statewide population goal and establish prairie dog focus areas by June 2002.

Strategy 1.1: Review scientific and popular literature for historical prairie dog acreage.

Progress toward objective:

A companion document (Dowd Stukel 2001) describes a number of publications relevant to historical prairie dog acreage in South Dakota. Each estimate of historical abundance, whether based on landscape features, plant communities, estimates by local weed and pest or animal damage personnel, or prairie dog acreage controlled, has inherent biases and limitations. It is unlikely that agreement will ever be reached on estimated historical prairie dog acreage in South Dakota, although the Service presented the best available information in its 12-Month Finding (Service 2000).

Strategy 1.2: Determine current prairie dog acreage in South Dakota.

Progress toward objective:

Section IIIB of this document describes current inventory efforts and estimated prairie dog acreage by agency, with the exception of Native American tribes in South Dakota, which are largely providing their information directly to the U.S. Fish and Wildlife Service.

Although not specifically a prairie dog inventory, Sidle et al. (in press) described results of a survey to estimate the extent of black-tailed prairie dog colonies in the Northern Great Plains using a stratified aerial line intercept technique. For the area sampled, South Dakota prairie dog acreage coverage was estimated at 576 km^2 (222.3 mi^2) of active colonies and 152.9 km^2 (61.2 mi^2) of inactive colonies at the time of the 1997-1998 fieldwork. Sidle estimated South Dakota's prairie dog acreage at 142,000 acres, with a standard error of 7% (J. Sidle, pers. comm.).

A second source of information is a summary of responses received by the U.S. Fish and Wildlife Service used in preparing a draft "Evaluation of opportunities for development of umbrella candidate conservation agreement with assurances for the black-tailed prairie dog in South Dakota." This document has been distributed at several black-tailed prairie dog coordination meetings during 2000 to serve as a potential template for candidate conservation agreement with assurances planning in South Dakota. In the document, the USFWS states that: "Until statewide and site specific estimates can be fine-tuned and are consistent with each other, we will assume a statewide estimate of 160,000 acres for Tribal and non-tribal lands. This estimate is within the standard error noted by USFS and includes an additional 5,000 acres occupied habitat that is believed to be scattered throughout the western half of the State. The State (non-tribal) portion of this total is estimated to be 68,500 acres."

For planning purposes the SDGFP, SDDA, and the SD Prairie Dog Working Group accepted the Sidle et al. estimate of 142,000 acres, with a standard error of 7% as a minimum population estimate for 2000.

Strategy 1.3: Investigate potential existing data sources for use in setting prairie dog acreage goals.

Progress toward objective:

Figures 1-2 and Tables 2-4 contain information related to an evaluation of the use of cropland capability classes and their relationship to suitable prairie dog habitat in South Dakota. Although this data source was examined, SDGFP has chosen to adopt the prairie dog acreage goal generated with the use of Bailey's ecoregion concept (See Strategy 1.4).

With assistance from David Schmidt, NRCS State Range Conservationist, SDGFP has evaluated the use of cropland capability classes (Table 2) as an indication of suitable prairie dog habitat in South Dakota. Cropland capability classes I, IIc, IIe, IIIc, IIIe, and IVe were included for counties west of the Missouri River and counties adjoining the Missouri River in eastern South Dakota as far east as Charles Mix County (Figure 1 and Table 3). The assumption is that limitations to crop cultivation, such as slope; topographic features; and soil depth, drainage, and other soil characteristics also limit prairie dog occupation to some extent.

Using this technique, a total of 12,435,800 acres are considered suitable prairie dog habitat in the area analyzed. A breakdown by general land ownership for these counties is included in Table 4.

Figure 1. Counties included in analysis of cropland capability classes as indicators of suitable black-tailed prairie dog habitat in South Dakota

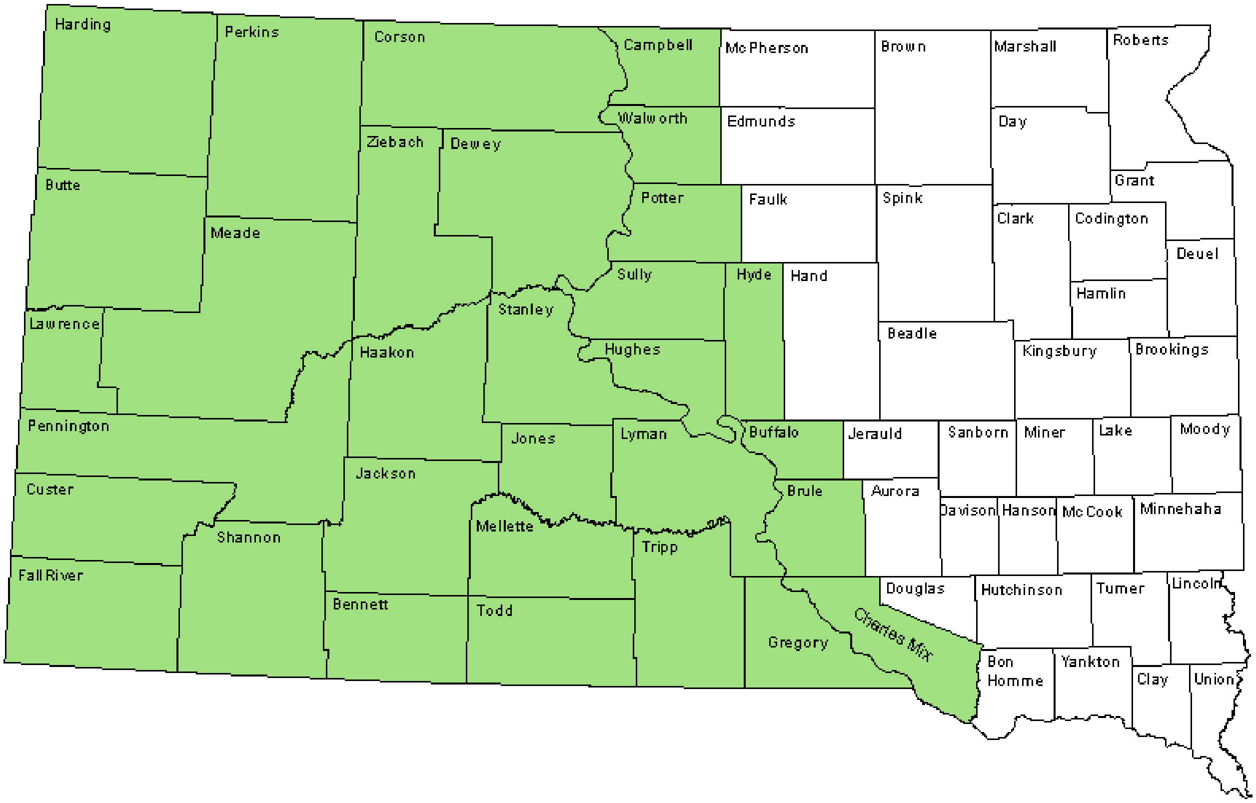


Figure 2. South Dakota’s physiographic regions (Van Bruggen 1985)

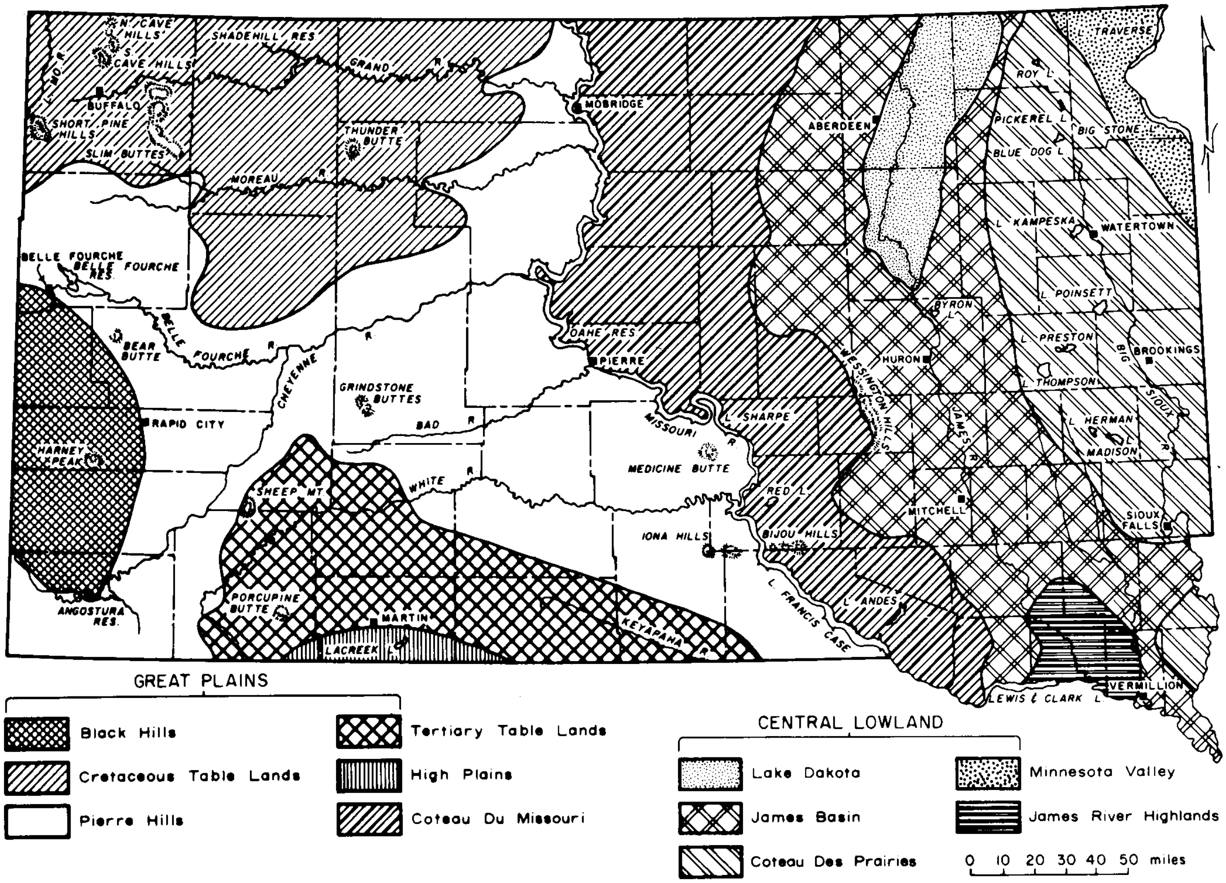


Table 2. Definitions of capability classes and subclasses used by Natural Resources Conservation Service in soil survey development (Bachman 1990)

Class I	Soils have few limitations that restrict their use.
Class II	Moderate limitations that reduce the choice of plants or that require moderate conservation practices.
Class III	Soils have severe limitations that reduce the choice of plants or that require special conservation practices, or both.
Class IV	Soils have very severe limitations that reduce the choice of plants or that require very careful management, or both.
Class V	Soils are not likely to erode but have other limitations, impractical to remove, that limit their use.
Class VI	Soils have severe limitations that make them generally unsuitable for cultivation.
Class VII	Soils have very severe limitations that make them unsuitable for cultivation.
Class VIII	Soils and miscellaneous areas have limitations that nearly preclude their use for commercial crop production.
Subclass modifiers	e: main limitation is risk of erosion unless close-growing plant cover is maintained w: water in or on the soil interferes with plant growth or cultivation s: soil is limited mainly because it is shallow, droughty, or stony c: chief limitation is climate that is very cold or very dry

Table 3. Suitable prairie dog acreage in South Dakota as determined by analysis of cropland capability classes.

Cropland Capability Units - I, IIc, IIe, IIIc, IIIe, IVe								
		Cultivated	**Non-Cult.**			**Minor**		
County	**Code**	**Cropland**	**Cropland**	**Pastureland**	**Rangeland**	**Land Uses**	**CRP**	**Total (A)**
Bennett	46007	118,600	20,200	32,100	122,400	0	7,900	301,200
Brule	46015	194,100	42,600	18,600	101,100	9,500	5,800	371,700
Buffalo	46017	37,200	14,400	5,100	80,200	2,800	2,900	142,600
Butte	46019	21,800	49,500	15,300	196,300	0	13,300	296,200
Campbell	46021	173,000	33,200	9,000	95,900	4,800	27,900	343,800
Charles Mix	46023	337,900	41,900	61,900	59,900	11,800	5,700	519,100
Corson	46031	134,800	81,700	25,300	334,900	9,800	60,700	647,200
Custer	46033	7,600	15,100	23,300	162,300	1,900	0	210,200
Dewey	46041	129,200	51,600	14,300	197,600	0	54,800	447,500
Fall River	46047	41,700	19,900	38,400	187,100	500	400	288,000
Gregory	46053	97,400	47,200	27,200	59,400	8,000	800	240,000
Haakon	46055	189,000	50,800	37,200	271,900	3,700	43,600	596,200
Harding	46063	65,100	53,900	27,100	546,300	1,400	19,800	713,600
Hughes	46065	191,200	7,400	1,300	96,500	4,200	2,100	302,700
Hyde	46069	90,800	19,400	26,100	215,200	9,100	8,600	369,200
Jackson	46071	81,900	54,400	25,800	248,200	2,100	25,600	438,000
Jones	46075	90,400	15,300	12,900	73,400	2,300	27,400	221,700
Lawrence	46081	6,500	16,200	21,400	12,900	1,500	0	58,500
Lyman	46085	185,700	7,400	0	112,100	12,400	74,600	392,200
Meade	46093	183,500	157,400	25,400	467,100	13,100	16,700	863,200
Mellette	46095	104,000	13,200	4,900	146,200	3,200	7,100	278,600
Pennington	46103	102,400	38,700	26,100	252,500	3,100	600	423,400
Perkins	46105	118,400	22,400	72,200	535,300	1,500	55,600	805,400
Potter	46107	253,000	5,800	16,600	78,700	11,800	36,800	402,700
Shannon	46113	51,800	11,600	11,500	170,200	6,500	7,300	258,900
Stanley	46117	115,700	27,400	5,100	122,200	3,500	30,800	304,700
Sully	46119	373,300	12,400	17,800	79,100	11,200	15,500	509,300
Todd	46121	24,600	66,600	24,600	255,600	3,800	0	375,200
Tripp	46123	169,700	95,400	20,300	194,400	13,600	50,400	543,800
Walworth	46129	195,200	5,900	11,200	81,100	6,800	31,800	332,000
Ziebach	46137	86,300	4,600	10,200	318,600	1,800	17,500	439,000
TOTAL		**3,971,800**	**1,103,500**	**668,200**	**5,874,600**	**165,700**	**652,000**	**12,435,800**

Table 4. General land ownership for counties considered within the state distribution range for black-tailed prairie dog.

County	Code	County Land Area Non Federal	County Land Area Federal	County Land Area Total	Tribal Trust Land Total[1]
Bennett	46007	745,800	16,300	762,100	248,985
Brule	46015	533,900	7,900	541,800	0
Buffalo	46017	304,000	8,000	312,000	68,237
Butte	46019	1,290,200	160,300	1,450,500	0
Campbell	46021	482,800	10,900	493,700	0
Charles Mix	46023	716,900	19,300	736,200	36,701
Corson	46031	1,570,500	48,400	1,618,900	546,011
Custer	46033	594,800	403,100	997,900	0
Dewey	46041	1,525,900	39,400	1,565,300	837,299
Fall River	46047	821,700	297,800	1,119,500	0
Gregory	46053	661,500	12,700	674,200	23,621
Haakon	46055	1,165,800	3,800	1,169,600	1,091
Harding	46063	1,611,100	102,600	1,713,700	0
Hughes	46065	499,400	12,900	512,300	33,777
Hyde	46069	554,000	700	554,700	24,188
Jackson	46071	1,075,700	122,000	1,197,700	416,678
Jones	46075	601,900	20,000	621,900	0
Lawrence	46081	238,100	274,100	512,200	0
Lyman	46085	986,900	105,700	1,092,600	115,735
Meade	46093	2,147,500	81,400	2,228,900	757
Mellette	46095	838,300	0	838,300	284,820
Pennington	46103	1,014,500	767,500	1,782,000	0
Perkins	46105	1,705,000	145,200	1,850,200	480
Potter	46107	570,400	4,600	575,000	0
Shannon	46113	1,202,300	139,600	1,341,900	1,105,706
Stanley	46117	893,800	77,100	970,900	29,094
Sully	46119	645,100	40,000	685,100	0
Todd	46121	889,500	700	890,200	502,256
Tripp	46123	1,035,200	0	1,035,200	66,639
Walworth	46129	468,900	7,400	476,300	0
Ziebach	46137	1,258,900	2,700	1,261,600	555,407
TOTAL		**28,650,300**	**2,932,100**	**31,582,400**	**4,897,482**

[1] Source: Dept. of the Interior, Bureau of Indian Affairs w[1]eb-site, www.doi/gov/bia/realty/report97.html

Strategy 1.4: Coordinate state population goals with standards established by Interstate Black-Tailed Prairie Dog Conservation Team.

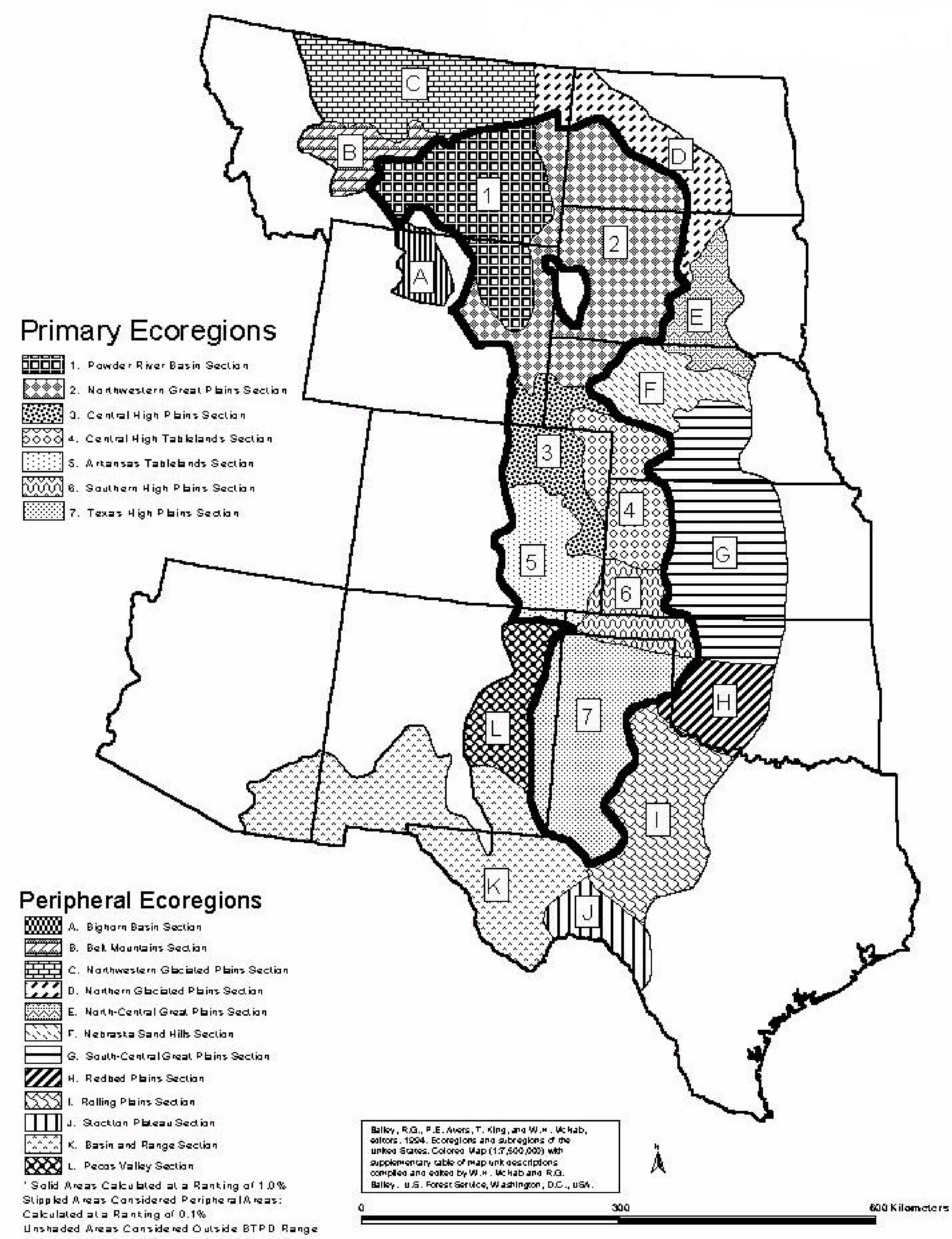
Progress toward objective:

SDGFP has participated in interstate prairie dog management planning since 1998, when representatives from the state wildlife and agriculture departments from South Dakota, Wyoming, and Montana met in Gillette, Wyoming. SDGFP has also participated in the Interstate Black-tailed Prairie Dog Conservation Team since its inception. In this role, SDGFP has participated in developing and testing various proposals for setting a national standard for prairie dog acreage goals as a percentage of historical potential habitat.

During a March 8-9, 2001 meeting of the Interstate BTPD Team, Team members evaluated the usefulness and biological defensibility of Bailey's ecoregions (Bailey et al. 1994) as a base map for determining state and rangewide prairie dog acreage goals (Figure 3). Acreages by ecoregion were determined for each state. A rank of 0.1 or 1.0 was assigned based on the relative importance of an ecoregion to prairie dogs. Four ecoregions found in South Dakota occur within the historical range of the black-tailed prairie dog and were ranked according to their suspected importance to prairie dog distribution. Since the northwestern great plains ecoregion section contains the majority of South Dakota's prairie dog range, this technique apportions 1% of this acreage to the state's historical prairie dog goal. Acreages in other ecoregion sections on the periphery of the state's prairie dog range are apportioned at a rate of 0.1% to the state's prairie dog goal. Using this technique, South Dakota's estimated statewide acreage goal is 220,681 (Table 5). NOTE: The Black Hills ecoregion section was not included during the mapping analysis with Bailey's ecoregion, even though black-tailed prairie dogs occur within this area. This omission will be remedied during the next mapping analysis, and South Dakota's prairie dog acreage goal will increase slightly as a result.

Using acreage estimates determined by cropland capability classes in central and western South Dakota, a goal of 220,681 acres represents 1.8% of suitable habitat. Assuming a current estimate of 160,000 acres, this goal is a 38% increase in statewide acreage. To accommodate the separate prairie dog planning by Native American tribes in South Dakota, the acreage goal of 220,681 must in some way be apportioned between tribal and nontribal lands. A subgroup of the Resource Staff (Appendix 8) has agreed to work cooperatively on apportionment of acreages between tribal and nontribal lands. Preliminary discussions have resulted in an estimate that approximately 15% of potential prairie habitat in South Dakota occurs on tribal lands, resulting in an acreage goal on nontribal lands (federal, state, and private lands combined) of 187,579 acres.

Figure 3. Bailey’s Ecoregions overlaid on black-tailed prairie dog range.



' Solid Areas Calculated at a Ranking of 1.0%
Stippled Areas Considered Peripheral Areas:
Calculated at a Ranking of 0.1%
Unshaded Areas Considered Outside BTPD Range

Bailey, R.G., P.E. Avers, T. King, and W.H. McNab, editors. 1994. Ecoregions and subregions of the United States. Colored Map (1:7,500,000) with supplementary table of map unit descriptions compiled and edited by W.H. McNab and R.G. Bailey. U.S. Forest Service, Washington, D.C., USA.

Table 5. State acreage goal components by ecoregions within historical black-tailed prairie dog range in South Dakota

Ecoregion sections	Rank	Total acres in ecoregion in SD within historical prairie dog range[1]	Ranked acres in ecoregion in SD[2]
Black Hills[3]	N/A		
Central Dissected Till Plains	N/A		
Northcentral Glaciated Plains	N/A		
Northeastern Glaciated Plains	N/A		
Western Glaciated Plains	N/A		
Red River Valley	N/A		
Nebraska Sand Hills	0.1	131,297	131 (131,297 * .001 = 0.1%)
Northcentral Great Plains	0.1	8,146,940	8,147 (8,146,940 * .001 = 0.1%)
Northern Glaciated Plains	0.1	2,560,201	2,560 (2,560,201 * .001 = 0.1%)
Northwestern Great Plains	1.0	20,984,316	209,843 (20,984,316 * .01 = 1%)
TOTAL		**31,822,754**	**220,681**

[1] Includes acres within specific ecoregion sections, regardless of prairie dog occupancy.

[2] Ranked acreage formulas determined by relative importance of the ecoregion section to prairie dogs.

[3] The Black Hills were not included in the initial calculation, but will be added when revised figures are available.

Strategy 1.5: Coordinate with federal, state, tribal, and private land managers in establishing acreage goals and focus areas.

Progress toward objective:

SDGFP has sought input from state, federal, tribal, and private landowners with land holdings large enough to warrant prairie dog conservation plans or to support long-term management areas (focus areas). A subgroup of the Resource Staff has agreed to work cooperatively on determining the appropriate allocation of acreage goals between tribal and nontribal lands. This subgroup includes representatives of the Service, the Bureau of Indian Affairs, The Nature Conservancy, and SDGFP. SDGFP will continue to work with interested cooperators in delineating focus areas and in identifying priority areas for landowner incentive funding.

A preliminary list of management areas of ≅5,000 acres by landowner is as follows*:

site	location	owner
Badlands National Park	Pennington, Jackson, and Shannon cos.	National Park Service
Fall River Ranger District	Fall River County	Nebraska National Forest
Wall Ranger District	Custer, Jackson, and Pennington cos.	Nebraska National Forest

*Several potential focus areas exist on tribal lands in South Dakota, which will be addressed by individual tribes in cooperation with the U.S. Fish and Wildlife Service.

A preliminary list of management areas of >1,000 acres but <5,000 acres by landowner is as follows:

site	location	owner
Wind Cave National Park	Custer County	National Park Service
Grand River National Grassland	Perkins County	Custer National Forest
Bad River Ranches	Jones and Stanley cos.	Ted Turner

Strategy 1.6: Assist with establishment of focus area management goals, monitoring schedules, and management strategies.

Strategy 1.7: Complete necessary formal agreements associated with focus area management.

Strategy 1.8: Implement necessary legal measures to assist in meeting and maintaining statewide population goal.

SDGFP and SDDA have various authorities to implement needed legal measures to help meet and maintain population goals on lands under state jurisdiction in South Dakota. The following substrategies detail progress to date in exercising these authorities.

NOTE: When the private landowner incentive program is being developed for South Dakota, the issues of prairie dog shooting and prairie dog control restrictions will be considered as they relate to individual landowner agreements. A specific issue to resolve will be whether a landowner meeting prairie dog acreage goals on his or her property will be subject to Strategies 1.8a and 1.8c.

Strategy 1.8a: Establish a prairie dog shooting closure to protect litters.

Progress toward objective:

On January 11, 2001, the South Dakota Game, Fish and Parks Commission finalized a proposal to prohibit prairie dog shooting on public lands in South Dakota from March 1 through June 14. This closure will allow litters to be reared by females before shooting begins. The closure does not apply to private or tribal lands, which may implement their own closures. The closure is in addition to year-round shooting restrictions on state parks and recreation areas, lands owned by the National Park Service and U.S. Fish and Wildlife Service, and black-footed ferret reintroduction areas, presently located on Cheyenne River Reservation and Conata Basin, located within the Forest Service's Buffalo Gap National Grassland.

Since shooting restrictions on nontribal lands can be made via SDGFP Commission action, more restrictive closures could be implemented if needed due to major population declines.

Strategy 1.8b: Determine an alternative to state declared pest species status.

Progress toward objective:

Senate Bill 64 (Appendix 3) was signed by Governor Bill Janklow on March 5, 2001 and became effective on July 1, 2001. This bill was designed to replace the state pest status of the black-tailed prairie dog in South Dakota with the designation of "species of management concern." Follow-up actions included preparation of rules by the South Dakota Departments of Agriculture and Game, Fish and Parks for implementing this law, which will treat prairie dog complaints as nuisance cases for civil resolution, as contrasted with the former punitive aspect of the pest species designation.

The South Dakota Game, Fish and Parks Commission finalized its rule creating the species of management concern category at the June 7-8, 2001 meeting (Appendix 4). Administrative Rule 41:10:03:01 (Appendix 5) became effective on August 28, 2001, which resulted in the removal of the black-tailed prairie dog from the state list of declared animal pests.

Strategy 1.8c: Provide a minimum base population level at which prairie dog control with pesticides will be affected to help assure that a minimum population will be maintained in South Dakota.

Progress toward objective:

The South Dakota Departments of Agriculture and Game, Fish and Parks have determined a minimum prairie dog population range to be used as a baseline below which prairie dog control with pesticides will be affected. This population level will be based on population estimates for prairie dogs occurring on private, federal and state lands. Tribal land acres will not be included in this minimum population threshold. However, privately held land in Indian Country would be included.

Progress toward objective:

The Departments of Agriculture and Game, Fish and Parks agree to draft administrative rules to limit pesticide use for the control of prairie dogs if the prairie dog population level falls below minimum thresholds established.

Under the proposed rules the following triggers would be in place based on the prairie dog population:

a) If the prairie dog population drops below 75,000 acres - the South Dakota Department of Agriculture will discontinue the manufacture and sale of its Zinc Phosphide Prairie Dog Bait and discontinue the sale of any other products used for prairie dog control.
b) If the prairie dog population continues to drop below 65,000 acres - after deliberations with the South Dakota Department of Game, Fish and Parks, the South Dakota Department of Agriculture will promulgate rules to prohibit the use of all pesticide control products used for the control of prairie dogs in South Dakota. Exceptions may need to be made in certain situations where human health would become an issue. These rules would remain in effect until the prairie dog population recovered to 85,000 acres.

General authority to promulgate rules is provided under §1-26. Chapters 38-21-15 and 38-21-51(3) also provide pesticide rule-making authority to the secretary of agriculture under these conditions. As with all administrative rules, the proposed rules will include a public hearing after appropriate notice is given.

IV-B. Population monitoring

Objective 2: Determine an effective population monitoring tool by June 2002.

Strategy 2.1: Evaluate existing data sources for their usefulness in monitoring South Dakota's prairie dog populations.

Progress toward objective:

In December 2000, SDGFP contracted with the Wildlife and Fisheries Sciences Department at South Dakota State University to conduct a feasibility study to determine whether landsat satellite imagery is a viable alternative for prairie dog population monitoring in western South Dakota (Project No. W-75-R, Amendment No. 134, Study No. 100). SDSU staff are working with the U.S. Geological Survey's EROS Data Center in Garretson, South Dakota and coordinating with personnel in other states also involved in this task. The specific study objective is to determine the season when spectral, chromatic and infrared characteristics of satellite imagery differentiate prairie dog towns from other western South Dakota land or vegetation categories.

The study area includes Wind Cave National Park, Badlands National Park and portions of Buffalo Gap National Grassland. Six high-resolution scenes are being photo-interpreted and accuracy assessed with ground-truthing and compared to digital data collected by the Forest Service for Buffalo Gap National Grassland. The study will be completed by December 31, 2001, when project leaders Jon Jenks and Dan Hubbard will make a recommendation to SDGFP on the usefulness of this technique for western South Dakota.

If this technique does not prove useful or feasible for population monitoring in South Dakota at three-year intervals, SDGFP will explore other options, such as a partnership arrangement with other agencies as proposed by John Sidle, US Forest Service, using Ikonos satellite imagery with designated sites for ground-truthing and evaluation at established intervals.

Strategy 2.2: Evaluate supplemental data sources for their usefulness in monitoring South Dakota's prairie dog populations

Progress toward objective:

Following discussions at several South Dakota Prairie Dog Work Group meetings, SDGFP and SDDA met to discuss the need for monitoring and estimating the amount of chemical control of prairie dogs being conducted in South Dakota. SDGFP will provide the expertise of Larry Gigliotti, Planning Coordinator and Human Dimensions Specialist, to help SDDA design a valid annual survey of certified pesticide applicators to estimate prairie dog toxicant use in South Dakota.

SDGFP will conduct an annual prairie dog shooting survey to estimate shooting mortality and other aspects of prairie dog shooting, such as activity by month, total days of participation, and landownership of lands visited. The survey sample will be derived from predator/varmint licensees and a sample of small game licensees. Survey results will provide an estimate of the number of prairie dog shooters, total days of shooting, and total prairie dogs taken by shooters.

Tables 6 and 7 include results from 2000, based on a survey of holders of the following license types: Predator/Varmint, Combination, Junior Combination, and Resident and Nonresident Small Game (Gigliotti, 2001).

Table 6. Total number of recreational days and total number of prairie dogs killed in South Dakota in 2000 by state licensed hunters.

License Type	**Recreation Days (excluding tribal)**	**Prairie Dogs Killed (excluding tribal)**
Resident Predator/Varmint ONLY	**1,034 (936)**	**19,278 (17,447)**
Nonresident Predator/Varmint ONLY	**5,177 (4,773)**	**250,388 (230,858)**
Resident Combination License	**58,587 (56,185)**	**552,129 (529,492)**
Resident Small Game License	**16,953 (16,173)**	**247,489 (236,105)**
Resident Junior Small Game License[1]	**13,299 (12,674)**	**110,861 (105,650)**
Nonresident Small Game License[2]	**4,000 (4,000)**	**66,720 (66,720)**
Total Number[3]	99,050 DAYS	1,246,865
Total on Non-tribal Land	**94,741 Days**	**1,186,272**

[1] Includes Resident Youth Small Game License (n=8,999)

[2] Includes Nonresident Youth Small Game License (n=2,489)

[3] Total does not include the number killed by hunters/shooters on tribal lands that do not have a valid South Dakota state hunting license.

Table 7. Total estimated number of prairie dogs killed in South Dakota (2000) by state licensed hunters.

Land Type	Estimated Number of Prairie Dogs Killed		
	RESIDENTS	**NONRESIDENTS**	**TOTAL**
Private Land	737,742	263,545	1,001,287
Public Land	141,873	32,781	174,654
Tribal Land[1]	41,061	19,530	60,591
Don't Know	9,078	1,252	10,330
Total	929,754	317,108	**1,246,862**
Estimated kill on non-tribal land	888,693	297,578	**1,186,271**

[1] This does not include the number of prairie dogs killed by shooters that do not have a valid South Dakota hunting license; i.e., shooters with <u>only</u> a tribal license.

Strategy 2.3: Implement selected monitoring tool to estimate South Dakota’s prairie dog populations at three-year intervals.

Strategy 2.4: Evaluate effectiveness of selected monitoring tool by comparison with other data sources.

Progress toward objective:

SDGFP will continue to participate on the Interstate Black-tailed Prairie Dog Conservation Team to benefit from findings in other states related to effective population monitoring tools.

IV-C. Disease monitoring and contingency plan

Objective 3: Develop a disease monitoring protocol by January 2002 for detecting sylvatic plague and other diseases detectable on prairie dog colonies, to include a contingency plan in case sylvatic plague is detected in South Dakota.

Strategy 3.1: Review existing information on plague occurrence in South Dakota.

Progress toward objective:

In association with the black-footed ferret reintroduction on the Conata Basin/Badlands site in South Dakota, carnivores have been sampled for diseases during 1990 and from 1993 through 2001. To date, plague has been detected at only extremely low levels among predators. Plague has not been detected in prairie dogs that died during quarantine periods or were found dead on-site (Williams et al. 1991, Williams et al 1996, Williams et al. 1998).

The second black-footed ferret reintroduction project in South Dakota began in 2000 on the Cheyenne River Sioux Tribe Reservation. An associated activity has been predator sampling for disease analysis, which begin in 1999. No plague has been detected to date (H. Dikeman, pers. comm.).

Strategy 3.2: Survey other agencies for input on protocol development.

Strategy 3.3: Contact wildlife disease experts for input on protocol development, including the need to monitor other diseases potentially dangerous to prairie dogs, such as turlaremia.

Strategy 3.4: Contact state human health officials for input on protocol development.

Progress toward objective:

The Interstate Black-tailed Prairie Dog Team is presently drafting plague-monitoring protocol. In association with this activity, SDGFP contacted the South Dakota Department of Health for information on human health aspects of this disease. Dr. Lon Kightlinger, SD Department of Health, shared a copy of the protocol that his agency follows (CDC 1996). Dr. Kightlinger also summarized plague occurrence in humans in South Dakota in an email dated October 8, 2001, in which he stated: “There has not been a case of human plague in South Dakota since 1923, according to our records.”

Strategy 3.5: Contact SDGFP Wildlife Damage Management staff and APHIS-Wildlife Services staff for input on incorporating protocol into existing activities.

Strategy 3.6: Develop plague contingency plan, to include consideration of prairie dog colony dusting, quarantine procedures, follow-up surveillance strategies, public awareness strategies, and interagency coordination, particularly with agricultural interests.

Strategy 3.7: Participate in national plague reporting system established by Interstate BTPD Conservation Team.

IV-D. Landowner incentive program

Objective 4: Develop and implement a private landowner incentive program to further statewide prairie dog management goals by June 2002 (implementation goal – October 2002).

This objective is dependent upon whether additional acres must be protected/managed on private lands in South Dakota in addition to commitments made by cooperating public and private entities. Suggested components of a landowner incentive program will be solicited from the South Dakota Prairie Dog Work Group and will benefit from experiences of other agencies involved in implementing similar or comparable programs. General components will include voluntary participation, proximity to identified focus areas, specific legal description of enrolled land, prairie dog acreage to be maintained on enrolled land, allowable activities on enrolled land, and responsibilities for prairie dog control within and adjacent to the enrolled land.

Strategy 4.1: Determine landowner attitudes about prairie dogs and acceptance conditions.

Progress toward objective:

Gigliotti (1998) analyzed results of an attitude survey on environmental and wildlife attitudes of South Dakota residents. Eighty-seven percent of respondents who identified themselves as farmers or ranchers agreed or strongly agreed that wildlife presence on their property was important to them. When the same individuals were asked if financial incentives would encourage them to protect or restore wildlife habitats on their properties, 65.1% agreed or strongly agreed, and 26.4% were uncertain. These results indicate that enhancement or protection of prairie dogs on private lands in South Dakota likely depend greatly on financial incentive payments.

Strategy 4.2: Build coalition of landowners and other affected parties to support legislative efforts to establish private landowner incentive program.

Strategy 4.3: Review existing and potential revenue sources to determine funding level for private landowner incentive program.

Strategy 4.4: Develop priorities for apportioning available funding for private landowner incentive program.

Progress toward objective:

SDGFP participated in the development of a multi-state grant proposal titled “Conserving black-tailed prairie dog populations through private landowner incentives,” which was submitted to the U.S. Fish and Wildlife Service for funding through the State Wildlife Grants Program. The objective of this proposal is to restore and provide long-term protection for approximately 217,000 acres of black-tailed prairie dog habitat on private lands, with a three-year goal of restoring and protecting 650,000 acres of occupied private land habitat. Assuming this grant has a successful outcome, SDGFP proposes to apportion the private landowner incentive funds in the following general step-down manner:

First priority: Private lands identified as focus areas and private lands adjacent to federal or state lands that are identified as prairie dog focus areas in the context of statewide planning. SDGFP will depend on input from government agencies via specific maps that indicate current and recent prairie dog occupancy. These sites are considered first priority for private landowner funding for the following reasons:

- These general areas are likely to be identified as long-term prairie dog management areas by government agencies, with dedicated funds for inventory and management;
- These private land areas are likely to be sites with chronic prairie dog migration patterns;
- SDGFP and SD Department of Agriculture are legally required to control prairie dogs moving from public onto adjacent private lands.

Second priority: Private lands intermingled with tribal prairie dog sites involved in black-footed ferret reintroduction or covered by a Candidate Conservation Agreement with Assurances (CCAA). Limited funding will not allow private landowner incentives for all private lands intermingled with tribal lands, so this priority is an attempt to identify those situations where these incentives could be applied.

Third priority: Other private lands.

Potential participants will be evaluated based on the following criteria:

- colony or complex size;
- location of property and proximity to other prairie dog complexes;
- presence of state or federal sensitive, candidate or listed species;
- evaluation of potential population threats, including sylvatic plague, toxicant use, and shooting;
- sociological factors, such as level of support of surrounding landowners.

At the time of preparation of this draft plan, no legal document had been signed between SDGFP and any South Dakota tribe agreeing to cooperative prairie dog management. If such a future agreement is reached, the funding prioritization described above will change to reflect an expansion beyond nontribal private lands.

<u>Strategy 4.5</u>: Design and implement specific private landowner incentive program, if funded, to include eligibility requirements, deadlines and contact information.

<u>Strategy 4.6</u>: Evaluate effectiveness of private landowner incentive program following completion of first major sign-up increment; i.e., five- or ten-year easement period.

IV-E.   Public outreach

Objective 5: Increase public awareness of positive and negative impacts of prairie dog ecosystem (timeframe – ongoing).

Strategy 5.1: Establish South Dakota Prairie Dog Working Group

Progress toward objective:

The South Dakota Prairie Dog Working Group was formed as a citizens working group representing a cross section of interests to provide input in the development of a South Dakota Black-tailed Prairie Dog Management Plan, which will follow the *Black-tailed Prairie Dog Conservation Assessment and Strategy*.

On December 23, 1999 SD Secretary of Agriculture Darrell Cruea and SD Secretary of Game, Fish and Parks John Cooper invited 12 South Dakotans to participate on a citizen advisory group called the South Dakota Prairie Dog Working Group. The Working Group met for the first time on February 15, 2000, when ground rules and general agreements were reached under the facilitation of Donna Fjelstad of Coterie Consulting (Appendices 6 and 7). Personnel from state, federal, and tribal agencies and private organizations constitute resource personnel, who assist the Working Group by providing technical information and advice (Appendix 8).

The Working Group met 9 times during 2000 and will continue to meet as necessary to provide citizen input on state prairie dog management planning. Primary discussion topics during 2000 were prairie dog shooting regulations, alternatives to prairie dog designation as a statewide declared animal pest, techniques for determining current prairie dog acreage, strategies for providing balanced information in public outreach activities, and private landowner incentives.

Strategy 5.2: Develop priorities for enhancing public awareness

Progress toward objective:

Ten general strategies were taken from the *Black-tailed Prairie Dog Conservation Assessment and Strategy*, with slight revisions. Appendix 7 contains each strategy, followed by suggested activities or guidelines for implementing the strategy in South Dakota.

Strategy 5.3: Implement public awareness activities of highest priority and those most easily incorporated into existing information outlets.

Beginning in 2001 and each year thereafter, SDGFP will send results of prairie dog shooting survey to all survey participants, which will include additional information about current prairie dog topics.

Strategy 5.4. Develop public involvement plan to target landowners and managers in and near prairie dog focus areas

Strategy 5.5: Evaluate effectiveness of public outreach efforts.

IV-F. Research Needs

Objective 6: Identify and prioritize research needs in South Dakota for consideration by state, tribal, and federal agencies and private organizations interested in prairie dog management (timeframe – ongoing).

Strategy 6.1: Summarize results of relevant studies conducted in South Dakota

Progress toward objective:

A companion document (Dowd Stukel 2001) includes summaries of a number of studies related to the prairie dog ecosystem in South Dakota. This review will be revised as new studies are conducted and as additional reports are made available to SDGFP.

Strategy 6.2: Determine perceived research priorities among group of interested and informed participants

Progress toward objective:

Research topics identified in Van Pelt (1999) were circulated to members of South Dakota's Prairie Dog Working Group and Resource Staff (Appendices 7 and 8) for prioritization as research topics of high, medium, and low importance. Appendix 9 indicates with the use of asterisks the number of times a specific topic was rated high, medium, or low.

Strategy 6.3: Seek additional, specific input on research priorities from wildlife and range science researchers.

Strategy 6.4: Make research priority lists available to individuals, agencies, and universities.

Strategy 6.5: Prepare pre-proposals for highest priority topics to make use of available research funding sources.

Strategy 6.6: Investigate opportunities for multi-state or multi-agency research projects.

IV-G. Wildlife components of prairie dog ecosystem

Objective 7. Determine and attempt to accommodate conservation needs of species dependent on prairie dog ecosystem (timeframe – ongoing).

Strategy 7.1. Review available information on state status of species dependent on prairie dog ecosystem.

Progress toward objective:

Although many species may inhabit prairie dog colonies at various times, few are as dependent on the prairie dog ecosystem in South Dakota as the black-footed ferret and burrowing owl.

The black-footed ferret is a federal and state endangered species. Its state heritage rank is G1/S1, indicating imperiled global and state statuses because of extreme rarity or because certain factors make it especially vulnerable to extinction. Heritage ranks range from 1 to 5, with 1 assigned to species that are most imperiled and 5 assigned to species that are most abundant and secure.

The black-footed ferret was considered extirpated in South Dakota prior to reintroduction into the Conata Basin/Badlands site located in portions of Badlands National Park and Buffalo Gap National Grassland, Wall Ranger District. The second reintroduction in South Dakota began in 2000 on the Cheyenne River Reservation. Both reintroduction projects have the advantage of using black-tailed prairie dog habitat that is presently plague-free and that is distributed in large, densely-populated colonies.

The burrowing owl is monitored by the South Dakota Natural Heritage Program. Its state heritage rank is G4/S3S4B/SZN. This status indicates that it is globally secure, although the species may be rare in parts of its range and a cause for long-term concern. The S3S4 breeding rank indicates that state nesting populations may be locally abundant but are distributed within a restricted range or vulnerable to extinction and cause for long-term concern. The SZN portion of the rank indicates that the species does not winter in South Dakota or occur in protectable nonbreeding populations. The burrowing owl is included on sensitive species lists for Bureau of Land Management lands in South Dakota and South Dakota portions of Black Hills National Forest, Custer National Forest, Dakota Prairie Grasslands, and Nebraska National Forest.

Strategy 7.2. Determine inventory needs for species dependent on prairie dog ecosystem.

Black-footed ferret populations resulting from reintroductions on the Conata Basin/Badlands site and Cheyenne River Reservation are presently being monitored with spotlight surveys and snowtracking surveys at a minimum. Other monitoring techniques have included reading implanted transponder chips and radio telemetry. An additional method of detecting movements has been reports from adjoining landowners, particularly near the Conata Basin/Badlands site. As reintroduced populations expand beyond the designated experimental areas, cooperating agencies will need to determine monitoring strategies for black-footed ferret populations. These strategies and respective agency roles have not yet been determined.

The South Dakota Breeding Bird Atlas project included fieldwork from 1988-1993 to document statuses of breeding bird species in the state. A total of 25 burrowing owl nests were confirmed, 53 nests were judged probable, and 33 nests were considered possible. Evidence of burrowing owl nesting was documented in 28 of South Dakota’s 66 counties (Peterson 1995).

Analyses of breeding trends for the burrowing owl indicate a negative trend on USFWS Breeding Bird Surveys conducted in South Dakota, although the trends were not statistically significant. From 1966-1999, the survey trend for the burrowing owl in South Dakota was -7.1, interpreted as estimated percent change per year (Sauer et al. 2000). Considering that breeding bird survey routes are located along permanent roads, this species is likely not adequately sampled with this method. Specific surveys of prairie dog or ground squirrel colonies are needed to determine breeding trends at a more specific level than those detected during USFWS breeding bird surveys.

<u>Strategy 7.3</u>. Incorporate conservation needs of dependent species into prairie dog management opportunities.

<u>Progress toward objective</u>:

Although smaller prairie dog complexes may be considered for future black-footed ferret reintroductions, projects to date have occurred on large (>10,000 acres) prairie dog complexes. Therefore, commitments to maintain substantial prairie dog complexes on public and private lands in South Dakota will likely benefit reintroduced populations of black-footed ferrets. In addition, disease monitoring (Objective 3) will help detect prevalence of plague and canine distemper, diseases with serious ramifications for black-footed ferrets.

Griebel (2000) studied nesting burrowing owls on black-tailed prairie dog colonies on the Wall Ranger District of Buffalo Gap National Grassland. A description of pertinent findings is included in Dowd Stukel (2001). A finding of interest to prairie dog colony conservation planning pertained to colony size. When data were analyzed at the colony level, larger prairie dog colonies with sufficient desirable habitat for nest spacing allowed early arrivers to select the most desirable colonies and experience the highest reproductive success. Larger colonies allowed lower nesting owl pair densities, larger mean clutch sizes, and a larger number of fledged young.

Although his study began soon after the Forest Service closed certain prairie dog colonies to recreational shooting, Griebel speculated that shooting restrictions on Buffalo Gap are benefiting nesting burrowing owls. SDGFP and other agencies receive a number of anecdotal reports each year of burrowing owls being killed by prairie dog shooters. The extent of direct loss or indirect impacts of shooting disturbance to nesting burrowing owls is unknown and a potential research need in planning for the conservation needs of this species.

Increased efforts to provide long-term commitments to prairie dog colonies, in some cases in areas closed to recreational shooting, are likely to benefit burrowing owls nesting in South Dakota.

Strategy 7.4. Investigate opportunities for cooperative conservation activities.

Progress toward objective:

This is an ongoing activity, and SDGFP has worked cooperatively with a number of entities on projects of mutual interest in the area of rare species conservation. A firmer commitment in terms of specific plans and concomitant funding will hopefully broaden SDGFP’s ability to participate in future activities that benefit species dependent on the prairie dog ecosystem.

IV-H. Evaluation of planning effort.

Objective 8. Use adaptive management method to evaluate progress of prairie dog planning effort and adjust as needed to accomplish program goals.

Strategy 8.1. Formulate interagency team to review progress toward meeting objectives at three-year intervals to coincide with population monitoring intervals.

IV-I. Relevance of conservation strategies in addressing federal listing factors

In its Notice of 12-Month Petition Finding (USFWS 2000), the U.S. Fish and Wildlife Service described threats to the black-tailed prairie dog as follows:

- habitat loss and fragmentation (moderate magnitude);
- overutilization via recreational shooting (low magnitude);
- disease (moderate magnitude);
- inadequate existing regulatory mechanisms (moderate magnitude);
- control programs conducted largely in response to concerns related to potential forage competition with domestic livestock (moderate magnitude).

Habitat loss and fragmentation:

On a national scale, pastureland acres declined by 12 million acres and rangeland acres declined by nearly 11 million acres from 1982-1997. Most of the declines in pastureland and rangeland acreage resulted from conversion to cultivated cropland. At a state level, South Dakota's pastureland acreage declined from 2,710,900 acres to 2,108,200 acres (22%) from 1982 to 1997. South Dakota's rangeland acreage declined from 22,965,700 acres to 21,876,400 acres (5%) during the same time frame (NRCS 2000).

Considering the array of economic and demographic factors involved in land conversion, South Dakota's prairie dog management plan is unlikely to significantly alter land conversion. However, the private landowner incentive program (Conservation Strategy D) will potentially influence landowners to maintain rangeland acres if acres qualify for the incentive payments. In addition, public outreach efforts (Conservation Strategy E) that present a balanced message about prairie dogs will allow landowners to make informed decisions about land conversion.

Overutilization via recreational shooting:

On January 11, 2001, the South Dakota Game, Fish and Parks Commission finalized a proposal to prohibit prairie dog shooting on public lands in South Dakota from March 1 through June 14 (Objective 1.8a and Appendix 2). This closure will allow litters to be reared by females before shooting begins. The closure does not apply to private or tribal lands, which may implement their own closures. In addition to the shooting closure, the SDGFP has begun annual surveys of prairie dog shooters to help determine impacts of this activity (Strategy 2.2).

Disease:

Conservation Strategy C addresses the need for a coordinated system to monitor sylvatic plague in South Dakota. Because of the presence of two reintroduced black-footed ferret populations, this monitoring system will also include canine distemper.

Inadequacy of existing regulatory mechanisms:

Senate Bill 64 (Objective 1.8b and Appendix 3) was signed by Governor Bill Janklow on March 5, 2001 and became effective on July 1, 2001. This bill will replace the state pest status of the black-tailed prairie dog in South Dakota with the designation of “species of management concern.” The South Dakota Departments of Agriculture and Game, Fish and Parks have prepared rules for implementing this law, which will treat prairie dog complaints as nuisance cases for civil resolution, as contrasted with the former punitive aspect of the pest species designation.

The South Dakota Game, Fish and Parks Commission finalized its rule creating the species of management concern category at the June 7-8, 2001 meeting (Appendix 4). The Administrative Rule that designated the black-tailed prairie dog as a species of management concern became effective on August 28, 2001, an action that removed this species from the state list of declared pests (Appendix 5).

Control programs conducted largely in response to concerns related to potential forage competition with domestic livestock (moderate magnitude):

In its draft proposal for a range-wide approach to BTPD management, the Interstate BTPD Conservation Team included recommended scenarios for implementation when state population estimates fall to certain levels and appear to be declining further. Strategy 1.8c in this draft plan describes proposed scenarios for limiting pesticide control of prairie dogs in South Dakota under at various population levels.

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Appendix 1. South Dakota Department of Game, Fish and Parks Rodent Control Policy

DIRECT CONTROL

The Department of Game, Fish and Parks will provide “Direct Control,” at no initial cost to the landowner, when rodents encroach on their private land from adjacent, previously uncontrolled public land. Once control has been achieved on both the private and public land, maintenance responsibility will then become the responsibility for the landowner.

TECHNICAL ASSISTANCE PROGRAM

The Department of Game, Fish and Parks will provide “technical assistance” to landowners in controlling large rodent colonies. Rodent infested lands, 160 acres or larger in size, will qualify for assistance from our field personnel. This will include equipment and manpower to supervise in both pre-bait and bait application. Landowners will be responsible for cost of bait material and will be required to do the bait application. Follow-up treatment and continued maintenance will also be the responsibility of the landowner.

EXTENSION CONTROL

The Department of Agriculture and Department of Game, Fish and Parks will jointly develop and “Extension Control” program. This will include the services of the county agent and local Weed and Pest Control boards. Educational programs as well as actual field demonstrations will be made available upon request. We will be able to show landowners proper bait application, timing of application, necessity for pre-baiting and desirable bait quality, all necessary for good, consistent control. This function will be for those who do not have a problem too large for them to handle themselves.

Established by the Joint Review Committee -- 1984

Appendix 2. SDGFP Commission action finalized on January 11, 2001 to establish a regulated prairie dog shooting season on public lands

GAME, FISH AND PARKS COMMISSION ACTION
FINALIZATION
Prairie Dog Shooting Season
Chapter 41:06:57

Commission Meeting Dates:	**Proposal**	**December 7-8, 2000**	**Pierre**
	Public Hearing	**January 11-12, 2001**	**Pierre**
	Finalization	**January 11-12, 2001**	**Pierre**

COMMISSION PROPOSAL

Establish a prairie dog shooting season as follows:

Open unit: Statewide except Conata Basin* in the Buffalo Gap National Grasslands

Season: Closed beginning March 1, 2001, through April 30, 2001;
Open beginning May 1, 2001, through February 28, 2002, and June 15 through last day of February thereafter, except that landoperators** may shoot anytime on the land they own or operate. This is not in Conata Basin.

Daily and possession limits: No restrictions

Shooting hours: No restrictions

License requirements: Residents: Predator/varmint license, or
Any resident hunting license or the furbearer license

Nonresidents: Nonresident predator license, or
Any nonresident hunting license

* Conata Basin is described as that portion of Buffalo Gap National Grassland east and south of Badlands National Park, north of Pine Ridge Indian Reservation, and west of the Jackson County line.

** Landoperator is a person, and immediate family residing with the person, who owns or operates land.

STAFF COMMENTS

Proposed changes from last year: Provision for prairie dog shooting restrictions as noted above.

Recommended changes from proposal:

1. Change season closure so that it would apply only to public lands, and also not allow lessees of public land to shoot prairie dogs on public lands during the closed period.
2. End the season closure in 2001 on June 14 rather than April 30.

SUPPORTIVE INFORMATION

The black-tailed prairie dog is presently a federal candidate species. The U.S. Fish and Wildlife Service has determined that the species is warranted for listing as a federal threatened species, but its listing is precluded by higher endangered species listing priorities within the Service. South Dakota has been working cooperatively with 10 other states within the present and historical range of the black-tailed prairie dog to promote retention of state management authority for this species. An identified area of vulnerability for state wildlife agencies is the failure of agencies to set limits on prairie dog shooting. During periods of prairie dog abundance, lack of limits was rarely questioned. However, the spread of sylvatic plague within the range of the black-tailed prairie dog and the increasing rarity of several species dependent on prairie dogs have drawn attention to the issue of prairie dog shooting regulations. This vulnerability is enhanced by the fact that state agencies, such as the SD Department of Game, Fish and Parks, have not monitored the prairie dog populations on which the agencies have allowed unlimited take.

Resident prairie dog shooters in South Dakota must have a predator/varmint license, a furbearer license, or any resident hunting license. Nonresident prairie dog shooters must have a nonresident predator license or any nonresident hunting license. Tribal fish and game departments have their own license requirements. Prairie dogs can presently be shot at any time of the year in any quantity, except for closed areas such as state parks, national parks, and black-footed ferret reintroduction sites.

In the northern Great Plains, black-tailed prairie dog pups typically first appear above ground from mid-May to early June, or about 5-8 weeks after birth. They are weaned a week or more after emergence. The pups are approximately half the size of adults at the time of emergence aboveground and reach adult size by fall. A closure from March through June 15 would provide protection for young of the year following their emergence from natal burrows.

Gigliotti (Prairie Dog Shooting in South Dakota {1999}, HD-4-00.SAM) estimated that 19% of residents and 2% of nonresidents shot prairie dogs in 1999. Resident shooting activity was highest from June through October with an average of 2.6 months of prairie dog shooting during 1999. A small sample size did not allow the same estimates for nonresidents. After sampling adjustments were made, Gigliotti estimated that 17,800 resident prairie dog shooters and 3,319 nonresidents harvested an estimated1.4 million prairie dogs in South Dakota in 1999.

Some landowners shoot prairie dogs on their lands or allow shooters access to their lands to keep their local towns in check and perhaps avoid use of toxicants. For this reason, the shooting closure would not apply to landowners shooting prairie dogs on their own property. Also, since some landowners have already booked prairie dog hunters for May and June, 2001, these months will not be closed to hunting in 2001 but will be closed through June 15 thereafter, along with the months of March and April.

Appendix 3. South Dakota species of management concern bill (S-64)

State of South Dakota

SEVENTY-SIXTH SESSION
LEGISLATIVE ASSEMBLY, 2001

AN ACT

ENTITLED, An Act to authorize the Department of Agriculture and the Department of Game, Fish and Parks to designate certain species as needing both control and protection.

BE IT ENACTED BY THE LEGISLATURE OF THE STATE OF SOUTH DAKOTA:

Section 1. Terms used in this chapter mean:

(1) "Departments," the Department of Game, Fish, and Parks and the Department of Agriculture;

(2) "Species of management concern," a species designated by the secretary of the Department of Agriculture and the Game, Fish and Parks Commission as a species which shares the dual status of requiring both control and protection.

Section 2. The secretary of the Department of Agriculture and the Game, Fish and Parks Commission shall establish, by rules promulgated pursuant to chapter 1-26, a list of species of management concern. In determining whether a species should be listed, the following factors are to be considered:

(1) Whether the species or its habitat, or both are of value ecologically and aesthetically and at the same time burdensome for property owners; and

(2) Whether the species may warrant protection at times and control at others depending on the rate of reproduction, climate, disease, population viability, and other factors.

Section 3. Rules promulgated pursuant to section 2 of this Act shall be conducted jointly by both the Department of Agriculture and the Game, Fish and Parks Commission, including joint notice, publication, hearings, and decision-making.

Section 4. If so requested, the departments may render assistance and advice regarding species of management concern including:

(1) Providing information to the public and property owners regarding the species of management concern and its characteristics, ecosystem values, and habitat; and

(2) Providing assistance in the development of conservation plans or control projects regarding the species of management concern.

Section 5. The following acts or omissions constitute nuisances:

(1) Engaging in practices which allow or cause a species of management concern to encroach upon the property of another or injure or endanger the property of another; or

(2) Failure to control the species of management concern thereby causing encroachment on the property of another or causing injury to or endangering the property of another.

Section 6. In addition to any other remedies at law, the remedies set forth in chapter 21-10 apply to the nuisances described in section 5 of this Act. These remedies include civil action, including injunctive relief and recovery of damages, and abatement. Abatement, if ordered by the court, shall include reimbursement for any reasonable and necessary costs incurred in abating the nuisance.

Section 7. Designation as a species of management concern abrogates any previous designation as a weed or pest.

Appendix 4. South Dakota Game, Fish and Parks Commission Action to create species of management concern rules.

GAME, FISH AND PARKS COMMISSION ACTION

FINALIZATION

Species of Management Concern

Chapter 41:15:01

Commission Meeting Dates:	**Proposal**	**May 3-4, 2001**	**Custer State Park**
	Public Hearing	**June 7-8, 2001**	**Lemmon**
	Finalization	**June 7-8, 2001**	**Lemmon**

COMMISSION PROPOSAL

Establish black-tailed prairie dogs (Cynomys ludovicianus) as a species of management concern.

STAFF COMMENTS

Proposed changes from last year: Establishment of this chapter and designation of black-tailed prairie dog as a species of management concern as noted above.

Recommended changes from proposal: None.

SUPPORTIVE INFORMATION

Legislation enacted this year allows the GFP Commission and the Secretary of the Department of Agriculture to designate a species as a “species of management concern”. The legislation basically provides recognition that a species can have both positive and negative impacts and provides a process where both the GFP Commission and the Secretary of Agriculture, shall jointly add or remove a species to this list by formal rule. The law also more clearly defines how the species is considered nuisance as it applies to civil court action and removes the species from the list of noxious weeds and declared pests.

Prairie dogs clearly meet these categories. In cooperation with the Dept. of Agriculture, we are both working to make this a joint rule process.

Finally, this action will remove prairie dogs from the declared pest list while still providing a measure of protection for private landowners. Not having prairie dogs listed as a declared pest also helps with our efforts to better manage the species and hopefully assists in efforts to avoid listing the species as a federally threatened species.

Appendix 5. Administrative Rule to establish species of management concern list

CHAPTER 41:10:03
SPECIES OF MANAGEMENT CONCERN

Section 41:10:03:01 List of species of management concern.

41:10:03:01. List of species of management concern. The following species of animals, which are determined by the Department of Agriculture and the Game, Fish and Parks Commission to be valued ecologically and aesthetically, burdensome at times for property owners, and subject to and warranting protection and control at certain times, are deemed to be species of management concern:
(1) Black-tailed prairie dog, ***Cynomus ludovicianus***.

Source: 28 SDR 24, effective August 28, 2001.

General Authority: SDCL 34A-8A-2.

Law Implemented: SDCL 34A-8A-2.

Appendix 6. Ground rules and general agreements of South Dakota Prairie Dog Working Group

GROUND RULES

1. Press releases will be agreed upon by the group.
2. There will be no individual or individual group statements.
3. There will be respect for individual and individual group opinions.
4. The group will operate from a consensus model with a "set aside" for serious conflict issues.
5. The emphasis is on the work group itself and staff will serve primarily as resources.
6. It is understood that our mission is to provide input and recommendations and that our results go to the Secretaries of the Departments of Game, Fish and Parks and Agriculture and ultimately the Governor for the final say.
7. The Facilitator, Donna Fjelstad, is in charge.

GENERAL AGREEMENTS:

1. The individuals present will constitute the core group of the "Statewide Prairie Dog Working Group."
2. Focus will be on ALL prairie dogs in the state regardless of residence.
3. There will be continuation of invitation and information to the tribes.
4. Others may be included for dissemination of information or as they are invited and choose to participate in the sharing of information. Those groups include: Tribes (Standing Rock, Cheyenne River, Lower Brule, Crow Creek, Rosebud and Pine Ridge), US Fish and Wildlife Service, USDA Forest Service, USDI Bureau of Indian Affairs, USDI Bureau of Land Management, USDI Park Service, USDI Bureau of Reclamation, South Dakota School & Public Lands.
5. While the next meeting needs to be held in Pierre, there is a need for discussion and consideration of other locations including somewhere near prairie dog habitat.
6. A time (thirty minutes) should be allowed for public comment prior to each PDWG meeting.

Appendix 7. Public awareness strategies for South Dakota.

1. Develop and distribute informational brochures targeting general public and land managers.
   - Brochures will emphasize need for prairie dog conservation and contain description of prairie dog natural history and lists of beneficial and detrimental management practices.
   - Management discussions will include practices allowing for livestock and prairie dog management and incorporation of nonlethal prairie dog control and concepts of integrated pest management.
   - Brochure will recognize potential detrimental impacts and benefits of prairie dogs to private landowners and explain state management needs and challenges.

   SD-specific ideas:
   - Important to determine target audience and specific message.
   - History must be accurate and supportable.
   - State management plan explanation should state clearly that prairie dog acreage will have upper and lower limits and that control will be implemented at upper limit level.
   - Investigate whether there are balanced information pieces that could be customized for South Dakota; i.e., "Prairie Dogs and Their Ecosystem," University of Nebraska, Lincoln.
   - Brochure should be short, neutral, and linked to appropriate web-sites.
   - Cooperate with stockgrowers and local agricultural programs, such as Bootstraps.

2. Develop and distribute fact sheet explaining effects of sylvatic plague on prairie dog colonies and possible transmission to humans.

   SD-specific ideas:
   - If funding and expertise are available, include fact sheet in a larger information package about wildlife diseases and related precautions to avoid infection.
   - Use maps to show advance of plague, such as at 50-year intervals.
   - Investigate whether an existing fact sheet could be customized for South Dakota.
   - Support program to support research on ways to control plague.
   - Fact sheet should be specific to South Dakota and plague.

3. Distribute state updates to public and private land managers within the state's prairie dog range.
   - Update would inform land managers of conservation issues and new technology related to prairie dog conservation.
   - Update would serve as avenue for working group members to solicit and receive input from stakeholder groups.

   SD-specific ideas:

- Determine outlet for this information, such as a web-site, newsletters, distribution through county extension agents, NRCS range managers, etc.
- Maintain current information.
- Use annual or semi-annual update that will be made available for publication in various outlets, such as the “South Dakota Conservation Digest.”
- Integrate into appropriate web-sites, such as those maintained by the SD Department of Agriculture and the SD Department of Game, Fish and Parks.
- Encourage constructive input from stakeholder groups.

4. Use demonstration areas to inform land managers about prairie dog habitat components, prairie dog habitat management approaches, and other integrated uses of prairie dog colonies, such as livestock grazing.

   <u>SD-specific ideas:</u>
   - Solicit input from Nebraska National Forest, Wind Cave National Park, and Badlands National Park for specific sites to serve as demonstration areas. National Grassland site could serve as a demonstration area representing a large prairie dog complex.
   - Use demonstration area to demonstrate the concepts of Integrated Pest Management, with such components as grazing management and non-chemical lethal prairie dog control.
   - Determine if prairie dog demonstration areas are appropriate components of such events as Rangeland Days, etc.
   - Develop a South Dakota-specific list of species associated with prairie dogs.
   - Explore concept of “Prairie Ecosystem Rancher of the Year” award.

5. Use newspaper, radio, and television media to share information about prairie dog management.

   <u>SD-specific ideas:</u>
   - Seek expertise in developing a communications plan and media strategies.
   - Investigate appropriateness of existing media outlets, such as agriculture and sports shows, “Ag-Day” on South Dakota Public Television and Tony Dean’s radio and television shows.

6. Integrate prairie dog conservation into existing school curricula. Components may include development of teacher packet for use during prairie dog colony visits and video on prairie dog ecology and controversy.

   <u>SD-specific ideas</u>:
   - Promote and assist with class field days.
   - Determine ways to integrate balanced prairie dog management message into existing outlets, such as Project Learning Tree, Project WILD, the Natural Source, and South Dakota Game, Fish and Parks’ Outdoor Campus.

- Use existing news and video development services, such as the Agriculture Communications Office at South Dakota State University, South Dakota Public Television, Greater Dakota News Service, and South Dakota Department of Game, Fish and Parks.
- Determine whether existing prairie dog ecology video is appropriate for South Dakota.
- Ensure that a balanced message is presented.
- Don't limit the strategy to the black-tailed prairie dog alone. Education units could focus on grasslands or prairie, with the prairie dog as a component.
- Videos could be produced at different levels, with a higher level video used at farm and ranch organization meetings.

7. Develop and maintain database on historical and current prairie dog information.

   SD-specific ideas:
   - Assure that historical information is accurate and supportable.
   - Make use of current information of federal and tribal entities with active prairie dog monitoring programs.
   - Definitely needed to contain prairie dog acreage figures.
   - Integrate with strategy c.
   - Investigate whether an agency, such as U.S. Geological Survey-Biological Resources Division, is prepared to maintain a centralized database for information throughout the range of the black-tailed prairie dog.

8. Develop and maintain prairie dog web-site to present balanced messages about prairie dog ecosystem. Components may include updates from working group members and links to related web-sites.

9. Develop and distribute watchable wildlife maps to direct public to prairie dog viewing sites or areas closed to shooting.

   SD-specific ideas:
   - Work cooperatively with city and area tourism boards to distribute maps.
   - Work cooperatively with federal, tribal and private entities interested in promoting prairie dog ecosystem viewing opportunities.
   - Explore interest of private conservation organizations.

10. Conduct landowner meetings to identify issues and concerns and seek constructive solutions that are consistent with conservation objectives.

    SD-specific ideas:
    - Previous strategies (a-i) must have been productive to have constructive landowner meetings.
    - Determine schedules and specific focuses for meetings to assure they provide constructive input rather than serve as gripe sessions.
    - Highlight "habitat partners."

- Showcase balanced ranches with natural grazing systems.
- Develop and use a PowerPoint presentation.

Appendix 8. Membership of South Dakota Prairie Dog Working Group

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Appendix 9. Resource Staff for South Dakota Prairie Dog Working Group

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Appendix 10. Prioritization of prairie dog research topics by SD Prairie Dog Working Group and Resource Staff

	High	**Medium**	**Low**
Plague			
The extent and cycle of plague throughout the black-tailed prairie dog range.	****	*****	**
The amount of time needed for a prairie dog complex to fully recover from plague and whether smaller complexes are more vulnerable.	***	*****	***
The mechanisms that allow some prairie dogs to survive an epizootic within a colony; whether some individuals have a level of resistance to the disease.	****	*****	**
The effect of colony size and spacing on the severity of the spread of plague.	******	****	*
Whether plague is more virulent in the southern or western portion of the black-tailed prairie dog range.	**	***	******
The factors that have limited the spread of plague to areas and prairie dog colonies unaffected by the disease.	****	*****	**
The factors that allow plague to enter a prairie dog town; how plague affects the town and repopulation of the town.	****	******	*
Whether periodic dusting of burrows with an insecticide is an effective means of plague control; other potential methods of plague control.	*****	*****	*
Methods to monitor and control plague efficiently and economically.	******	****	*
Land Conversion/Loss of Habitat			
The importance of prairie dog occupied habitat patches in maintaining local populations of associated species.	***	****	***
Whether prairie dogs can be sustained in areas of repeated summer fallow or dry land cultivation.		***	*******
The degree to which black-tailed prairie dog populations are influenced by cattle and native grazing species.		****	*****
Whether habitat conditions can be altered to enhance reintroduction/translocation efforts once burrow systems have deteriorated.	**	*****	***
Grazing Competition			
Whether cattle and wild ungulates preferentially graze on prairie dog towns.	*******		****
Whether cattle grazing in pastures occupied by black-tailed prairie dogs gain as much weight as cattle grazing in similar pastures without prairie dogs.	********		***
Whether black-tailed prairie dog foraging and burrowing activities reduce grass and increase forb and shrub abundance and if range conditions improve with prairie dogs present.	******	**	***
Whether soil churning by prairie dogs increases plant diversity and nutrition, thereby benefiting cattle and other wildlife.	****	***	****
Whether the more closely cropped vegetation within a prairie dog town is substantially more nutritious than adjacent rangeland.	*******		****

Determine the occurrence of livestock injuring themselves in prairie dog burrows.	*****	*	******
Determine if the potential benefits of increased nutritional value of the vegetation when prairie dogs are present offsets the potential losses to forage quantity and availability for livestock when prairie dogs are absent.	********		***
Prairie Dog Control			
Whether prairie dogs are capable of population recovery following extensive control efforts.	****	*	******
Determine the effect of prairie dog poisoning on nontarget species.	****	**	*****
Determine the effective level of control for reducing potential competition with livestock.	*****	****	**
Whether nonlethal control measures are as effective as lethal methods.	*****	***	***
Determine the amount of time or minimal colony size needed for a prairie dog complex to recover following control efforts.	*****	***	***
Recreational Shooting			
Determine the degree of shooting pressure on prairie dogs that will force them to spend a greater proportion of time in alert postures and less time foraging.	*	***	*******
Determine the effect of colony population dynamics and colony maintenance by having prairie dogs spending more time in alert positions.	*	*****	*****
Whether there is a minimum threshold of prairie dogs required to keep vegetation clipped and to watch for predators, and if shooting reduces the prairie dog colony population below that threshold.	*	*****	*****
Whether intensive shooting has a statistically significant impact on the density and composition of local prairie dog colonies and social structure and interactions	***	*****	***
Determine the effects of shooting on other nontarget wildlife.	**	****	*****
Whether extensive shooting, especially of pregnant or nursing females, significantly reduces annual recruitment and the ultimate population dynamics of a colony.	**	****	*****
Population Viability Analysis			
Whether smaller isolated prairie dog towns have higher extinction rates than larger towns within complexes.	****	**	*****
Whether isolated prairie dog colonies result in the loss of additional genotypes.	*	***	*******
The minimum viable population.	***	***	*****
The degree of colony interconnectivity and maximum dispersal capabilities.	**	****	*****
The genetic integrity of the species.	*	***	*******
Relationship between colony size, isolation and spread of plague.	******	**	***
Prairie Dog Associated Species/Shortgrass Prairie Keystone Species			
Whether the estimated decline of occupied black-tailed prairie dog habitat in the Great Plains has initiated changes in ecosystem structure resulting in a decline of overall species diversity.	****	*****	**

Other prairie dog obligate species besides the black-footed ferret.	***	***	*****
Whether habitat associated species occur in higher densities on towns as opposed to on suitable habitat without prairie dog towns.	*	******	****
Whether suspected prey- and habitat-associated species abundance are linked to prairie dog towns throughout the entire prairie dog range or only in localized areas an situation.		*******	****
Ideal prairie dog complex size including town size and proximity for obligate species.	****	*****	**
Commercial Use of Prairie Dogs			
The amount of commercial trade that is occurring within each state.		*	**********
The effects of commercial take methods on nontarget species.		**	*********
Additional suggested topics: • Determine effects of Canada thistle expansion on prairie dog colonies. • Develop list of animal species found on a prairie dog town that are not found on a healthy prairie range site. • Evaluate economics of maintaining and growing prairie dogs on private land by developing cost and manpower requirements for prairie dog management, including easements, control, monitoring, etc. • Assess relative long- and short-range impacts to the species from chemical control vs. recreational shooting. • Evaluate burrowing owl populations in controlled and uncontrolled prairie dog colonies. • Prairie dog movement barriers (nonlethal barriers to prairie dog migration).			

3

The Role of Top Carnivores in Regulating Terrestrial Ecosystems

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The vast majority of species inhabiting the earth today have existed for more than a million years (Stanley 1987; May et al. 1995). Significantly, the last million years have been, climatically, among the most turbulent of the last 500 million years, with major and often abrupt changes in mean temperature, rainfall, glaciation, sea level, and extent of sea ice (Pielou 1991). Notwithstanding the extraordinary climatic instability of the recent past, extinction rates have not been particularly high (Coope 1995). In the absence of human beings, therefore, most plant and animal species are remarkably resilient to natural environmental instabilities of the kinds that prevailed over the Pleistocene era. How can we account for this resilience to extinction of wild species? If we knew the answer, it would be of immeasurable help in reducing the rate of extinction in our own time. Extinction rates are acknowledged to be hundreds or thousands of times higher today than they were in the prehuman past (Wilson 1992; May et al. 1995; Ehrlich 1995). Scores of studies have asked why a particular species or population went extinct or became endangered. In some cases—as in the overharvest of the dodo and great auk (Diamond 1982)—the cause is obvious. But in many others, it is hard to distinguish proximate from ultimate causes (Caughley 1994).

Both physical and biological processes are important in preserving biodiversity. An appropriate disturbance regime, for example, is considered essential to maintaining diversity in plant communities (Connell 1978). In a variant on the same theme, natural grasslands often depend on herbivores for opening sites that help plants colonize, but today livestock have widely replaced native herbivores—often with devastating impacts on plant communities. Predation can play an analogous role in reducing inter- and intraspecific competition for resources among prey species. Simple predator/prey models describe feedback processes leading to a stable point or stable limit cycle, in which the numbers of predators and prey come to equilibrium or oscillate within circumscribed limits. But widespread elimination of top predators from terrestrial ecosystems the world over has disrupted the feedback process through which predators and prey mutually regulate each other's numbers.

In this chapter we focus on predation as a key process in the natural maintenance of biodiversity. The role of predation has become a matter of intense interest to conservationists because mounting evidence, as we shall see, points to the pivotal role of predation in helping to preserve the biodiversity of terrestrial communities. On every continent, top predators are now restricted to tiny fractions of their former ranges so that the integrity of biological communities over large portions of the earth's terrestrial realm is threatened by grossly distorted predation regimes. Even where they are present, population densities of top predators tend to be so low, and their behavior so secretive, that sightings are infrequent. Most biologists prefer to study species that are common, small, and easily manipulated. Many academics dismiss field studies of large carnivores as "unscientific" because sample sizes are typically small and controlled experimentation difficult. Carnivore biology has thus been left to a small coterie of hardy devotees whose work, if not ignored, lies well outside the mainstream. The role that top predators play in terrestrial ecosystems, therefore, remains ill defined and contentious. (See Erlinge et al. 1984, 1988; Kidd and Lewis 1987; Terborgh 1988; Hunter and Price 1992; Power 1992; Strong 1992; Wright et al. 1994; Estes 1996.) At the end of a literature review, for example, Polis and Strong (1996) conclude "that trophic cascades and top-down community regulation as envisioned by trophic-level theories are relatively uncommon in nature." Here, after reviewing an overlapping body of literature, we come to the opposite conclusion.

Whether contentious or not, it is crucial to define the role of top predators because the stakes are enormous. If, as we conclude here, top predators are often essential to the integrity of ecological communities, it will be imperative to retain top predators or restore them to as many parts of the North American continent as practical. Failure to do so will result in distorted ecological interactions that, in the long run, will jeopardize biodiversity.

Theory

What is at issue in the current debate over "top-down" versus "bottom-up" processes (Matson and Hunter 1992)? "Top-down" means that species occupying the highest trophic level (top carnivores) exert a controlling influence on species at the next lower level (their prey) and so forth down the trophic ladder. The definition can be made operational in a thought experiment. Under top-down regulation, the removal of a top predator (or better, the entire guild of top predators) results in an appreciable population increase in the prey. It is thereby demonstrated that productivity (the food supply available to the prey) was not the proximal factor limiting prey numbers. Conversely, if removal of the guild of top predators does not lead to increases in the numbers of prey, we must conclude that the prey were proximally limited by something else—most likely the food supply.

We can ask parallel questions about the bottom rung on the trophic ladder. Suppose we could increase the long-term productivity of an ecosystem experimentally—let us say by adding water to a desert or nutrients to a barrens (Wedin and Tilman 1993). If the increase in plant growth resulting from the artificial input then led to an increase in the biomass of consumers (herbivores such as rabbits and deer), we could conclude that the consumers were under bottom-up control. If we found no increase in consumer biomass, this would imply that something other than productivity was limiting—plant antiherbivore defenses, or predators, to mention two possibilities (Oksanen 1983). Even by the admittedly simple operational criteria just presented, it should be evident that top-down versus bottom-up is not merely an either/or proposition. If we could add water or fertilizer to an ecosystem, the number of consumers could increase even in the presence of predators—implying bottom-up regulation. Simultaneously, say, in a different experimental plot, consumers could increase in response to predator removal without external inputs such as water or fertilizer—implying top-down regulation (Brett and Goldman 1997).

Both top-down and bottom-up regulation can operate concurrently in the same system. In the presence of predators, herbivores are secretive and act as time-minimizers, thereby maximizing their survival. That is, they endeavor to spend as little time feeding (when they are exposed to predators) as possible. Most of the time is spent in secure places—in burrows or dense thickets, for example, or in naturally protected spots such as steep mountain slopes or ledges (bighorn sheep and mountain goats). If predators are removed, then the quest for security ceases to be the leading regulator of prey behavior; now consumers are free to feed when and where they want, becoming energy-maximizers, thereby maximizing fecundity. The switch in prey behavior from time-minimizer to energy-maximizer in response to differing levels of perceived predator threat introduces complexity into the system and allows both top-down and bottom-up regulation to operate simultaneously or to varying degrees. (See Power 1992; Werner and Hall 1988; Abrams 1993; Werner and Anholt 1993; Englund 1997.) Another layer of complexity is added by herbivory-induced plant defenses. Damage to foliage can stimulate plants to increase levels of herbivore-deterring chemicals in their tissues—thereby reducing the food supply available to herbivores (a bottom-up effect). It is the extraordinary complexity of trophic interactions that has made the issue of top-down versus bottom-up a matter of so much contention among ecologists.

Top-down effects have been shown to act on communities in two fundamentally different ways. One is through preferential feeding on a prey species that, in the absence of predation, is capable of competitively excluding other species that depend on a limiting resource. Thus, over an intermediate range of predation intensities, species diversity in the prey guild is enhanced over that which occurs in the overabundance or absence of predators. Here we refer to this process as the "Paine effect." A more generalized form of this process, known as the intermediate disturbance model of species diversity, has been demonstrated in a variety of systems (Connell 1978, Sousa 1984).

The second way in which predators influence their communities is through a cascade of interactions extending through successively lower trophic levels to autotrophs at the base of the food web (Carpenter and Kitchel 1993). In trophic cascades, the autotrophs are either enhanced by reduced herbivory or limited by increased herbivory, depending on whether the number of trophic levels is odd or even (Power 1992). The top-down model predicts that each trophic level is potentially limited by the next level up. For intact three-level systems, therefore, predators limit herbivores, thus releasing producers from limitation by herbivory. Since there is little unambiguous evidence from terrestrial systems for trophic cascades involving three or more levels, a number of studies have looked only at component steps—for instance, evidence that herbivores limit

plants when the predators are missing and evidence that herbivores are limited by predators (Estes 1996).

Empirical Foundations: The Paine Effect

If terrestrial carnivores were not so inherently difficult to study, we might have understood their roles long ago. The simpler conditions characteristic of certain aquatic systems have facilitated investigation, however, and the keystone role of predators is now established beyond dispute. Paine (1966) was the first to provide incontrovertible evidence. By removing the predatory starfish *Pisaster ochraceous* from sections of the intertidal zone of the rocky Washington coastline, he showed that the diversity of the attached invertebrates subsequently declined as a superior competitor, the mussel *Mytilus californicus*, gradually occupied all available space, thereby excluding other species from the community. It is important to note that *Mytilus* is the preferred prey of *Pisaster*, so that the action of the predator is selective removal of the dominant competitor—an act that exposes attachment sites that can be exploited by other species. Further studies of sessile intertidal communities have amply supported Paine's result (with some geographical variation and local exceptions). The effect of a top predator is reduced, for example, when it does not feed preferentially on the dominant competitor among the potential prey species (Menge 1992; Menge et al. 1994; Menge 1995). The primary effect of a top predator in the intertidal system is thus seen in regulating the diversity of the prey community. This is the Paine effect.

The presence/absence of a predator influences the productivity and biomass of the intertidal prey community because space (attachment sites) is the limiting resource. The productivity that supports the intertidal community is almost entirely imported from the open ocean—an example of a spatially subsidized food web. Interactive links between sessile intertidal predators and the productivity of the system are thus weak to nonexistent. Terrestrial and aquatic systems involving mobile organisms may show different dynamics, however, because consumers and predators are free to come and go and many of the component species have long lifetimes. And unlike Paine's rocky intertidal system, which can be studied on the scale of a few square meters, terrestrial and open-water aquatic systems must be studied on vastly larger spatial scales because the important predators and consumers may have low population densities and range over large areas. These daunting obstacles to the careful analysis of mobile predator/prey systems have been major impediments to scientific progress. Now, with results emerging from some long-term studies and the first large-scale predator-exclusion experiments, the time is ripe for a synthesis.

Anecdotal Evidence

In the hope of arriving at some general conclusions, we now review evidence relevant to understanding the role of top carnivores. Our emphasis is on terrestrial ecosystems and large vertebrates, especially mammals. Although open aquatic systems provide many parallels, they are mentioned here only briefly. The evidence can be broadly categorized as anecdotal or experimental, though the dividing line between the two categories is not always distinct. Here we refer to evidence derived from natural perturbations and experiments lacking controls as "anecdotal."

Herbivore release onto predator-free islands. Sailors of yore introduced herbivores to predator-free islands throughout the Seven Seas to ensure themselves of a supply of meat on subsequent voyages. Horses, cattle, caribou, sheep, goats, pigs, and rabbits are among the animals introduced, singly or in combinations, to countless islands around the world (Carlquist 1974; Bramwell 1979; Coblentz 1978, 1990; Crosby 1986; Vitousek 1988). Few of these introductions were carefully monitored, so they can hardly be considered scientific studies. Nevertheless, in numerous instances (Ascension, Aldabra, Juan Fernández, California Channel Islands, St. Mathews Island, St. George Island) the introduced herbivores increased without check until they devastated the native vegetation of the island—at which point populations of the herbivores themselves often crashed (Klein 1968; Carlquist 1974; Coblentz 1980; Cronk 1980).

Destruction of the vegetation of predator-free islands by herbivores is unambiguously a top-down effect. Herbivores do not ordinarily destroy the vegetation of large landmasses supporting top predators, so it is tempting to attribute their massive impacts on islands to the absence of predators (Hairston et al. 1960). Another interpretation is possible, however, so the conclusion of top-down regulation is not the only one that can be drawn. The vegetation of islands lacking native vertebrate herbivores must experience relaxed selection for antiherbivore defenses and hence might be exceptionally vulnerable to introduced herbivores (Carlquist 1974; Bowen and van Vuren 1997). Without additional information, we cannot distinguish the two interpretations; but under the right circumstances, both may be correct.

Predator elimination. Humans have eliminated top predators over much of the globe, drastically reducing the geographical ranges of many species, including wolves, bears, tigers, lions, and many less intimidating beasts. Nevertheless, herbivores have generally not overrun predator-free portions of the planet, as we would expect if herbivore populations were indeed under top-down control. The reason in this case appears obvious. Large vertebrate herbivores are also the prey of human beings, and in many places they have been reduced to low densities or extirpated by human overhunting (Redford 1992). In many regions, introduced livestock substitute for missing native ungulates. Untangling the effects of predator removal from those of hunting and introduced livestock is an almost impossible task in most situations.

One common, nonexperimental situation that conforms to the requirements of a proper test of top-down control is increasingly attracting scientific attention. It is found in suburban areas and parklands in the United States from which top predators were eliminated long ago and where hunting is now prohibited. Mammals that would have been part of the prey pool of missing carnivores such as wolves and cougars have, despite high rates of roadkill, become notoriously abundant to the point that some of them are now nuisances: by being road hazards (deer, moose); by browsing ornamental shrubbery (deer); by raiding trash cans (opossums, raccoons); by preying on birds (house cats) and their nests (cats, raccoons); by destroying vegetable gardens (deer, woodchucks, ground squirrels), and by flooding people's yards (beaver; Garrott et al. 1993). The problem of mammalian overabundance in predator-free portions of North America has become so widespread and so severe that it was recently the topic of a major symposium hosted by the Smithsonian Institution (McShea et al. 1997).

If top-down processes, as elucidated by Paine, are important in terrestrial ecosystems, then the removal of top predators must lead to reduced diversity in the next lower trophic level. The obvious experiment to test this proposition was preempted long ago, however, by megafaunal overkill. What is now the eastern United States once supported an impressive galaxy of large herbivores—including elephants, tapirs, ground sloths, capybaras, giant beaver, and others—but today it supports only one or two, the white-tailed deer and moose. Certainly white-tailed deer, raccoons, woodchucks, and beaver have proliferated dramatically in the absence of large carnivores, but it seems highly unlikely that any of these animals could ever drive another to extinction via exploitation competition (depletion of the food supply). Are we to conclude, then, that the Paine mechanism is inoperative on land?

This conclusion is not inevitable. The Paine effect operates through the monopolization of space, not resource competition. The few examples from terrestrial ecosystems that resemble a Paine effect involve small rodents. Small island communities of native rodents are conspicuously vulnerable to invasion and monopolization by a behaviorally dominant species. Small, eighty-year-old islands in Lake Gatun, Panama, are today occupied only by the spiny rat, *Proechimys semispinosus,* even though central Panamanian forests support sixteen species of rodents, at least some of which were presumably present on these islands at isolation (Adler and Seamon 1991). Other examples emanate from predator-free islands where introduced rats, particularly *Rattus rattus,* or mice have replaced other rodent species (Brosset 1963; Berry and Tricker 1969; Lynam 1997). Even on the large landmass of Madagascar, where a wide complement of predators is present, there is mounting evidence that introduced *Rattus* is displacing native rodents (Goodman 1995). Such competitive displacements of several species by one are not true Paine effects, because space is not limiting, but like the Paine mechanism they do occur in the absence of normal predation.

Although biologists have not fully documented the exact mechanism by which a single rodent species can, in the absence of predators, replace a community of other species, some rat species (such as *Rattus rattus*) are aggressive toward other rodents and are known to attack their nests and kill the young. If overt aggression is involved, then the takeover of predator-free islands by an aggressive rodent species would involve a form of spatial monopolization analogous to the Paine mechanism. Under mainland conditions where animals are free to disperse and are at risk of predation, densities of all rodent species might be held to low enough levels to reduce or eliminate interspecific aggression between them, thereby permitting coexistence (Grant 1972).

Thus there is limited evidence that the Paine effect may operate among certain terrestrial consumer guilds, but demonstrating it seems to require rather exacting conditions: predator-free environments and strong interspecific aggression within the guild of consumers. We therefore doubt that the Paine effect has much conservation significance in terrestrial communities except perhaps on predator-free islands where, in many cases, ecological conditions have already deteriorated beyond repair. As we shall see, the Paine effect may operate more commonly at the producer level of terrestrial and benthic ecosystems through changes in the abundance of consumers.

PREDATOR INTRODUCTION. Another kind of uncontrolled experiment is performed when predators are intentionally or unintentionally introduced into predator-free environments. The recovery of the sea otter from near extinction is a classic example. In the absence of sea otters, sea urchins, abalones, and other benthic grazers had nearly eliminated the kelp forests that once dominated the inshore environment along the Pacific rim of North America. Gradual recovery of the sea otter during the middle portion of the twentieth century has led to sharp declines of benthic grazers, accompanied by dramatic recovery of kelp forests and associated fauna (Estes et al. 1978, 1989). Experimental removal of benthic grazers, simulating otter predation, led to rapid growth of benthic algae, followed by progressive domination of a single kelp species, *Laminaria groenlandica,* demonstrating a strong Paine effect at the level of herbivore/plant interactions (Duggins 1980).

The introduction of alien top predators has wreaked havoc in freshwater aquatic systems around the world. Some particularly notorious cases are the introductions of sea lamprey to the Great Lakes, of Nile perch to Lake Victoria in East Africa, of rainbow trout to Lake Titicaca in the Andes, and of peacock bass to Lake Gatun, Panama. (See Zaret and Paine 1973; Zaret 1980; Kaufman 1992; Goldschmidt et al. 1993; Mills et al. 1994.) In these and countless additional well-documented examples, top-down effects have been dramatic and unequivocal—typically with devastating consequences for native fauna.

The introduction of exotic predators to predator-free islands provides further evidence for the operation of top-down regulation. Mongooses introduced onto islands of the tropical Pacific and Antilles have contributed to the collapse of native faunas (King 1984). Inadvertent introduction of the brown tree snake onto Guam led to a population explosion of the snake and consequent extinction of most of the island's native birds (Savidge 1987). Introduced domestic cats have had strong effects in Australia and on certain temperate islands, as have foxes in boreal to arctic regions (Bailey 1993).

On the North American mainland, the growing gray wolf population has been associated with a concurrent decline in elk and white-tailed deer densities. Most known ungulate mortality in these areas was caused by wolf predation (D. Pletscher, pers. com.). The recent reinvasion of the northern Midwest by wolves has reduced the distance from aquatic habitats that beavers can forage—a behavioral modification that in turn reduces the impact of beaver on plant associations (Naiman et al. 1994; Pollock et al. 1995). Similarly, the reestablishment of wolves in other areas has been followed by declines in caribou, moose, elk, and deer (Bergerud 1988; Messier and Crête 1985; Hatter and Janz 1994).

Long-term monitoring of predator/prey interactions. A compelling case for a terrestrial trophic cascade is that of the gray wolf/moose/balsam fir interaction on Isle Royale, Michigan (McLaren and Peterson 1994; Messier 1994). The number of wolves determines the intensity of wolf predation on moose populations on Isle Royale. Growth rings in young fir trees showed depressed plant growth rates when wolves were rare and moose abundant—from which McLaren and Peterson (1994) infer the existence of a wolf-induced trophic cascade. Broad ramifications within the forest ecosystem are suggested from known linkages among moose, microbes, and soil nutrients (Pastor et al. 1988).

The anecdotal evidence cited here is consistent with top-down regulation as a predictable feature of terrestrial and many aquatic communities. But without rigorous controls, anecdotal evidence, by its nature, is open to alternative interpretations. Uncontrolled changes in the quality or distribution of habitats concurrent with predator elimination or reintroduction especially complicates the interpretation of causes and effects that may be separated in time by decades. For these reasons, scientists put greater stock in controlled comparisons and experiments.

Experimental Evidence

Few well-controlled comparisons of prey populations at sites with and without top predators have been made—presumably because the conditions required are so rarely available. The sites being compared must have similar climate and vegetation and differ only in the presence/absence of top predators. Hunting or complicating management interventions must be absent.

One carefully documented comparison is between two sites in the neotropics: one is Barro Colorado Island (BCI), Panama, a research preserve of the Smithsonian Institution; the other is Cocha Cashu Biological Station (CCBS) in the Manu National Park of Perú. Located respectively at 10° north and 12° south latitude, the two sites have a similar climate and fauna. The dominant habitat at both is primary tropical moist forest. BCI is a 1600-hectare island created by flooding during the construction of the Panama Canal. It has been isolated since the canal's creation. Due to its limited area, BCI lost top predators—jaguar, puma, and harpy eagle—more than fifty years ago (Glanz 1982). CCBS is located in the heart of a 2-million-hectare biosphere reserve that retains an intact flora and fauna, including all top predators.

The terrestrial and arboreal mammals of both BCI and CCBS have been censused on multiple occasions (Glanz 1990; Janson and Emmons 1990; Wright et al. 1994). Counts made by different observers at different times consistently agree in registering higher mammal densities on BCI than at CCBS (Terborgh 1988, 1992; Wright et al. 1994). In several cases, the differences in abundance are striking—exceeding an order of magnitude, particularly for the agouti, paca, armadillo, and coatimundi (terrestrial) and the three-toed sloth and tamandua (arboreal). Differences for other species are less extreme—as for the collared peccary and rabbit (terrestrial) and howler monkey (arboreal)—or negligible (deer, tapir). Whenever there are appreciable differences, they consistently favor BCI.

Differences in abundance are most pronounced in medium to large species that are prey of the top predators missing from BCI. Small mammals (rodents and marsupials weighing less than 1 kilogram) show similar abundances at the two sites, but these species do not appear in the prey of the top predators (Rettig 1978; Emmons 1987). Instead these animals are prey to small carnivores (ocelot, snakes, raptors) that are well represented at both sites. The higher densities of medium and large mammals on BCI have been interpreted as evidence of a top-down effect resulting from missing top predators (Terborgh and Winter 1980; Terborgh 1988, 1992). This conclusion, however, has been questioned by Wright et al. (1994) who emphasize that other interpretations are possible, including uncontrolled differences in productivity between the two sites.

The only certain way to exclude possible influences of uncontrolled variables is with strictly controlled experiments that include censusing before and after. For terrestrial predator/prey systems, the appropriate spatial scale on which to conduct the critical experiments is that of square kilometers—a fact that has precluded such experiments until very recently (Englund 1997). There are now two experimental efforts under way that promise to overcome certain weaknesses of correlational analysis and geographical comparisons. One of these efforts employs isolated remnants of a formerly intact landscape; the other uses large (1 square kilometer) fenced exclosures to exclude terrestrial predators. For reasons to be explained, neither set of experiments is perfect. But both represent major advances over previous efforts to isolate the effects of predators on terrestrial communities.

The creation in 1986 of one of the world's largest hydroelectric impoundments (Lago Guri) in the Caroni Valley of east-central Venezuela has resulted in the inundation of a hilly forested landscape with the consequent isolation of hundreds of erstwhile hilltops as islands. The impoundment is 120 kilometers long and up to 70 kilometers wide. Islands ranging in size from less than 1 hectare to more than 1000 hectares are scattered throughout the vast expanse of water—a number of them as far as 7 kilometers from the mainland. Small size and isolation by water assure that many of the more remote islands in Lago Guri are free of vertebrate predators except for certain small raptors and, perhaps, snakes.

Systematic surveys of the vertebrate faunas of a dozen Lago Guri islands were conducted seven years after isolation, along with control surveys on the nearby mainland (Terborgh et al. 1997). Roughly 75 to 90 percent of the species of terrestrial vertebrates that occupy the same forest type on the mainland were absent from islands between 1 and 10 hectares in size within seven years after isolation. With few exceptions, species that persisted became hyperabundant compared to their densities on the mainland. The absence of many species and the hyperabundance of others has created animal communities unlike any that would ever occur naturally—communities that are grotesquely imbalanced from a functional standpoint. These communities lack vertebrate predators and are deficient in pollinators and seed dispersers; but they contain abnormally high densities of seed predators (small rodents) and generalist herbivores (howler monkeys, iguanas, and leaf-cutter ants). The excess of herbivores is particularly striking, as all three species occur at densities between one and two orders of magnitude above those found on the mainland.

Larger Lago Guri islands (between 100 and 1000 hectares) still retain nearly complete vertebrate faunas (all primates and ungulates known for the region, for example), lacking only resident populations of the top predators (jaguar, puma, harpy eagle). Mammal densities on the two large islands being monitored have not yet increased conspicuously, but one and perhaps both of these islands are visited regularly by jaguars that swim over from the mainland, so they are not strictly predator-free. As for the smaller, more isolated islands that assuredly are predator-free, the hyperabundance of persistent vertebrates is consistent with the top-down effect of release from predation.

Further support for these observations is the documentation of hyperabundant rodent populations on numerous predator-free islands in both temperate and tropical regions (Adler and Levins 1994; Adler 1996). Nevertheless, the possibility remains of a confounding effect of missing species. The absence of other seed predators and herbivores that are present in the mainland fauna, for example, may have made available additional resources that allowed the persistent species to achieve hyperabundance. As in the previous examples considered here, the findings are consistent with a top-down effect but an airtight case remains elusive.

Finally, we come to the most carefully constructed test of top-down regulation conducted to date. Charles Krebs, Tony Sinclair, and their associates are conducting the experiment in southern Yukon, Canada, where they have been monitoring snowshoe hare populations for nearly a decade in 1-square-kilometer plots. Two of the plots are surrounded by electric fencing that excludes mammalian predators but is permeable to hares. Plots have been assigned to five treatments: control, food supplementation, fertilizer, predator exclusion, and predator exclusion with food supplementation (Krebs et al. 1995). Hares exhibited strong positive demographic responses to food supplementation and (partial) predator exclusion while continuing to follow the classic ten-year cycle of abundance. Averaged over the peak and decline phases, hare density was double that of controls under predator exclusion, triple with food supplementation, and eleven times greater under predator exclusion coupled with food supplementation (Krebs et al. 1995). The results strongly implicate both bottom-up and top-down regulation. This interpretation is complicated, however, by the free passage of hares in and out of predator exclosures and by the exposure of hares within exclosures to predation by goshawks and great horned owls. Nevertheless, the effort represents a bold attempt to conduct an experimental test of bottom-up and top-down regulation on an appropriate spatial scale with a natural predator/prey system.

Another series of large-scale experiments has been conducted to test the role of top-down regulation in freshwater aquatic systems (Carpenter and Kitchell 1993). Entire lakes in Wisconsin have been seined free of piscivorous or planktivorous fishes and the respective hauls exchanged between lakes in a series of dramatic whole-lake perturbations (Carpenter et al. 1985; Carpenter and Kitchell 1988). Removal of piscivorous fish (large-mouthed bass, the top carnivore in this system) leads to order-of-magnitude increases in planktivorous fish, decreases in the size and number of zooplankton (cladocerans), and strong increases in the standing crop of phytoplankton in a textbook top-down trophic cascade.

A variety of efforts designed to assess the polarity of trophic regulation in terrestrial and aquatic ecosystems have consistently produced results consonant with strong top-down effects. To date, however, most or all of these efforts have fallen short of making an airtight case because of the overwhelming logistical challenge of removing or excluding only the guild of top predators without altering anything else. Carpenter's studies of Wisconsin lakes provide the most unambiguous evidence. On land, perhaps the closest approximation yet achieved to the ideal experimental condition is found in areas like BCI in Panama and in North American parks and suburbs where mammal communities complete except for top predators live under protection from hunting (McShea et al. 1997). In both these situations, densities of medium and large mammals are much higher than can be considered normal, though other potentially complicating factors preclude drawing an unequivocal link to missing predators.

Admittedly many questions remain to be answered by future research. Nevertheless, in the spirit of metaanalysis, if one considers the entire collection of controlled and uncontrolled comparisons and experiments cited here, the consonance of the results suggests a much stronger conclusion than a single case standing alone. With so much evidence pointing in the same direction, the conclusion that top predators play a major regulatory role seems inescapable.

Countercurrents

Although the evidence that top predators commonly limit the densities of their prey is compelling, one would be wrong to conclude that predators limit the numbers of all consumers. There are a variety of situations in nature that allow consumers to escape predation to varying degrees—often to the extent that top-down control by large carnivores does not operate. These probable exceptions, as we shall see, include both megaherbivores and herd-forming migratory ungulates. Moreover, one should not assume that because top predators play major roles in regulating prey populations in many ecosystems, they play equivalent roles in all ecosystems.

Prior to the late-Pleistocene and Holocene megafaunal overkill, nearly every ecosystem on earth included very large herbivore species too big (at least as adults) to be killed by the largest carnivores in the system. The prime living example is that of elephants, which were once distributed on all continents (except Australia and Antarctica) and a number of islands. Nearly all the earth's once abundant megaherbivores have been driven to extinction and only a few survive (Martin and Klein 1984). In Africa there are rhinos and hippos, in addition to elephants, that, as adults, enjoy immunity to lions. In the north, adult moose repel gray wolves; in the neotropical forest, tapirs shrug off jaguars. Elsewhere, Madagascar had its elephant birds, New Zealand its moas, the Antilles their hutias and ground sloths, and the Seychelles, Galápagos and Aldabra Island their tortoises. Lacking any population control from the top, megaherbivores must be regulated from below. But to the extent that megaherbivores regulate vegetation, they too exert a top-down force, that is independent of predation (Kortlandt 1984; Owen-Smith 1988). What fraction of the earth's land surface still supports megaherbivores? Ubiquitous and abundant to the point of dominating mammalian biomass over most of the globe for millions of years, megaherbivores have been so systematically persecuted that they have become almost irrelevant to today's ecosystems and conservation concerns, except in dwindling portions of Africa and Asia.

Sheer size enables a few of the world's largest mammals to escape predation. But size is not the only successful antipredator strategy to have arisen through evolution. Some species are able to reduce (but not eliminate) predation through social mechanisms. The list of these mechanisms is long. It includes the formation of herds and flocks, sentinel behavior, and the giving of alarm calls (Bertram 1978; Harvey and Greenwood 1978; Terborgh 1990). Social mechanisms can be very effective at limiting predation. Consider the fabled wildebeest of Serengeti. These antelopes aggregate in huge mixed herds that can be within the territories of only one or two lion prides at a time. Lions are consequently unable to make much of a dent in wildebeest numbers, killing only about 8 percent of the population per year (Sinclair and Norton-Griffiths 1979; Sinclair and Arcese 1995). In a bad year, wildebeest die en masse from starvation and malnutrition, as has been convincingly documented by Sinclair and his associates. The conclusion follows that wildebeest—and, by analogy, other herd-forming migratory ungulates—are regulated from the bottom up (Fryxell et al. 1988). But again, how much of today's earth is occupied by herd-forming migratory ungulates? Not much more than is occupied by megaherbivores. Both of these major agents of top-down forces in terrestrial ecosystems are becoming Pleistocene relics. Hence we should give special attention to top carnivore processes, because it seems likely that they are crucial to preserving what bits and pieces of wild nature we have left.

Top predators play structuring roles in many ecosystems. Exceptions, however, may be found in extreme environments, such as deserts or barrens, where low plant productivity or chemical toxicity of foliage limits large herbivores to such a degree that predators are unable to exploit them. Other factors, such as a severe disturbance, can temporarily upset normal trophic relationships. A stand-replacing fire, for example, may result in lowered herbivore densities and a switch from top-down to bottom-up regulation until the vegetation recovers (McLaren and Peterson

1994). In the world at large, however, productivity-limited (pure bottom-up) systems appear to be rare. Moderate to strong top-down regulation appears to be the norm for terrestrial ecosystems.

Indirect Effects and Trophic Cascades

Having made a case for top-down regulation as a nearly ubiquitous force in terrestrial ecosystems, we now ask about the role played by top predators in maintaining ecosystem integrity. From a conservation perspective, we are concerned about the destabilizing forces that are unleashed in ecosystems from which top predators have been eliminated. It is a concern that extends over the large fraction of the earth's surface from which we have diminished or expunged the influence of these key animals. If there are no predictable ecological consequences of predator loss, we need not be concerned. But we have already reviewed convincing evidence to the contrary, so we know there are consequences. What are these consequences and how severe might they be?

The intellectual groundwork for studying "indirect effects" or "trophic cascades" in terrestrial ecosystems was laid in the 1970s and 1980s by James Brown and Diane Davidson in a major series of exclosure experiments conducted in the Chihuahuan Desert of southeastern Arizona. Experimental enclosures were open to aerial predators and certain mammals (coyotes) but closed to certain terrestrial predators (snakes) and to the movements of small rodents. Treatments included open and enclosed control plots, plus food supplementation and removal of rodents, ants, and both rodents and ants. (See Brown and Davidson 1977; Brown et al. 1986; Heske et al. 1994.) Rodents and ants live at the same trophic level: both subsist on the seeds of desert plants.

Partial exclusion of rodent predators led to increased densities of rodents, but not of ants. Selective removal of rodents or ants (or both) resulted in changes in the abundance and species composition of annual plants. In short, manipulation of a guild of consumers, in this case seed predators, resulted in large and often unanticipated changes in the composition of the plant community. Integrity of plant communities is essential to preserving biodiversity, so the Brown and Davidson experiments raised an early warning flag to conservationists. Perhaps other changes in consumer guilds mediated through top-down effects could have similarly drastic consequences.

In many parts of North America, extirpation of dominant predators has resulted in a phenomenon known as "mesopredator release" in areas supporting other small to midsized predators (foxes, skunks, raccoons, opossums, feral and domestic housecats: Soulé et al. 1988; Palomares et al. 1995). In such areas, mesopredators act by default as surrogate top predators. This has resulted in modified niche exploitation, altered diversity, and other ripple effects in the population structure of the community. Local elimination of coyotes, for example, allows the guild of mesopredators to increase in number, thereby imposing added predator pressure on the prey. Widespread reduction of ground-nesting birds, such as quail, pheasants, grouse, ducks, nightjars, and certain warblers, has been attributed to mesopredator release (Côté and Sutherland 1997). Mesopredator release has also been blamed for the decline or disappearance of gamebirds, songbirds, and other small vertebrates from a number of North American terrestrial ecosystems—including scrub habitats (Soulé et al. 1988), grasslands (Vickery et al. 1994), prairie wetlands (Sovada et al. 1995; Garrettson et al. 1996a, 1996b), and eastern deciduous forest (Wilcove 1985; Faaborg et al. 1995; Peterjohn et al. 1995).

Reintroduction or recolonization of predators influences the composition and structure of carnivore guilds as well. Wolf recovery in the Rocky Mountains has resulted in interference and exploitation competition among intraguild carnivores, resulting in changes in behavior, abundance, and distribution of affected species (Cohn 1998). As a rule, generalized predators, like the wolf, can be expected to exert stronger top-down effects than specialists like the fisher and pine martin or omnivores such as bears.

Extirpation of top predators has released herbivore populations in parts of the United States with consequences that are just beginning to come to light. Overbrowsing by white-tailed deer is decisively altering the pattern of tree regeneration in some eastern forests and is threatening certain endangered plants with extinction (Alverson et al., 1988, 1994; Miller et al. 1992; McShea et al. 1997; Rooney and Dress 1997). Elsewhere in North America, introduced ungulates, especially Eurasian boar *(Sus scrofa)*, have increased to such a degree that they are destroying wildflower beds and altering tree regeneration patterns in forests (Abramson 1992). It hardly needs to be emphasized that rapid, large-scale, and unpredictable changes in forest composition represent a chilling threat to biodiversity.

For another case, let us return to Lago Guri in Venezuela, where recently created islands in a hydroelectric impoundment are experiencing cataclysmic biological change. In a predator-free environment, three generalist herbivores have each increased in abundance by more than an order of magnitude. Howler monkeys on some islands have attained densities equivalent to 500 per square kilometer whereas mainland densities are typically between 20 and 40 per square kilometer (Crockett and Eisenberg 1986). Densities of iguanas and leaf-cutter ants have similarly exploded (Terborgh et al. 1997; Rao 1998).

Ongoing studies of forest regeneration on these islands reveal little successful reproduction of canopy trees. On some islands fewer than five species are represented by saplings in the understory, despite the presence of sixty to seventy species in the canopy. The mechanisms by which tree reproduction on these islands is being suppressed are currently under investigation. Preliminary results suggest the simultaneous involvement of several mechanisms: deficiencies of pollination and seed dispersal; excessive seed predation; decimation of seedlings by leaf-cutter ants; and repeated defoliation of canopy trees by howler monkeys, iguanas, and leaf-cutter ants (Terborgh et al., unpublished results). In the absence of "normal" biological interactions, the remnant ecosystems of these islands have spun out of control. It seems inevitable that most of the plant and animal species that survived the initial contraction in area will go extinct within one or two tree replacement cycles.

Vegetation change in the Lago Guri islands and in portions of the United States occupied by hyperabundant populations of white-tailed deer and Eurasian boar offer startling examples of trophic cascades—examples that mirror findings from deserts (Brown et al. 1986), lakes (Carpenter and Kitchell 1993), and Pacific kelp forests (Estes et al. 1989). To prevent ecosystems all over North America from experiencing similar convulsions brought about by trophic cascades, the full spectrum of ecological processes that operates to perpetuate biodiversity, especially predation, must be widely maintained.

Where top predators have been extirpated and their reestablishment is impractical, can trophic cascades be avoided? Perhaps worst-case scenarios can be avoided through interventions of various sorts. But no human effort can accurately simulate the effects of real predators, because these animals have impacts on many prey species simultaneously and interact with prey populations in complex ways that are seldom understood. Nevertheless, the worst consequences of trophic cascades might be forestalled or ameliorated though the hunting of herbivores and trapping of mesopredators. The most severe impacts of hyperabundant mesopredators and consumers appear in localities where predators are absent and hunting and trapping are prohibited.

A contrasting situation arises in countries lacking enforced game laws, where all medium and large birds and mammals are systematically overhunted (Redford 1992). The resulting "defaunation," like hyperabundance, results in distorted or disrupted plant/animal interactions—including seed dispersal, seed predation, and herbivory. Little is known about the consequences of wholesale defaunation, though preliminary evidence from Mexico points to highly aberrant patterns of plant regeneration (Dirzo and Miranda 1991).

Predators prevent prey populations and mesopredators from exploding into hyperabundance while rarely, if ever, driving prey to extinction. Prey species, such as seed dispersers, seed predators, or herbivores, are thereby regulated within definite upper and lower bounds. The operation of such feedback mechanisms can be likened to "a balance of nature." Nature stays in balance so long as a fauna remains intact and the full suite of ecological processes operates unhindered. It is when nature falls out of balance—when there are too many consumers and mesopredators (or not enough)—that species begin to disappear and humans begin to notice. But what humans notice is only that some favored species or another has disappeared. Hidden in the workings of a nature we are only beginning to understand, the cause remains obscure.

Another Key to Biodiversity

Despite the complexity of food web linkages, interactions across trophic levels define a subset of these links that are of particular importance to the functioning of natural ecosystems. In terrestrial ecosystems, top-down and bottom-up processes operate simultaneously. This seemingly contradictory statement results not only from the complexity of food web structure but from flexibility in the behavior of individual species—such as the tendency for prey to act as time-minimizers in the presence of predators and the ability of plants to increase their investment in antiherbivore defenses in response to herbivory.

Although megaherbivores (those large enough to be invulnerable to predators) and herd-forming migratory ungulates tend to be regulated from the bottom up, megaherbivores concurrently exert top-down forces through their effects on vegetation. Both groups of species may have been prominent over much of the earth's surface prior to megafaunal overkill, but they have been reduced by human persecution to a tiny fraction of their former geographical occurrence. What remains nearly everywhere else are drastically truncated mammal communities that are regulated largely through top-down processes.

The evidence reviewed here overwhelmingly supports the strong top-down role of top carnivores in regulating prey populations—and thereby stabilizing the trophic structure of terrestrial ecosystems. Loss of top predators results in hyperabundance of consumers playing a variety of trophic roles (herbivores, seed dispersers, seed predators) and in mesopredator release. Hyperabundance of consumers and mesopredators, in turn, results in trophic cascades that lead to multiple effects—including the direct elimination of plant populations from overbrowsing/grazing, reproductive failure of canopy tree species, and the loss of ground-nesting birds and probably other small vertebrates.

In sum, then, our current knowledge about the natural processes that maintain biodiversity suggests a crucial and irreplaceable regulatory role of top predators. The absence of top predators appears to lead inexorably to ecosystem simplification accompanied by a rush of extinctions. Therefore, efforts to conserve North American biodiversity in interconnected mega-reserves will have to place a high priority on reestablishing top predators wherever they have been locally extirpated. If steps are not taken in the interim to restore the full gamut of natural abiotic and biotic processes that maintain biodiversity, efforts to halt extinction through legislated mechanisms (such as the Endangered Species Act) will be overwhelmed by irresistible biological forces. It is only by providing the conditions that allow nature to remain in balance that biodiversity can be perpetuated over the long run.

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User behaviour, best practice and the risks of non-target exposure associated with anticoagulant rodenticide use

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ABSTRACT

Usage of anticoagulant rodenticides (ARs) is an integral component of modern agriculture and is essential for the control of commensal rodent populations. However, the extensive deployment of ARs has led to widespread exposure of a range of non-target predatory birds and mammals to some compounds, in particular the second-generation anticoagulant rodenticides (SGARs). As a result, there has been considerable effort placed into devising voluntary best practice guidelines that increase the efficacy of rodent control and reduce the risk of non-target exposure. Currently, there is limited published information on actual practice amongst users or implementation of best practice. We assessed the behaviour of a typical group of users using an on-farm questionnaire survey. Most baited for rodents every year using SGARs. Most respondents were apparently aware of the risks of non-target exposure and adhered to some of the best practice recommendations but total compliance was rare. Our questionnaire revealed that users of first generation anticoagulant rodenticides rarely protected or checked bait stations, and so took little effort to prevent primary exposure of non-targets. Users almost never searched for and removed poisoned carcasses and many baited for prolonged periods or permanently. These factors are all likely to enhance the likelihood of primary and secondary exposure of non-target species.

1. Introduction

Commensal rodents contaminate and consume crops (Daniels et al., 2003; Stenseth et al., 2003), damage property through gnawing wires and cables (Leung and Clark, 2005) and act as vectors of human and animal diseases such as leptospirosis, trichinosis and salmonellosis (Daniels et al., 2003; Meerburg et al., 2009; Webster and Macdonald, 1995). The control of rodent populations is therefore common and widespread. It is a critical component of modern agricultural practice as farmers seek to prevent rodents spoiling and consuming animal feed and stored grain, damaging buildings and transmitting disease. In the developed world, the primary means of controlling rodent populations, and their impacts, is with anticoagulant rodenticides (ARs)(Stenseth et al., 2003). There are two generic groups of ARs, so called first and second-generation anticoagulant rodenticides (FGARs and SGARs). The latter are more acutely toxic and persistent than FGARs and were developed during the 1970s and 1980s to combat the emerging problem of resistance to FGARs (Rowe et al., 1981; Lund, 1988,). SGARs are now the primary means of controlling rodents in Great Britain (Dawson et al., 2001; Dawson and Garthwaite, 2003) and in many other regions (e.g. Eason et al., 2002).

SGARs can be a highly effective means of controlling rodent populations. Nonetheless, their use can also lead to the unintended exposure of non-target species (Berny et al., 1997; Stone et al., 2000; Fournier-Chambrillon et al., 2004). Exposure occurs either directly via consumption of bait (primary exposure) or indirectly when predators or scavengers consume an animal that has already been exposed (secondary exposure). In Britain, secondary exposure has been identified in a variety of non-target mammals and birds. Polecat (*Mustela putorius*), stoat (*M. erminea*), weasel (*M. nivalis*), red fox (*Vulpes vulpes*), hedgehog (*Erinaceous europeaus*), barn owl (*Tyto alba*), tawny owl (*Strix aluco*), kestrel (*Falco tinnunculus*), buzzard

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(*Buteo buteo*) and red kite (*Milvus milvus*) populations have all been found to be exposed to varying extents (Dowding et al., 2010; McDonald et al., 1998; Newton et al., 1999; Shore et al., 1996, 2003a,b, 2006a,b; Walker et al., 2007, 2008a,b). However, the effect of exposure on species at both the individual and population level remain poorly understood (Burn et al., 2002; Knopper et al., 2007).

The relationship between AR usage and secondary exposure of predatory birds and mammals is complex (Eason et al., 2002; Shore et al., 2006a). Factors that are likely to contribute to the risk of non-target exposure include the persistence and toxicity of the rodenticides, level of usage, and how and where they are used (Shore et al., 2003a,b, 2006a). In the United Kingdom (UK), voluntary and regulatory measures relating to AR usage have been introduced to reduce the level of risk to non-target wildlife. The measures include the promotion of voluntary best practice guidelines and the confinement of the more toxic and persistent SGARs, flocoumafen and brodifacoum, to use indoors. A number of guidelines are promoted by government and industry (Anonymous, 1999, 2001; Think Wildlife, 2005), and are designed to increase awareness of the risks associated with AR use and increase the efficiency of rodent control. Examples of best practice include bait protection, fixed duration of baiting campaigns followed by bait removal, and searches for and removal of poisoned carcasses (Anonymous, 1999, 2002). While overall levels of AR usage in Great Britain have been monitored in the past (for example, Dawson and Garthwaite, 2003) there are limited published data on end user behaviour (McDonald and Harris, 2000). The extent to which best practice guidelines are adhered to is unknown.

The objective of the current study was to use a questionnaire to determine how end-users applied ARs and whether they followed best practice guidelines designed to maximise efficacy and reduce the risk of non-target exposure. By gathering this information, we aimed to identify current usage practices that contribute to the risk of non-target exposure but which could be modified to mitigate such risks.

2. Methods

We conducted a survey of farmers in Northern Ireland (NI) in conjunction with a statutory biennial survey of pesticide use on farms. Farms were considered for survey if they reported in the Northern Ireland Agricultural Census, June 2005 (Anonymous, 2006) that they grew one of the following: barley, wheat, oats, oilseed rape, peas and beans, lupins or potatoes. The process of selecting the farms to be surveyed is detailed by Withers et al. (2006) and is described briefly here. Farms were first stratified into six size classes according to the total area of arable crops grown. Holdings were then selected at random within each of the size classes with the number of holdings being proportional to the total area of arable crops grown. A total of 273 farms were notified by letter that they had been selected to take part in the compulsory survey. Letters were followed up by personal interviews between November 2006 and April 2007. Farmers are obliged to take part in the statutory pesticide usage survey, but the additional questions on rodenticide usage were non-compulsory.

Prior to the main survey, a pilot study of ten farmers was used to improve the relevance and design of the questionnaire. This process resulted in a thirty-four question, closed format questionnaire, with contingency questions (Supplementary Information, Appendix I). This format of questionnaire was chosen as it provides a greater uniformity of responses and is easily processed (Babbie, 1990). Questions asked related to behaviours identified by best practice guidelines that reduce the risk of non-target exposure and increasing the efficiency of control (Anonymous, 1999, 2002; Think Wildlife, 2005). The main points were: maintenance of records (number of baiting points and quantity of bait used), protection of bait from non-target species, removal of bait at the end of treatment and searching for dead rodents at the end of treatment periods. In addition, we asked questions relating to usage (product used, period used). All responses are given as a percentage of the total number of questionnaires returned unless otherwise stated.

A multiple correspondence analysis (MCA) was used to analyse patterns in behaviour of respondents using ARs. An MCA was chosen due to its ability to analyse patterns of relationships for several categorical variables. The factors included in the model were: type of AR used (first or second-generation), period of use (periodic or permanent), location used (indoor or outdoor), protection of bait (yes or no), bait removed (yes or no), periodicity of bait checks (frequency), records kept of location used (yes or no), records of amount of bait used (yes or no), bait replenished (yes or no), training (level) and searches for dead rodents (yes or no). Strata size was initially included in the exploratory analysis for the MCA but did not help differentiate the responses and so was not included in the main analysis. Records with missing responses for the factors analysed were removed from the analysis. The number of dimensions was chosen based on examination of the contributory factors to each dimension. All statistical analyses were conducted using SPSS 17.0.0 (August 23rd, 2008).

3. Results

A total of 162 (59%) of the 273 farmers approached agreed to participate in the rodenticide survey. Information provided by 158 (57.9%) respondents was analysed as four forms were completed incorrectly. Of the 111 (41%) non-participating farms, 36 were asked to answer a reduced number of questions over the telephone but only two did so.

Most respondents (n = 127, 80%) undertook rodent control themselves but a few (n = 10, 6%) employed contractors. Only 21 (13%) did not use any chemical to control rodents. SGARs were most commonly used (n = 117, 74%) but a few respondents used FGARs (n = 8, 5%) or other rodenticides (n = 3, 2%). Seven (4%) respondents did not know what type of rodenticide they used. Rodent control was usually undertaken using one product but 9 (6%) respondents used two or three products together. The SGARs licensed for outdoor use, difenacoum and bromadiolone, were used by 54.5% of respondents and indoor products (flocoumafen and brodifacoum) by 19.6% (Table 1). The FGARs used were chlorophacinone and coumatetralyl (Table 1).

Two (1%) farmers had attended a training course on AR use, and 25 (15%) received instruction through a leaflet (Table 2). The majority (n = 90, 57%), though, relied on guidelines on the manufacturers' packaging.

Few respondents selectively applied ARs in years when rodents were considered to be a problem; the majority applied baits every year (Table 2). Most (n = 91, 58%) respondents applied baits over short periods, typically four months or less (Fig. 1a) with few

Table 1
Percentage of respondents (n = 158) using different anticoagulant rodenticide products. Nine farmers used more than one AR (seven used two ARs and two used three ARs in combination). No Warfarin use was recorded.

Anticoagulant	N	% of total respondents
Difenacoum	52	33.0
Bromadiolone	34	21.5
Flocoumafen	25	15.8
Brodifacoum	6	3.8
Chlorophacinone	5	3.2
Coumatetralyl	4	2.5

Table 2
Proportion of adherence to best practice guidelines among survey respondents who answered the key questions relating to best practice. Single responses (yes or no) were only possible to these questions.

Question	Total responses	Yes	No
Has the farmer received instruction on how to use rodenticides?	123	118 (95.9%)	5 (4.1%)
Is the number of bait points and amount of bait laid recorded?	126	14 (11.1%)	112 (88.9%)
Are bait points checked?	125	118 (94.4%)	7 (5.6%)
Is bait protected from being eaten by other animals?	123	114 (92.7%)	9 (7.3%)
Is bait removed once an infestation has declined?	120	36 (30.0%)	84 (70.0%)
Is a search for dead rodents made following baiting?	120	1 (0.8%)	119 (99.2%)

baiting the entire year (Fig. 1a and b). Use varied seasonally, and peak usage was during autumn and winter (Fig. 1b).

Baits were applied within buildings by 68% of respondents and outside buildings by 48%. When used outside, baits were used mainly around buildings i.e. within the vicinity of the farm, although 10% ($n = 16$) applied bait away from buildings in fields or hedges. Products that were licensed for indoor use only (flocoumafen, brodifacoum) were also used around the outside of buildings by 12% of farmers and away from buildings in fields or hedges by 3% of respondents. Most respondents did not keep records of where baits were used and those that did were most likely to bait permanently (Table 2), and some ($n = 26$, 16%) did not know how much bait they used in a year.

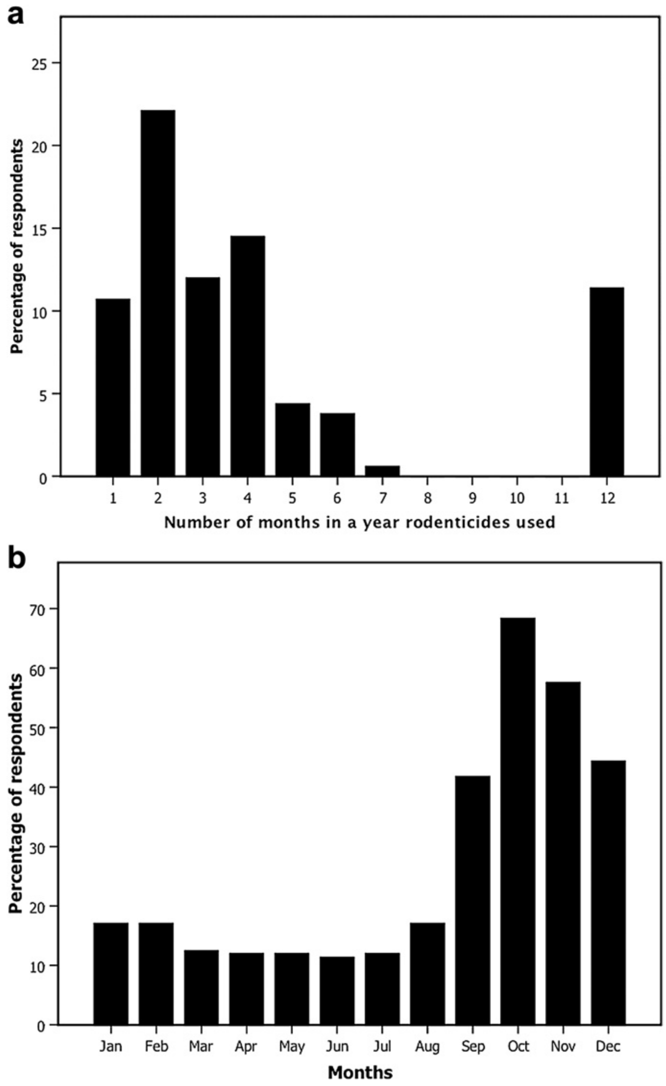

Fig. 1. Temporal variation in rodenticide usage among farmers. a) The typical number of months in a year that baits are applied by anticoagulant rodenticide users b) the percentage of anticoagulant rodenticide users ($n = 118$) that apply baits in each month of the year.

Despite the general lack of record keeping, baiting points were usually checked. Frequency of checks depended on the type of product used and the period over which baits were deployed (Table 2). FGAR users were less likely to check baits than SGAR users but the frequency of checks was highly variable. Half of respondents checked baits weekly but the frequency of checks varied on the duration of usage. Checks by permanent baiters were conducted either daily or fortnightly while periodic users (the bulk of respondents) checked baits weekly. Although bait was typically protected from non-target species (Table 2), this was less common amongst FGAR than SGAR users. Tubes or pipes ($n = 44$) were most commonly used to protect baits followed by bait boxes ($n = 30$) and a piece of wood/tile/glass ($n = 27$). Following treatment, bait was removed by over a third of respondents (Table 2), but baits were less likely to be removed by farmers that baited for prolonged periods. Only one user reported conducting a search for dead rodents following initiation of treatment but half of respondents ($n = 79$) reported finding dead animals without actively searching.

A total of 118 of the 127 respondents that used ARs answered all questions relating to best practice. Therefore, only responses from this group were included in the MCA. The factors, searching and training, were not included in the analysis as almost none of the respondents conducted searches and most had received no training other than the guidance on the product label (Table 2). In addition, replenishment of bait and records of amount of bait used were highly correlated (positively) with periodicity of checks and records of location of use respectively. Therefore, the latter were only included in the final analysis. Patterns in user behaviour were best explained by two dimensions in the MCA (Fig. 2a). The first dimension was most strongly characterised by the factors "Type of AR" (ie FGAR or SGAR), "bait protection" and "periodicity of checks", while the best discriminated responses in the second dimension were "periodicity of checks", "period used", "and "bait removed". The joint category plot (Fig. 2b) identified which categories were associated with each other (close together in the plot) and proximity to the origin was positively related to the number of respondents giving that response. It was evident from dimension 1 that most AR users apply SGAR baits (termed 2nd in the figure), protect them and check them weekly. In contrast, FGAR baits (1st) are used less often, are never checked and are not protected. Dimension 2 identified that the longer baits are used, the more variable checks become.

4. Discussion

By conducting an on-farm survey, we were able to obtain an outline pattern of rodenticide usage by a sample of farmers. Although our inability to engage non-respondents and determine their behaviour may have introduced some bias, as non-respondents can display different behaviours to respondents (White et al., 2005), our overall response rate was within acceptable limits for analysis (59%) (Babbie, 1990). Furthermore, the responses were credible with respect to the limited existing data on levels of rodenticide usage elsewhere in the UK (Dawson and Garthwaite, 2003; Dawson et al., 2001). Thus, this is the first published survey to document how the behaviour of end-users influences potential

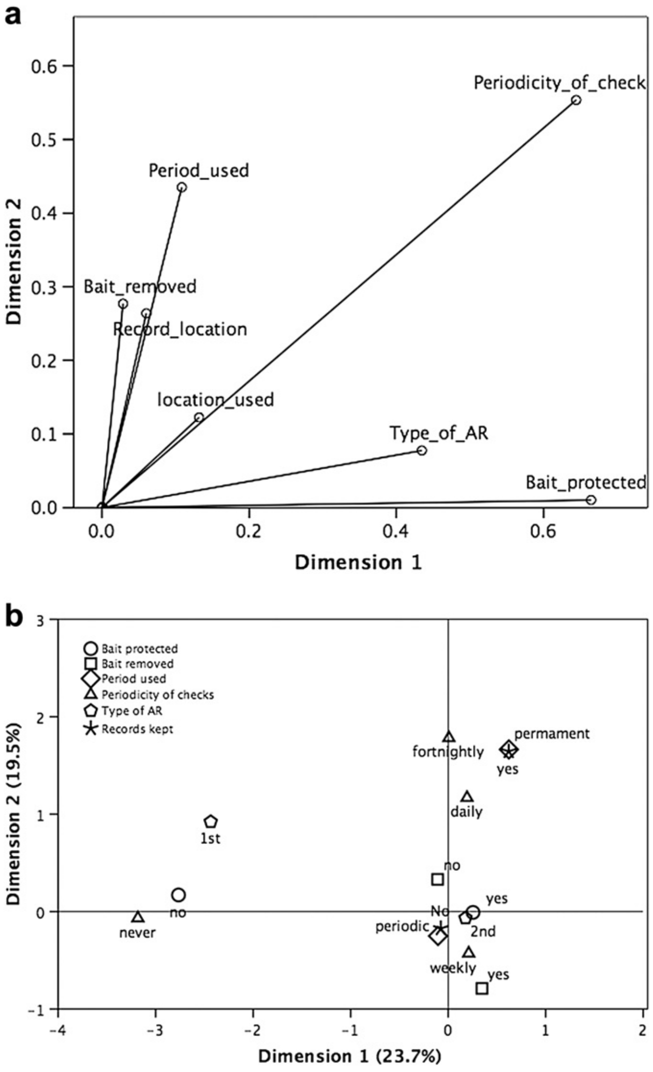

Fig. 2. a) Discrimination measure plot and b) joint category plot for a multiple correspondence analysis of behavioural traits amongst anticoagulant rodenticide users. *The amounts of variation explained by the two dimensions in the MCA are stated in the figure axes.*

risk to non-targets. It is also the first survey of rodenticide use in Northern Ireland; all previous surveys only covered Britain.

Most farmers used ARs every year as a means of preventing rodent infestations but a small proportion reported only using baits in years when rodents were perceived to be a problem. Farmers that bait every year appear to fall into two groups, permanent and periodic baiters. Periodic baiters use ARs for part of the year and are categorised by a high variation in the frequency with which they check bait stations, poor record keeping and baiting periods that extend beyond the 4–5 weeks recommended for controlling infestations (Anonymous, 1999, 2002). In contrast, permanent baiters apply ARs throughout the year, regularly check bait points and maintain records. The majority of permanent baiters do this apparently in response to the requirements of customers who specify that rodent control is practiced by suppliers. However, permanent baiting contravenes best practice recommendations, partly because it increases the risk of non-target exposure (Anonymous, 2001, 2002). Therefore, consumer requirements, combined with the failure of many periodic users to remove ARs following periods of treatment, extend the availability of baits to well beyond the autumn and winter period of peak rodenticide use. This may in part explain why ARs are detected in non-target wildlife at all times of the year and why exposure is not restricted to periods of peak AR use (Shore et al., 2003a).

If baits are not removed, or if baiting is permanent, the risk of primary non-target exposure can potentially be reduced by protecting baits. Most farmers protect bait from non-targets but FGAR users are less likely to do so than SGAR users. Although the risk of non-target primary exposure is likely to be low in NI because FGAR use is uncommon, this may not be the case in Great Britain where nearly a quarter of farmers use FGARs (Dawson et al., 2001). Although FGARS are less acutely toxic than SGARs, they are still toxic to most vertebrates and direct consumption can lead to death (Fisher et al., 2003; Mendenhall and Pank, 1980). It is unclear if FGAR users do not protect bait because of a lack of awareness of the hazards of these rodenticides, but our results suggest that promotion of best practice may need to highlight that FGARs, as well as SGARs, present a risk to non-target species.

Despite widespread protection of SGAR baits, the risk of secondary exposure resulting from the scavenging of poisoned rodent carcasses is likely to be significant. This is because the results from our survey suggest that farmers rarely search for and remove carcasses, but many often see dead rodents on their farms. Furthermore, the number of dead rodents that farmers note from their casual observations is likely to be a fraction of the true number as many carcasses will be scavenged quickly and not be seen. The widespread exposure to rodenticides of scavengers, such as the red kite (Walker et al., 2008a), is consistent with the idea that scavenged carcasses are likely to be a significant exposure pathway for scavenging birds and mammals. Searches for poisoned rodents and removal of their carcasses are essential if secondary poisoning via scavenging is to be minimised.

Due to the longer half-lives of SGARs compared with FGARs, extensive usage of more persistent ARs potentially enhances the risk of secondary poisoning (Eason et al., 2002; Wyllie, 1995). The unexpectedly high level of flocoumafen use in NI increases the risks to non-targets from AR use compared to other regions of the UK, especially as this compound is more toxic and persistent than any of the other SGARs available in the UK (Fisher et al., 2003; Parmar et al., 1987). We suggest that a greater availability or marketing of flocoumafen based ARs explains their greater level of use in NI rather than a general preference of farmers towards the most toxic ARs. Flocoumafen use elsewhere in the UK is relatively low (Dawson et al., 2001; Olney et al., 1991; Thomas and Wild, 1996) and it is rarely detected in predatory birds and mammals (Shore et al., 2003a,b; Walker et al., 2007, 2008a,b). Given the greater use of flocoumafen in NI, we would predict that there would be greater exposure to flocoumafen in predatory birds and mammals in NI than elsewhere in the UK though whether this would result in a greater occurrence of mortalities is unknown.

Despite apparent variable adherence to best practice amongst users in our survey, the extent of misuse appears to be low and is comparable to elsewhere in the UK. In NI, misuse in part may arise from the greater availability, and use of, flocoumafen in the Republic of Ireland (RoI) (Eadsforth et al., 1996; Dawson et al., 2001; McDonald and Harris, 2000). At present, there are no restrictions on flocoumafen and brodifacoum use in RoI and labelling does not carry the same restrictions as in the UK, where these compounds are restricted to indoor use only. As our survey suggests that most users obtain guidance on use from the manufacturers' guidelines, misuse amongst users who purchase ARs from the RoI may result from a lack of awareness of restrictions that apply to the UK. Addressing the labelling and sale of these products to farmers in Northern Ireland may therefore reduce such misuse.

Despite low awareness of best practice campaigns (CAIP, 2009), it is unlikely that low awareness alone explains the variable adherence recorded. Most farmers employ at least one element of best practice that suggests farmers already recognise the need to bait efficiently and protect wildlife but other factors are preventing total adherence. The time required to bait correctly may be the largest obstacle as rodent control is labour intensive (Anonymous, 2009). Lack of time is already recognised as part of the many pressures of farm management and consequently rodent control may not be a priority for many (Parry et al., 2005). A preventative approach to baiting may also be a symptom of the inability of farmers to dedicate the time needed to control infestations, even though such practices may have poor efficacy, waste money and increase selection pressure for resistance (Cowan et al., 1995). Clearly, there is a need to improve awareness and uptake of usage practices amongst farmers to reduce both the risk to non-target species and enhance the efficacy of rodent control. However, any campaigns designed to achieve this may also need to focus on demonstrating how best practice can be achieved in a timely manner and the financial benefits this will construe.

5. Conclusions

The results of our study suggest that, despite the availability of best practice guidelines for ARs, the uptake of such practice is heterogeneous amongst farmers. Many farmers in our survey carried out baiting in a manner that potentially increased the risk of exposure of non-target wildlife species. Low awareness of best practice may in part explain this, suggesting that there is a continuing need for promotion schemes, such as the Campaign for Responsible Rodenticide Use. However, it is also important that reasons for low adherence to best practice are clearly identified if such campaigns are to be successful.

Acknowledgements

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Appendix. Supplementary data

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.jenvman.2010.12.014.

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Mexican Prairie Dog

Julián Treviño-Villarreal

Common Name: Mexican prairie dog
Scientific Name: *Cynomys mexicanus*
Order: Rodentia
Family: Sciuridae
Status: Classified as Endangered by the IUCN (1990), the U.S. Fish and Wildlife Service (USFWS 1991), and the Secretaría de Desarrollo Social (SEDESOL 1994); listed on Appendix I of CITES (1992).
Threats: Habitat fragmentation and destruction; competition from cattle grazing; agricultural pesticides; unauthorized eradication programs that make use of poisons.
Habitat: Valleys, prairies, and intermontane basins at elevations of 1,690 to 2,200 m and associated with loamy soils that are dominated by grasses, forbs, and bare soil (Treviño-Villarreal et al. 1997; Treviño-Villarreal & Grant 1998).
Distribution: Endemic, restricted, and relict distribution (Hall 1981) of less than 500 km^2 in the Mexican states of Coahuila, Nuevo León, and San Luis Potosí. The only prairie dog colony historically reported for the state of Zacatecas is now extinct (Treviño-Villarreal & Grant 1998).

DESCRIPTION

Five species of prairie dogs are found in North America: the black-tailed (*Cynomys ludovicianus*), white-tailed (*C. leucurus*), Gunninson's (*C. gunnisoni*), Utah (*C. parvidens*), and Mexican (*C. mexicanus*). White-tails, Utahs, and Gunnisons all have short tails (30–65 mm and less than 20% of total body length) with a variable amount of white or gray hair; Mexicans and black-tails have longer tails (60–110 mm and more than 20% of total body length) with a distinct black tip (Hoogland 1995).

The origin and isolation of the Mexican prairie dog presumably relate to post-Pleistocene climatic changes and the isolation of black-tailed prairie dog populations around 40,000 years ago (Baker 1956; McCullough & Chesser 1987). Hall (1981) noted that the Mexican prairie dog skull differs from that of black-tails by having inflated auditory bullae, triangular cheek-teeth, and broad and usually posteriorly truncate nasals. The dental formula for *C. mexicanus* is 1/1 incisors, 0/0 canines, 1/1 premolars, and 3/3 molars. Adult males average 1,011 g, whereas adult females average 955 g (Treviño-Villarreal 1990). Mexican prairie dog color is pinkish-buff above and streaked with numerous black hairs, producing a grizzled effect (Ceballos & Wilson 1985). Below, the hairs are dark basally and yellow distally. The tail has more individual black hairs extending proximally along the lateral margins of the tail as a dark border. There are two complete pelage (coat of hair) renewals (winter and summer) and two transition pelage periods (spring and autumn) (Treviño-Villarreal 1990).

NATURAL HISTORY

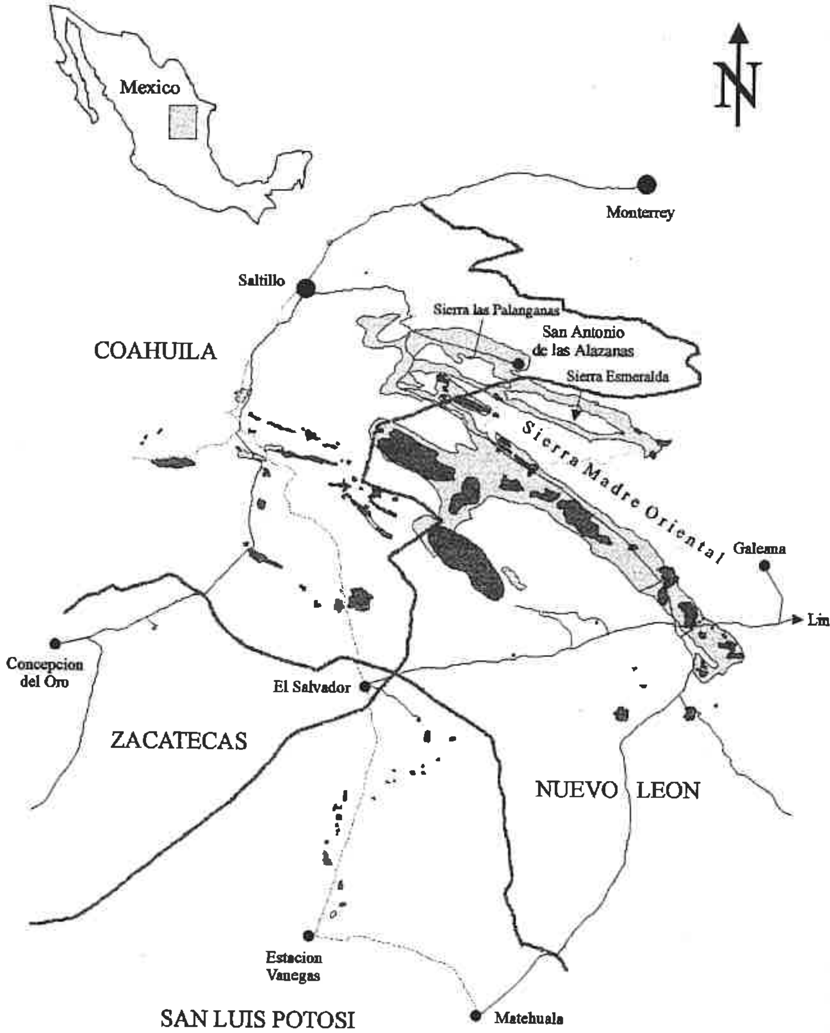
Treviño-Villarreal and Grant (1998) estimated that Mexican prairie dog current (1992–93), recent, and historical ranges are 478, 768, and 1,255 km^2, respectively. This indicates that the Mexican prairie dog has lost 62% of its historical, natural habitat as large and medium-size colonies have been fragmented into numerous, small, and isolated ones. Fully 74% of the current geographical range is in Nuevo León (354.7 km^2), 24% in Coahuila (112.5 km^2), and 2% in San Luis Potosí (9.5 km^2) (Figure 6).

Mexican prairie dogs are gregarious and social animals that live in colonies. A typical colony consists of distinct groups of individuals that occupy and protect small areas within the colony (Treviño-Villarreal 1990). Hoogland (1981a) and King (1955) referred to such groups in black-tailed prairie dogs as coteries. Groups are structured by age and usually consist of one or two adult males, one to four females, and 16 to 20 young of the year. Intergroup movements in Mexican prairie dogs involve not only individuals but also groups (Treviño-Villarreal 1990). Group formation apparently is associated with availability of resources, especially food. Dispersal behavior has been described for several members of the Sciuridae family; however, dispersal of Mexican (Treviño-Villarreal 1990) as well as black-tailed (Hoogland 1981a) prairie dogs is poorly understood. Chesser (1983) suggests that increased agricultural use of the land and associated ranching practices, widespread poisoning programs, and natural decimation of populations owing to disease (e.g., sylvatic plague) have reduced the distribution of black-tailed prairie dog populations.

Mexican prairie dogs begin to reproduce either during the first or second year of life depending on body weight, current social structure of the colony, and environmental conditions, with litter size ranging from 4.0 to 4.5 (Treviño-Villarreal 1990). Mild climatic conditions throughout the range of the Mexican prairie dog permit a longer reproductive season than in other species of *Cynomys* in North America, which either hibernate or are inactive throughout most of the winter (King 1955). Reproduction usually occurs between early January and early April depending on food availability, which, in turn, depends primarily on rainfall patterns (Treviño-Villarreal 1990).

No figures on longevity for Mexican prairie dogs are available; however, in black-tailed prairie dogs, females may live 5 to 6 years whereas males usually do not survive longer than 4 years (Hoogland 1981b). Mortality factors affecting Mexican prairie dogs include plague and other diseases,

Figure 6. Distribution of Mexican Prairie Dogs



accidents, starvation, weather, parasites, and predation (King 1955; Hoogland 1995; Garret 1982), but human activities have caused the greatest loss (Chesser 1983; Clark 1977; Treviño-Villarreal 1990).

A large and diverse number of plants and animals are present throughout the grasslands inhabited by Mexican prairie dogs. A total of 84 species of vertebrates and 163 species of plants have been reported within the geographical range of the Mexican prairie dog and surrounding habitats (Jiménez-Guzmán 1966; Scott-M. 1984; Treviño-Villarreal 1988). Specially protected species, such as rattlesnakes (*Crotalus scotulatus*) and red-tailed hawks (*Buteo jamaicencis*); threatened species, such as badgers (*Taxidea taxus*), kit foxes (*Vulpes macrotis*), prairie falcons (*Falco mexicanus*), and burrowing owls (*Athene cunicularia*); and endangered species, such as golden eagles (*Aquila chrysateos*) (SEDESOL 1994), rely on Mexican prairie dogs as an important source of food or on their burrows for habitats.

CONFLICTING ISSUES

Prairie dogs in the United States and Canada have been considered economic pests because they clip and eat plants utilized by livestock. Similarly, Mexican farmers consider Mexican prairie dogs pests because they feed on commercial and subsistence crops (Treviño-Villarreal et al. 1996). Therefore the establishment of croplands led to extensive, unauthorized poisoning programs to eradicate Mexican prairie dogs. These efforts are local in planning and implementation, and they are not sponsored or coordinated by government. Despite widespread practice, the published literature has documented only one Mexican prairie dog poisoning eradication program (Medina & De La Cruz 1976). Poisoning is generally accepted because prairie dogs are perceived to conflict with human needs.

An estimated 62% of Mexican prairie dog habitat has been destroyed over the past four decades as a result of agricultural activities, and remaining habitat is under heavy grazing pressure from cattle (Treviño-Villarreal & Grant 1998). Densities of Mexican prairie dogs began declining in 1955, at the same time that high technology agriculture was established in the region (Treviño-Villarreal et al. 1996). With the opening of several new highways, the human population has increased, there is easier access for heavy agricultural equipment, and crop production has become the most intensive activity in Nuevo León and Coahuila. If agriculture continues advancing at its present rate in these areas, there is a strong possibility that 98% of remaining Mexican prairie dog habitat will disappear in the near future. Large farms also are being established in northern San Luis Potosí.

The fragmented distribution of remaining Mexican prairie dog habitat also may play an important role in determining the fate of colonies. The proximate cause of abandonment of the six colonies that were identified as inactive by Treviño-Villarreal and Grant (1998) remains speculative—none were close to croplands, and local residents did not observe any of the factors that have caused abandonment of colonies in other areas, such as disease (Treviño-Villarreal et al. 1998), poisoning eradication programs (Medina & De la Cruz 1976), direct or indirect effects of cattle grazing within the colonies and adjacent desert scrub communities (Mellink 1989), or catastrophic events (Oldemeyer et al. 1993). Chances of recolonization may be low owing to the colonies' relative isolation (Treviño-Villarreal & Grant 1998).

FUTURE AND PROGNOSIS

Mexican prairie dogs are Endangered and therefore protected by the Mexican Law for the Ecological Equilibrium and the Protection of the Environment (LEPEMA); however, there has been only one case in which the Mexican government, through LEPEMA, fined a private landowner in the state of San Luis Potosí because his land use practices were destroying and fragmenting Mexican prairie dog habitat (Treviño-Villarreal et al. 1992).

Studies on the effects of competition with cattle grazing, agricultural pesticides, and sylvatic plague, as well as pilot prairie dog reintroduction programs, are urgently needed to help future plans for the conservation and management of the Mexican prairie dog. However, such plans will require a strict regulation of agriculture; enforcement of the endangered species legislation by the Mexican Ministry of the Environment, Natural Resources, and Fisheries; and resolution of conflicts among the Mexican Agrarian Reform Law, the Forestry Law, and the Law for Ecological Equilibrium and the Protection of the Environment.

Mexican Wolf

Jane M. Packard and José F. Bernal-Stoopen

Common Name: Mexican wolf
Scientific Name: *Canis lupus baileyi*
Order: Carnivora
Family: Canidae
Status: Endangered in Mexico and the United States; a reintroduced population is designated as experimental and nonessential (east-central Arizona and west-central New Mexico).
Threats: Human-related mortality; depletion of prey populations owing to human activities.
Habitat: Dependent on adequate populations of large-bodied mammalian prey; primary habitat is in mid-elevation oak woodlands, with surrounding grasslands as secondary habitat.
Distribution: Formerly located throughout the western mountains and high plateau region of Mexico (from Michoacán and Puebla to the border regions of Arizona/Sonora, Chihuahua/New Mexico/Texas/Coahuila) (Leopold 1959; Young & Goldman 1944); presently there are infrequent signs of a small remnant population in the mountains on the border between Sonora and Chihuahua, where it has been logistically difficult to verify the information (Crane 1989). Captive-raised family groups have been reintroduced to the Blue Range Area of the Apache National Forest in Arizona (Dinon 1998; U.S. Fish and Wildlife Service 1997).

DESCRIPTION

The Mexican wolf is a relatively small-bodied subspecies of the gray wolf (25–42 kg), varying in color from grizzled-gray to tawny-cinnamon on the upper parts of the body, with lighter underparts (Brown 1983; Young & Goldman 1944). This subspecies is morphologically and genetically distinct from red wolves (*Canis rufus*) and coyotes (*Canis latrans*) (Hedrick et al. 1997).

In a revision of the taxonomic status of three subspecies of wolves described from Mexico and the southwestern United States, no convincing morphological evidence was found to separate the Mexican wolf (*C. l. baileyi*) from the extinct subspecies found in New Mexico (*C. l. mogollonensis*) and Texas (*C. l. monstrabilis*) (Brown 1983; U.S. Fish and Wildlife Service 1997). Body size and skull size overlap considerably with the variation observed in other subspecies of gray wolves (Brown 1983).

United States
Department of
Agriculture
Forest Service

**Rocky Mountain
Forest and Range
Experiment Station**

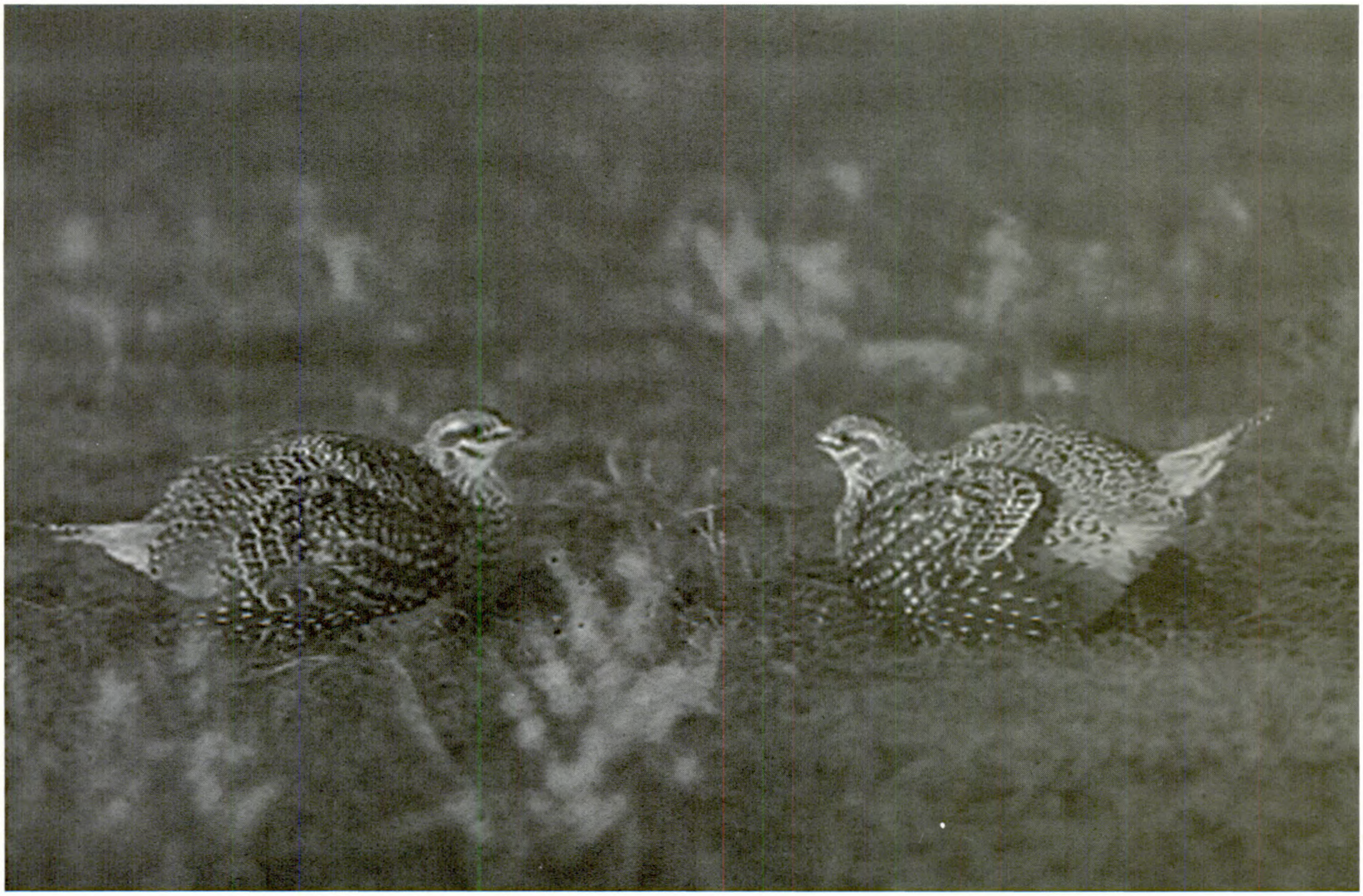
Fort Collins
Colorado 80526

**General Technical
Report RM-GTR-298**

Conserving Biodiversity on Native Rangelands: Symposium Proceedings

August 17, 1995

Fort Robinson State Park, Nebraska



Uresk, Daniel W.; Greg L. Schenbeck; James T. O'Rourke, tech coords. 1996. Conserving biodiversity on native rangelands: symposium proceedings; August 17, 1995; Fort Robinson State Park, Nebraska. General Technical Report RM-GTR-298. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 38 p.

Abstract: These proceedings are the result of a symposium, "Conserving biodiversity on native rangelands" held on August 17, 1995 in Fort Robinson State Park, NE. The purpose of this symposium was to provide a forum to discuss how elements of rangeland biodiversity are being conserved today. We asked, "How resilient and sustainable are rangeland systems to the increasing demands of a growing human population and to extended periods of drought?" Key programs and issues, identified by a program committee, were addressed by researchers and managers. Their papers provide research results, management findings, and describe management programs currently used to conserve rangeland biodiversity.

Keywords: biodiversity, rangeland, sustainability, drought, conservation

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USDA Forest Service
General Technical Report RM-GTR-298

September 1997

Conserving Biodiversity on Native Rangelands: Symposium Proceedings

August 17, 1995

Fort Robinson State Park, Nebraska

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Contents

Introduction

Rangelands embody biological diversity of profound ecological and social significance, yet it is the biological diversity of forests and wetlands that has been the focus of research by scientists and concern by the public. Recently, a broad array of people, from ecologists and biologists to ranchers and recreationists, have begun to realize the importance of rangeland conservation and biological diversity. Although these groups may not always share a common vision of rangelands, they share a common interest in the land that will foster a better understanding and appreciation of the value of diverse and healthy rangelands.

Ranchers have long practiced conservation of rangeland biological diversity. Most recognize the importance of both warm and cool season grasses to round out their forage programs, and many have noticed that in some years one grass will do poorly while another will thrive, thus balancing the production. Ranchers depend on native grasses coming back on their own after drought or a bad grasshopper year; some species will return quicker than others. Looking toward the future, ranchers manage their grass for a diverse rangeland community, not a monotypic one. This is conservation of rangeland biological diversity at the grass roots level.

Together, scientists and rangeland managers are traveling to new levels of conservation of rangeland biodiversity, but the journey has some formidable challenges. Herbivory, fire, drought, and other natural events and processes historically shaped rangeland biodiversity and ecological processes long before human action. However, human influence on the range has complicated and interrupted many naturally occurring mechanisms. The use and control of fire has altered its frequency and intensity. The pattern, frequency, and intensity of herbivory by large animals has been modified by the conversion from free-ranging bison and other large ungulates to confined domestic livestock and a proliferation of livestock water developments. Cultivation has fragmented and isolated rangelands and often natural processes no longer function. An insidious challenge to rangeland biodiversity is the invasion of exotic plants into native range often at the expense of native biota.

The purpose of this symposium was to provide a forum to discuss how elements of rangeland biodiversity are being conserved today. We asked, "How resilient and sustainable are rangeland systems to the increasing demands of a growing human population and to extended periods of drought?" One way to begin answering this question is to look at our successes and failures in conserving all parts of rangeland systems. Key programs and issues, identified by a program committee, were addressed by researchers and managers. Their papers, which have received statistical and peer review, are presented here and provide research results, management findings, and describe management programs currently used to conserve rangeland biodiversity. The paper "Gap Analysis in the Great Plains: A Large-Scale Geographic Strategy for Conservation of Biodiversity" by Dennis Jelinski, Michael Jennings, and James Merchant was withdrawn by the authors before publication of this workshop proceedings.

This symposium was held concurrently with the Annual Meeting of the Central Mountains and Plains Section of The Wildlife Society. We thank the organizers of that event for suggesting this symposium. Thanks are also extended for the well-attended field trip to review northern swift fox management in southwestern South Dakota that concluded the workshop.

A Neotropical Migratory Bird Prioritization for National Forests and Grasslands

Dick Roth[1] and Richard Peterson[2]

Abstract.—The Rocky Mountain Region of the USDA Forest Service provides nesting habitat for 146 species of neotropical migratory birds. Interactive, prioritization databases were developed for each National Forest and National Grassland in the Region to assist land managers in making informed decisions about resource allocations. The data was processed using Paradox software. This paper summarizes the uses and application of the database for the Oglala and Ft. Pierre National Grasslands.

METHODS

We used data provided by Colorado Bird Observatory and ranked according to the Partners-In-Flight (PIF) ranking scheme for initial prioritization of neotropical migratory birds (NTMBs). The approach ranks species by their relative susceptibility to extinction (Carter and Barker 1993, Hunter et al. 1993). There are many factors that contribute to extinction probability. The PIF prioritization scheme uses seven criteria as the most important in gauging a species susceptibility to extirpation or extinction: 1) importance of area of consideration (IA), (percentage of a species range that is within a state or geographic area under consideration); 2) global abundance (GA); 3) the degree of threat to the species' persistence on the breeding ground (TB); 4) the degree of threat to species' persistence on the wintering ground (TW); 5) breeding distribution (BD); 6) extent of wintering distribution (WD); 7) population trend in area of consideration (PT); based upon U.S. Fish and Wildlife Service Breeding Bird Survey (BBS) data. Each of the seven criteria is weighted equally. An individual species is assigned a score in each of the seven categories ranging from one (low concern) to five (high concern). Each species is ranked according to the average of the seven scores. The importance of area score (IA) was modified for our use to include a rank based upon the percentage of the area under consideration which meets breeding habitat requirements for a given species.

Uncertainty values are assigned to each species in conjunction with values assigned for threats to breeding (TBU) and wintering (TWU), and population trend (PTU). These uncertainty values reflect the extent of the available information for each of the associated criteria. They indicate the extent and location of gaps in our knowledge of neotropical migrant biology. These values help us differentiate between species with definite management concerns and those requiring additional monitoring or research in order to more clearly reflect their status.

Several criteria were modified for the Oglala and Ft. Pierre National Grasslands. Population trend (PT) and Population trend uncertainty scores were determined from USFWS Breeding Bird Survey (BBS) for the 10-year and 26-year scores. Data from physiographic region 39 (Missouri Plateau-Unglaciated) were used for both grasslands. Other population trend data more specific to the area under consideration can be used for these criteria if available. Threats to breeding habitat (TB) and Threats to breeding habitat uncertainty (TBU) criteria provided by PIF were used (Carter and Barker 1993). Additionally, known local threats were also considered such as reduction of prairie dog towns as a threat to burrowing owl habitat. In this case, a TB score of 5 was used because loss of prairie dog towns would result in elimination of burrowing owl habitat (Peterson 1994).

Several methods have been developed to determine priorities for community based conservation (Millsap et al. 1990, Master 1991, Reed 1992). The technique developed by Partners in Flight is essentially one that ranks individual species first, and secondarily ranks habitats based on individual species scores grouped by habitat preference. This ranking can then be used to develop and justify community based conservation programs. The determina-

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tion of breeding occurrence and habitat preference of neotropical migratory landbirds on the Oglala and Ft. Pierre Grasslands was made using local expertise.

The habitat types and conditions developed for the Grasslands and assigned to each species have three levels:

1) Appropriate habitat contains six major breeding bird habitat types. They include trees/woodlands, shrubs/shrublands, grass/grasslands, edge-tree/grass-shrub/grass, wetlands and special topographic structure.
2) Suitable habitat, in general, additional conditions are needed for appropriate habitat to be suitable breeding habitat for a given species. For grasslands, additional conditions could be related to a given height and density of grasses or forbs. For trees/woodland habitat, additional conditions could include deciduous trees, cavities or a multi-layered canopy.
3) Special conditions includes topographic structures such as cliffs and cutbanks, but also includes features such as riparian areas and prairie dog towns.

These habitat categories enable development of habitat ranking based on a species' use of a wide variety of habitat types and variables.

Coding used for habitats and special features is as follows:

Habitats T-(t)rees/woodlands, coni(f)erous, (d)eciduous, (o)ld growth, m(u)ltilayer canopy, and
(c)avities.
E-(e)dge, tree-grass/shrub-grass.
S-(s)hrubs, (b)ig sagebrush, (2) thorny shrubs-esp. plum,
G-(g)rass/grasslands-open areas-esp. s(h)ort and/or sparse, t(a)ll and/or de(n)se, mi(x)ed/mid.
W-(w)etlands/(w)ater-(1)riparian, (m)arsh/tall emergent, (3) wet meadow-tall grass/short emergent.

Specials s(P)ecial-topo/structure-(4)cliffs/caves/ledges and cutbanks, (5)buildings/bridges/chimneys and bird houses, (6)islands/bare shores.
s(p)ecial-other-(7)prairie dog towns, (i.e. burrows/bare ground/short grass and associated prey), forest fire locations-(B)urned areas, esp. large with tall snags, (9) cropland-esp alfalfa, (0)old crow/magpie nests.

The mix of numbers and letters used in the coding may appear to be confusing; however, familiarization with the application of those codes as displayed in the habitat columns of the accompanying tables reveals that they provide a logical fit.

RESULTS

The Oglala and Ft. Pierre National Grasslands support 79 and 68 species of neotropical migratory landbirds which regularly nest there, or a combined total of 84 regular nesters. These are listed in Appendix 1 and 2 along with all associated prioritization scores for the seven criteria and some of the associated uncertainty scores. Species with R10 or R26 ranks of 3.00 or greater should be given high priority for management considerations (Thompson et al. 1993). Analysis of the data reveals that 18 of the 84 species have a R10 or R26 rank of 3.00 or greater (Appendix 1 and 2). The R10 and R26rank scores along with importance of area, threats to breeding and breeding distribution scores help to provide a framework for setting management priorities. As an illustration, the chestnut-collard longspur has high R10 and R26 rank scores but has an importance of area (IA) score of only 3.00.

Consequently, other species with higher IA scores should be given higher management priority. The two top ranked species on both grasslands (burrowing owl and ferruginous hawk) have a preference for short-grass prairie and prairie dog towns. Other species on these two grassland have a preference for tall and mixed-grass prairie. Consequently, management of the National Grassland units for a diversity of heights and would provide habitat for both species.

The database contains scores for each criterion, for each species, for each unit where they are likely to occur. It is important that the data for each unit be analyzed separately for more specific insights into the top priority species and habitat for each unit. For example, what is the importance of the habitat on the unit being analyzed for a given species. What are the threats to that habitat? What is the status and trend of that habitat?

This prioritization system reveals that the highest ranked habitat on the Oglala National Grassland is big sagebrush and that is based on one species (table 1). The next highest ranked habitat is short and mixed-grass prairie and prairie dog towns respectively. These habitats support six and four high priority (= > 3) species respectively. Edge habitat and riparian habitat are both important because of the diversity of species that they support. These values are based upon the relative susceptibility to extinction of species found in each habitat. Information on species as presented in table 2 should also be considered along with the habitat information when weighing the consequences of management actions.

A total of 12 species from the Oglala National Grassland have a R26 Rank of 3.00 or greater. Brewer's Sparrow is the species in big sagebrush habitat which causes the high habitat rank in table 1. The rank of 1 for importance of area score (IA) indicates that only a small portion of the Oglala National Grassland provides suitable breeding habitat for Brewer's Sparrows. The two top-ranked species use prairie dog towns and the top five species also short to mixed grass prairie habitats.Therefore, the highest priority habitats for NTMBs on the Oglala National Grassland should be those that support these species.

Table 1. Habitat association scores for the Oglala National Grassland based on R26 species ranks.

Habitat	≤3	<3 to 2	<1.99	# Species	Average score	Total score
Short/Mix Grass	6	1	1	8	3.08	24.71
Prairie Dog Towns	4	2	1	7	2.94	20.57
Mix/tall Grass	2	7		9	2.81	29.00
Trees Deciduous	2	8	2	12	2.48	29.71
Shrub Big Sage	1			1	3.14	3.14
Shrub Dense		5		5	2.60	13.00
Edge	1	15	7	23	2.32	53.41
Water/marsh		7	4	11	2.18	24.00
Riparian	2	15	5	22	2.36	51.99

Table 2. Species on the Oglala National Grassland with R10 or R26 =≥3.00.

Species	Hab	IA	AB	TB	BD	R10	R26
Burrowing Owl	Gh7	5	4	5	3	3.57	3.86
Long-billed Curlew	Gxh7	5	3	3	4	3.86	3.71
Chestnut-collared Longspur	Gxh	3	3	3	4	3.29	3.57
Lark Bunting	Gxhs	5	2	3	4	3.29	3.43
Ferruginous Hawk	Gxht7	3	4	4	3	3.29	3.29
Black-billed Cuckoo	Tds12	2	3	4	3	3.29	3.14
Bobolink*	Ga39	1	2	4	3	3.14	3.14
Brewer's Sparrow	Sb	1	2	4	3	3.00	3.14
Loggerhead Shrike	Es2	3	3	4	2	3.00	3.14
Dickcissel*	Ga9	1	2	4	3	2.86	3.00
Great Crested Flycatcher	Tdc1	1	2	4	3	3.00	3.00
Prairie Falcon	Gxh47	4	3	3	3	3.14	3.00

** Species found in the area but not confirmed nester on National Grassland.*

Similar analysis of the data for the Ft Pierre National Grassland reveals somewhat different results (table 3). Ft Pierre is in a higher precipitation area and has taller grasses and more deciduous trees than the Oglala National Grassland. Bird species diversity is greater across habitat types than on the Oglala National Grassland and mixed/tall grass habitat higher priority. The burrowing owl is the highest ranked species on both units (table 4). Dickcissel , bobolink, grasshopper sparrow, northern harrier and upland sandpiper had higher prioritization scores on the Ft. Pierre National Grassland. Management of prairie dog towns and short grass habitat should have some priority on Ft. Pierre, but management for mixed to tall grass habitat is of higher priority based on this analysis.

Table 3. Habitat association scores for the Ft. Pierre National Grassland based on R26 species ranks.

Habitat	≥3	>3 to 2	>1.99	# Species	Average score	Total score
Short/Mix Grass	5	1	1	7	3.06	21.43
Prairie Dog Towns	3	2	1	6	2.81	16.86
Mix/Tall Grass	5	5		10	3.13	31.29
Trees Deciduous	2	9	2	13	2.50	32.58
Shrub Dense	1	5		6	2.26	13.57
Edge	1	9	7	17	1.98	33.70
Water/marsh	1	8	5	14	2.01	28.13
Riparian	3	14	5	22	2.39	52.58

Table 4. Species on Ft. Pierre National Grassland with R10 or R26 scores ≥ 3.00.

Species	Hab	IA	TB	BD	AB	R10	R26
Burrowing Owl	Gh7	4	5	3	5	3.57	3.86
Baird's Sparrow*(Historic)	Gx3	4	5	5	0	3.86	3.71
Chestnut-collared Longspur	Gxh	3	3	4	3	3.29	3.57
Dickcissel	Ga9	2	3	3	5	3.29	3.43
Ferruginous Hawk	Gxht7	4	4	3	4	3.43	3.43
Lark Bunting	Gxhs	2	3	4	5	3.29	3.43
Bobolink	Ga39	2	3	3	3	3.29	3.29
Long-billed Curlew*	Gxh7	3	4	4	1	3.43	3.29
Bell's Vireo*	Sn12	3	4	3	1	3.14	3.14
Black-billed Cuckoo	Tds12	3	4	3	2	3.29	3.14
Grasshopper Sparrow	Gxa	2	2	2	5	2.57	3.00
Great Chrested Flycatcher*	Tdc1	2	4	3	1	3.00	3.00
Loggerhead Shrike	Es2	3	4	2	2	2.86	3.00
Northern Harrier	Gasm	3	3	1	5	3.00	3.00
Sprague's Pipit*(historic)	Gxa	3	5	4	0	3.00	3.00
Upland Sandpiper	Gx	3	2	3	5	3.14	3.00

** Species found in the area but not confirmed nester on National Grassland.*

CONCLUSIONS

The PIF species ranking system is a helpful tool in establishing priorities for Neotropical Migratory Bird species and habitat based management efforts for those species. It should not replace human judgment or additional information which might be important in setting resource priorities. Refinement of the PIF data as was done on the Oglala and Ft. Pierre National Grasslands with local expertise increases the utility value of the system. Only a few analysis examples were given here. However, an endless variety of queries can be used to tease additional information from the data.

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Appendix 1. Prioritization scores for the Neotropical Migratory Landbirds of the Oglala National Grasslands.

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
American Goldfinch	Tdes1	1.00	2.00	3.00	1.00	1.00	2.00	3.00	3.00	2.00	3.00	1.43	1.57
American Kestrel	Ec8	1.00	1.00	2.00	2.00	1.00	4.00	1.00	1.00	2.00	3.00	1.71	1.57
American Robin	Ethw	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00	4.00	3.00	1.57	1.29
Barn Swallow	Pgw5	1.00	1.00	1.00	2.00	1.00	2.00	1.00	1.00	5.00	1.00	1.86	1.29
Belted Kingfisher	W4	2.00	4.00	2.00	2.00	1.00	1.00	4.00	3.00	3.00	4.00	2.00	2.14
Black-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	3.00	2.00	3.00	3.00	4.00	3.00	3.29	3.14
Black-headed Grosbeak	Tds1	2.00	3.00	4.00	2.00	3.00	2.00	2.00	3.00	2.00	2.00	2.57	2.57
Blue Grosbeak	Sn2	3.00	3.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.43	2.57
Bobolink	Ga39	2.00	4.00	2.00	3.00	3.00	1.00	5.00	2.00	5.00	2.00	3.14	3.14
Brewer's Blackbird	Es29	2.00	3.00	5.00	2.00	3.00	1.00	3.00	3.00	3.00	3.00	2.29	2.29
Brewer's Sparrow	Sb	2.00	4.00	3.00	4.00	3.00	1.00	5.00	1.00	4.00	3.00	3.00	3.14
Brown-headed Cowbird	Egsm	1.00	1.00	1.00	1.00	1.00	5.00	1.00	1.00	1.00	1.00	1.71	1.71
Burrowing Owl	Gh7	4.00	5.00	2.00	3.00	3.00	5.00	4.00	3.00	2.00	3.00	3.57	3.86
Cedar Waxwing	Ts	2.00	2.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.00	2.14
Chestnut-collared Longspur	Gxh	3.00	3.00	4.00	4.00	4.00	3.00	4.00	3.00	2.00	3.00	3.29	3.57
Chipping Sparrow	Efs	1.00	3.00	4.00	2.00	1.00	3.00	4.00	3.00	4.00	3.00	2.29	2.29
Cliff Swallow	Pw45	2.00	2.00	4.00	2.00	1.00	1.00	3.00	3.00	3.00	3.00	2.00	2.00
Common Nighthawk	Eh	2.00	2.00	4.00	2.00	1.00	5.00	3.00	3.00	4.00	3.00	2.43	2.29
Common Poorwill	Ef4	3.00	2.00	4.00	3.00	3.00	2.00	3.00	4.00	3.00	4.00	2.71	2.71
Common Yellowthroat	Wms1	1.00	3.00	2.00	2.00	1.00	2.00	4.00	3.00	5.00	2.00	2.29	2.14
Cooper's Hawk	To1	3.00	3.00	3.00	3.00	1.00	1.00	3.00	4.00	3.00	5.00	2.29	2.29
Dickcissel	Ga9	2.00	4.00	3.00	2.00	3.00	1.00	5.00	1.00	4.00	3.00	2.86	3.00
Eastern Bluebird	Ec85	2.00	3.00	2.00	3.00	3.00	1.00	3.00	4.00	3.00	4.00	2.43	2.43
Eastern Kingbird	E	1.00	1.00	2.00	3.00	2.00	3.00	2.00	3.00	1.00	1.00	2.00	2.14
Eastern Phoebe	Td15	2.00	4.00	4.00	3.00	3.00	1.00	3.00	4.00	3.00	5.00	2.57	2.57
Ferruginous Hawk	Gxht7	4.00	4.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.00	3.29	3.29
Golden Eagle	Et47	3.00	2.00	2.00	2.00	2.00	5.00	4.00	3.00	2.00	3.00	2.57	2.86
Grasshopper Sparrow	Gxa	2.00	2.00	3.00	2.00	2.00	4.00	5.00	1.00	2.00	3.00	2.43	2.86
Gray Catbird	Sn12	2.00	4.00	2.00	2.00	2.00	2.00	4.00	2.00	2.00	3.00	2.43	2.71
Great Crested Flycatcher	Tdc1	2.00	4.00	3.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	3.00	3.00
Horned Lark	Gh7	1.00	1.00	1.00	1.00	1.00	5.00	2.00	2.00	2.00	3.00	1.71	1.71
House Wren	Tc15	1.00	2.00	1.00	1.00	1.00	2.00	1.00	1.00	1.00	2.00	1.29	1.29
Indigo Bunting	Tds1	1.00	3.00	3.00	2.00	3.00	1.00	3.00	4.00	3.00	4.00	2.29	2.29
Killdeer	Gh67	1.00	2.00	2.00	1.00	1.00	5.00	4.00	1.00	5.00	1.00	2.29	2.14
Lark Bunting	Gxhs	2.00	3.00	3.00	3.00	4.00	5.00	4.00	2.00	3.00	3.00	3.29	3.43
Lark Sparrow	E	3.00	2.00	3.00	2.00	2.00	3.00	3.00	3.00	1.00	2.00	2.29	2.57
Lazuli Bunting	Ts1	2.00	3.00	4.00	2.00	3.00	2.00	4.00	3.00	2.00	3.00	2.57	2.86
Loggerhead Shrike	Es2	3.00	4.00	4.00	4.00	2.00	3.00	3.00	3.00	2.00	2.00	3.00	3.14
Long-billed Curlew	Gxh7	3.00	3.00	4.00	3.00	4.00	5.00	4.00	3.00	5.00	1.00	3.86	3.71
Long-eared Owl	Efo0	3.00	3.00	3.00	3.00	1.00	1.00	3.00	5.00	3.00	5.00	2.14	2.14

Appendix 1 (Continued).

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
Marsh Wren	Wm	2.00	4.00	2.00	4.00	3.00	2.00	3.00	4.00	3.00	4.00	2.71	2.71
Merlin	Ef0	4.00	4.00	4.00	3.00	2.00	2.00	3.00	4.00	3.00	4.00	2.86	2.86
Mountain Bluebird	Ec85	2.00	3.00	3.00	3.00	3.00	2.00	4.00	2.00	3.00	3.00	2.57	2.71
Mourning Dove	Ew	1.00	1.00	1.00	1.00	1.00	4.00	1.00	1.00	3.00	3.00	1.71	1.43
N. Rough-winged Swallow	Pw4	3.00	3.00	3.00	2.00	1.00	2.00	4.00	3.00	3.00	3.00	2.43	2.57
Northern Flicker	Ec8	1.00	2.00	1.00	1.00	1.00	2.00	4.00	2.00	3.00	3.00	1.57	1.71
Northern Harrier	Gasm	3.00	4.00	3.00	4.00	1.00	3.00	4.00	3.00	4.00	3.00	2.86	2.86
Northern Mockingbird	Eds12	1.00	2.00	2.00	1.00	2.00	1.00	3.00	4.00	3.00	4.00	1.71	1.71
Northern Oriole	Tds1	2.00	3.00	3.00	2.00	2.00	2.00	3.00	3.00	3.00	3.00	2.43	2.43
Orchard Oriole	Tds1	3.00	3.00	3.00	2.00	3.00	2.00	2.00	2.00	4.00	3.00	2.86	2.57
Ovenbird	Tu	2.00	4.00	4.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	2.86	2.86
Pine Siskin	Tfe	1.00	2.00	3.00	1.00	2.00	2.00	3.00	4.00	3.00	4.00	1.71	1.71
Prairie Falcon	Gxh47	3.00	3.00	3.00	3.00	3.00	4.00	3.00	3.00	4.00	3.00	3.14	3.00
Red-eyed Vireo	Tdu1	1.00	4.00	4.00	2.00	2.00	1.00	3.00	3.00	3.00	4.00	2.29	2.29
Red-tailed Hawk	Etg	1.00	2.00	2.00	2.00	1.00	5.00	3.00	3.00	3.00	3.00	2.14	2.14
Red-winged Blackbird	Wms1	1.00	2.00	1.00	1.00	1.00	2.00	4.00	2.00	4.00	3.00	1.71	1.71
Rock Wren	P4	3.00	2.00	2.00	2.00	3.00	3.00	4.00	2.00	4.00	3.00	2.71	2.71
Rufous-sided Towhee	Sn	1.00	3.00	4.00	2.00	2.00	2.00	4.00	3.00	4.00	3.00	2.29	2.29
Say's Phoebe	G45	3.00	2.00	3.00	3.00	2.00	3.00	3.00	3.00	3.00	3.00	2.71	2.71
Sharp-shinned Hawk	Tfo	3.00	3.00	2.00	3.00	1.00	1.00	3.00	4.00	3.00	4.00	2.14	2.14
Short-eared Owl	Gasm	3.00	4.00	4.00	4.00	1.00	2.00	2.00	3.00	4.00	3.00	2.71	2.43
Swainson's Hawk	Gxt9	3.00	2.00	2.00	3.00	2.00	5.00	2.00	1.00	2.00	3.00	2.86	2.86
Tree Swallow	Ec15	2.00	4.00	3.00	3.00	1.00	1.00	2.00	3.00	3.00	3.00	2.29	2.14
Turkey Vulture	E4	1.00	2.00	4.00	2.00	1.00	4.00	2.00	2.00	4.00	3.00	2.14	1.86
Upland Sandpiper	Gx	3.00	2.00	3.00	3.00	3.00	4.00	2.00	3.00	3.00	3.00	3.00	2.86
Vesper Sparrow	Gxs	3.00	3.00	4.00	2.00	2.00	2.00	4.00	3.00	4.00	3.00	2.57	2.57
Violet-green Swallow	Efc4	2.00	3.00	3.00	2.00	3.00	2.00	3.00	4.00	3.00	4.00	2.57	2.57
Warbling Vireo	Td1	2.00	3.00	4.00	2.00	2.00	2.00	5.00	1.00	4.00	3.00	2.57	2.71
Western Kingbird	E	1.00	1.00	2.00	2.00	3.00	3.00	1.00	1.00	1.00	2.00	2.14	2.14
Western Meadowlark	Gx7	1.00	2.00	2.00	3.00	2.00	5.00	3.00	3.00	3.00	3.00	2.43	2.43
Western Tanager	Tf	2.00	3.00	4.00	2.00	3.00	2.00	3.00	4.00	3.00	4.00	2.57	2.57
Western Wood-Pewee	T	2.00	3.00	4.00	3.00	2.00	2.00	2.00	2.00	1.00	1.00	2.43	2.57
White-throated Swift	P4	3.00	2.00	3.00	2.00	3.00	1.00	3.00	4.00	3.00	4.00	2.43	2.43
Willow Flycatcher	Sn12	3.00	4.00	3.00	3.00	3.00	1.00	3.00	5.00	4.00	3.00	3.00	2.86
Yellow Warbler	Tds1	1.00	4.00	3.00	2.00	1.00	2.00	2.00	3.00	2.00	3.00	1.86	1.86
Yellow-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	2.00	2.00	2.00	3.00	3.00	4.00	2.86	2.71
Yellow-breasted Chat	Sn12	2.00	3.00	3.00	3.00	2.00	2.00	3.00	3.00	1.00	1.00	2.29	2.57
Yellow-headed Blackbird	Wm	3.00	4.00	2.00	3.00	3.00	2.00	2.00	3.00	4.00	3.00	3.14	2.86
Yellow-rumped Warbler	Tf	1.00	2.00	2.00	1.00	1.00	2.00		4.00	3.00	4.00	1.71	1.29

Appendix 2. Prioritization scores for the Neotropical Migratory Landbirds of the Ft. Pierre National Grasslands.

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
American Goldfinch	Tdes1	1.00	2.00	3.00	1.00	1.00	2.00	3.00	3.00	2.00	3.00	1.43	1.57
American Kestrel	Ec8	1.00	2.00	2.00	2.00	1.00	4.00	1.00	1.00	2.00	3.00	1.86	1.71
American Robin	Ethw	1.00	1.00	1.00	1.00	1.00	2.00	2.00	2.00	4.00	3.00	1.57	1.29
Baird's Sparrow(historic)	Gx3	4.00	5.00	4.00	4.00	5.00	0.00	4.00	3.00	5.00	2.00	3.86	3.71
Bank Swallow	Pw4	3.00	3.00	4.00	2.00	1.00	1.00	2.00	3.00	2.00	2.00	2.14	2.14
Barn Swallow	Pgw5	1.00	1.00	1.00	2.00	1.00	2.00	1.00	1.00	5.00	1.00	1.86	1.29
Bell's Vireo	Sn12	3.00	4.00	3.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	3.14	3.14
Belted Kingfisher	W4	2.00	4.00	2.00	2.00	1.00	1.00	4.00	3.00	3.00	4.00	2.00	2.14
Black-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	3.00	2.00	3.00	3.00	4.00	3.00	3.29	3.14
Black-headed Grosbeak	Tds1	2.00	3.00	4.00	2.00	3.00	1.00	2.00	3.00	2.00	2.00	2.43	2.43
Blue Grosbeak	Sn2	3.00	3.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.43	2.57
Bobolink	Ga39	2.00	3.00	2.00	3.00	3.00	3.00	5.00	2.00	5.00	2.00	3.29	3.29
Brown-headed Cowbird	Egsm	1.00	1.00	1.00	1.00	1.00	5.00	1.00	1.00	1.00	1.00	1.71	1.71
Burrowing Owl	Gh7	4.00	5.00	2.00	3.00	3.00	5.00	4.00	3.00	2.00	3.00	3.57	3.86
Cedar Waxwing	Ts	2.00	3.00	3.00	2.00	2.00	1.00	4.00	3.00	3.00	4.00	2.14	2.29
Chestnut-collared Longspur	Gxh	3.00	3.00	4.00	4.00	4.00	3.00	4.00	3.00	2.00	3.00	3.29	3.57
Chipping Sparrow	Efs	1.00	3.00	4.00	2.00	1.00	1.00	4.00	3.00	4.00	3.00	2.00	2.00
Cliff Swallow	Pw45	2.00	2.00	4.00	2.00	1.00	1.00	3.00	3.00	3.00	3.00	2.00	2.00
Common Nighthawk	Eh	2.00	2.00	4.00	2.00	1.00	5.00	3.00	3.00	4.00	3.00	2.43	2.29
Common Yellowthroat	Wms1	1.00	3.00	2.00	2.00	1.00	2.00	4.00	3.00	5.00	2.00	2.29	2.14
Dickcissel	Ga9	2.00	3.00	3.00	2.00	3.00	5.00	5.00	1.00	4.00	3.00	3.29	3.43
Eastern Bluebird	Ec85	2.00	3.00	2.00	3.00	3.00	1.00	3.00	4.00	3.00	4.00	2.43	2.43
Eastern Kingbird	E	1.00	1.00	2.00	3.00	2.00	3.00	2.00	3.00	1.00	1.00	2.00	2.14
Eastern Phoebe	Td15	2.00	4.00	4.00	3.00	3.00	1.00	3.00	4.00	3.00	5.00	2.57	2.57
Ferruginous Hawk	Gxht7	4.00	4.00	3.00	3.00	3.00	4.00	3.00	3.00	3.00	3.00	3.43	3.43
Grasshopper Sparrow	Gxa	2.00	2.00	3.00	2.00	2.00	5.00	5.00	1.00	2.00	3.00	2.57	3.00
Gray Catbird	Sn12	2.00	4.00	2.00	2.00	2.00	1.00	4.00	2.00	2.00	3.00	2.29	2.57
Great Crested Flycatcher	Tdc1	2.00	4.00	3.00	4.00	3.00	1.00	3.00	4.00	3.00	4.00	3.00	3.00
Horned Lark	Gh7	1.00	1.00	1.00	1.00	1.00	5.00	2.00	2.00	2.00	3.00	1.71	1.71
House Wren	Tc15	1.00	2.00	1.00	1.00	1.00	2.00	1.00	1.00	1.00	2.00	1.29	1.29
Indigo Bunting	Tds1	1.00	3.00	3.00	2.00	3.00	1.00	3.00	4.00	3.00	4.00	2.29	2.29
Killdeer	Gh67	1.00	2.00	2.00	1.00	1.00	5.00	4.00	1.00	5.00	1.00	2.29	2.14
Lark Bunting	Gxhs	2.00	3.00	3.00	3.00	4.00	5.00	4.00	2.00	3.00	3.00	3.29	3.43
Lark Sparrow	E	3.00	2.00	3.00	2.00	2.00	2.00	3.00	3.00	1.00	2.00	2.14	2.43
Least Flycatcher	Td1	3.00	4.00	5.00	4.00	2.00	1.00	3.00	3.00	2.00	3.00	2.71	2.86

Appendix 2 (Continued).

Species	Hab	AB	TB	TBU	TW	BD	IA	PT26	PTU26	PT10	PTU10	R10	R26
Loggerhead Shrike	Es2	3.00	4.00	4.00	4.00	2.00	2.00	3.00	3.00	2.00	2.00	2.86	3.00
Long-billed Curlew	Gxh7	3.00	4.00	4.00	3.00	4.00	1.00	4.00	3.00	5.00	1.00	3.43	3.29
Long-eared Owl	Efo0	3.00	3.00	3.00	3.00	1.00	1.00	3.00	5.00	3.00	5.00	2.14	2.14
Marsh Wren	Wm	2.00	4.00	2.00	4.00	3.00	1.00	3.00	3.00	3.00	4.00	2.57	2.57
Mourning Dove	Ew	1.00	1.00	1.00	1.00	1.00	4.00	1.00	1.00	3.00	3.00	1.71	1.43
N. Rough-winged Swallow	Pw4	3.00	3.00	3.00	2.00	1.00	2.00	4.00	3.00	3.00	3.00	2.43	2.57
Northern Flicker	Ec8	1.00	2.00	1.00	1.00	1.00	2.00	4.00	2.00	3.00	3.00	1.57	1.71
Northern Harrier	Gasm	3.00	3.00	3.00	4.00	1.00	5.00	4.00	3.00	4.00	3.00	3.00	3.00
Northern Mockingbird	Eds12	1.00	2.00	2.00	1.00	2.00	1.00	3.00	4.00	3.00	4.00	1.71	1.71
Northern Oriole	Tds1	2.00	3.00	3.00	2.00	2.00	2.00	3.00	3.00	3.00	3.00	2.43	2.43
Orchard Oriole	Tds1	3.00	3.00	3.00	2.00	3.00	3.00	2.00	2.00	4.00	3.00	3.00	2.71
Red-eyed Vireo	Tdu1	1.00	4.00	4.00	2.00	2.00	1.00	3.00	3.00	3.00	4.00	2.29	2.29
Red-tailed Hawk	Etg	1.00	2.00	2.00	2.00	1.00	5.00	3.00	3.00	3.00	3.00	2.14	2.14
Red-winged Blackbird	Wms1	1.00	2.00	1.00	1.00	1.00	3.00	4.00	2.00	4.00	3.00	1.86	1.86
Rock Wren	P4	3.00	3.00	2.00	2.00	3.00	1.00	4.00	2.00	4.00	3.00	2.57	2.57
Rufous-sided Towhee	Sn	1.00	3.00	4.00	2.00	2.00	2.00	4.00	3.00	4.00	3.00	2.29	2.29
Savannah Sparrow	Gx3	3.00	4.00	4.00	3.00	1.00	1.00	5.00	1.00	5.00	1.00	2.71	2.71
Say's Phoebe	G45	3.00	2.00	3.00	3.00	2.00	1.00	3.00	3.00	3.00	3.00	2.43	2.43
Short-eared Owl	Gasm	3.00	3.00	4.00	4.00	1.00	5.00	2.00	3.00	4.00	3.00	3.00	2.71
Sprague's Pipit(historic)	Gxa	3.00	5.00	5.00	3.00	4.00	0.00	3.00	3.00	3.00	3.00	3.00	3.00
Swainson's Hawk	Gxt9	3.00	2.00	2.00	3.00	2.00	5.00	2.00	1.00	2.00	3.00	2.86	2.86
Tree Swallow	Ec15	2.00	3.00	3.00	3.00	1.00	1.00	2.00	3.00	3.00	3.00	2.14	2.00
Turkey Vulture (no nest?)	E4	1.00	2.00	4.00	2.00	1.00	1.00	2.00	2.00	4.00	3.00	1.71	1.43
Upland Sandpiper	Gx	3.00	2.00	3.00	3.00	3.00	5.00	2.00	3.00	3.00	3.00	3.14	3.00
Vesper Sparrow	Gxs	3.00	3.00	4.00	2.00	2.00	1.00	4.00	3.00	4.00	3.00	2.43	2.43
Warbling Vireo	Td1	2.00	4.00	4.00	2.00	2.00	2.00	5.00	1.00	4.00	3.00	2.71	2.86
Western Kingbird	E	1.00	1.00	2.00	2.00	3.00	3.00	1.00	1.00	1.00	2.00	2.14	2.14
Western Meadowlark	Gx7	1.00	2.00	2.00	3.00	2.00	5.00	3.00	3.00	3.00	3.00	2.43	2.43
Willow Flycatcher	Sn12	3.00	4.00	3.00	3.00	3.00	1.00	3.00	5.00	4.00	3.00	3.00	2.86
Yellow Warbler	Tds1	1.00	4.00	3.00	2.00	1.00	2.00	2.00	3.00	2.00	3.00	1.86	1.86
Yellow-billed Cuckoo	Tds12	3.00	4.00	3.00	3.00	2.00	1.00	2.00	3.00	3.00	4.00	2.71	2.43
Yellow-breasted Chat	Sn12	2.00	3.00	3.00	3.00	2.00	1.00	3.00	3.00	1.00	1.00	2.14	2.43
Yellow-headed Blackbird	Wm	3.00	3.00	2.00	3.00	3.00	2.00	2.00	3.00	4.00	3.00	3.00	2.71

Greater Prairie Chicken Nesting Habitat, Sheyenne National Grassland, North Dakota

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Abstract.—Greater prairie chicken (*Tympanuchus cupido pinnatus*) populations and habitats have declined dramatically in the Great Plains. The Sheyenne National Grassland (SNG) has the largest population of greater prairie chickens in North Dakota, but this population has declined over the past 15 years. Lack of nesting habitat has been identified as a significant factor contributing to the decline in greater prairie chicken populations throughout their range. We used the Habitat Suitability Index (HSI) model for greater prairie chickens to evaluate the nesting habitat conditions on the SNG. This population of greater prairie chickens appears to sustain itself on the brink of extirpation by nesting in the few areas that provide nesting cover and in private alfalfa fields. Encroachment of woody plants into the SNG, changes in private land-use patterns, removal of forage by domestic livestock contribute to the low suitability of the SNG for nesting by greater prairie chickens.

INTRODUCTION

The Sheyenne National Grassland (SNG) is approximately 28,745 ha of federally administered prairie in southeastern North Dakota. Within its administrative boundary there are an additional 25, 910 ha of interspersed private cropland and prairie. The SNG contains the largest population of greater prairie chickens (*Tympanuchus cupido pinnatus*) in the state of North Dakota (Kobriger et al. 1987). Greater prairie chickens are not native to the SNG, but are considered a naturalized immigrant in North Dakota (Johnson and Knue 1989). Prairie chickens apparently moved into North Dakota from the north-central part of the United States during the Euro-American settlement in the 1870's and 1880's (Johnson and Knue 1989, Evans 1968). Greater prairie chicken populations and their habitats (native tall grass prairie) have declined to a small fraction of their historical range (Hjertaas et al. 1993, Samson and Knopf 1994). Thus, the population of greater prairie chickens on the SNG has both regional and national importance.

Numbers of prairie chickens on the SNG increased from the early 1960's through the early 1980's (Kobriger et al. 1987). Since then, prairie chicken numbers on the SNG have declined from a high of 410 males in 1983 to a low of 84 males in 1994 (Kobriger et al. 1987, unpubl. data, Sheyenne National Grassland, Lisbon, ND). State and federal natural resource management agencies, and conservation groups are concerned that management of the SNG may be contributing to the decline in the greater prairie chicken population. Lack of suitable nesting habitat has been identified as the most significant factor limiting populations of greater prairie chickens across their range (Kirsch 1974, Westemeir 1973) and in North Dakota (Svedarsky 1979).

Habitat suitability index (HSI) models are an accepted method for quantifying species' habitats as numerical index (Schamberger et al. 1982) . Biological and habitat information are synthesized to formulate index values between zero (unsuitable) and one (optimum) for habitat requisites considered important to a species (U.S. Fish and Wildlife Service 1980). We conducted HSI analyses to assess habitat conditions for greater prairie chickens on the SNG at three scales: 1) the western portion of the SNG and adjacent private lands, 2) the Durler/Venlo Management unit, and 3) areas $\leq$1.6 km of the 14 active booming grounds.

METHODS

The HSI model for greater prairie chickens (Prose 1985) identifies two habitat components, nesting cover and winter food, as the most important habitat com-

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ponents for prairie chickens. The HSI for nesting cover is based on grassland vegetation height/density (expressed as visual obstruction measurements on a pole, Robel et al. 1970) for nesting cover in the spring (figure 1).

We mapped the lowland, midland, and upland grassland vegetation types (Manske and Barker 1987) on 1:24,000 aerial photos of the SNG. Most nesting by greater prairie chickens on the SNG occurs within 1.6 km of leks (Newell et al. 1987). The Custer National Forest Land Management Plan (U.S. Forest Service, Custer National Forest, Billings, MT, 1986) requires that nesting habitat for prairie grouse be assessed within 1.6 km of leks. During October and November, 1994, we estimated height/density of vegetation in these vegetation types from 81 transects within 1.6 km of greater prairie chicken leks in the northern and western portion of the SNG. At each of 10 stations on each transect, we recorded the height that vegetation obstructed 100 percent of a pole (VOR) marked in 0.5 dm increments when viewed from four directions (at 90° azimuths) at a distance of 4 m and a height of 1 m from the pole (Robel et al. 1970). VORs were averaged for each station and the average among stations was used to estimate transect VORs. We placed six transects in upland vegetation, 51 transects in midland vegetation and 26 transects in lowland vegetation. Data from these transects were used as VOR estimates in the mapped vegetation polygons they were collected in. For all other mapped vegetation polygons, these VOR data served as calibrations for ocular estimates of five VOR classes (0 - 0.50 dm, 0.51 - 1.0 dm, 1.01 - 1.5 dm, 1.51 - 2.0 dm, and >2.0 dm) during field reconnaissance. Maps of vegetation and VOR class assignments were transferred to 1:24,000 U.S. Geological Survey maps and the area of each vegetation was planimetered for use in the HSI estimates.

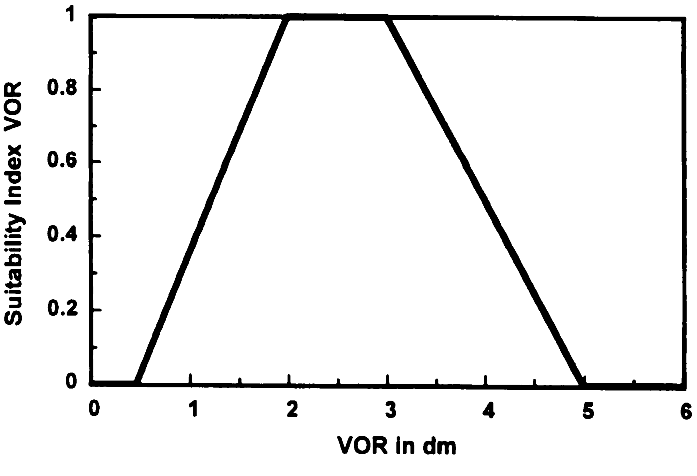

Figure 1. Relationship between average 100 percent obstruction of pole (VOR) marked in 0.5 dm increments and next cover suitability index for greater prairie chickens (from Prose 1985).

HSI for nesting cover is estimated in three steps (Prose 1985). First, a suitability index is estimated from the midpoint of the VOR classes of each vegetation type i (SI_{VORi}). Second, the percent of area providing equivalent optimal nesting habitat (EONH) is calculated using:

$$EONH = \sum_{i=1}^{n} (SI_{VOR_i})(N_i)$$

where n = total number of vegetation types, and N_i = percent of the area in vegetation type i. Third, HSI for nest cover is calculated from:

$$HSI = \frac{(0.735 * EONH) - 21.4}{37}$$

Characteristics of vegetation and winter snow accumulation influence the structure of vegetation in the spring for nesting by greater prairie chickens. VOR measurement collected in the fall decrease prior to spring nesting. This decrease is proportional to the height of vegetation and for the range of VOR 0.5 - 2.0 dm varies from 7-40 percent in mixed grass prairie (G. Schenbeck pers. commun., Nebraska National Forest, Chadron, NE). Over winter VOR losses on the SNG are probably different, but data are lacking. We selected 15 percent over-winter VOR losses to estimate spring nesting cover based on fall VOR estimates because the VORs for the SNG are near the lower end of the range.

Western SNG Analysis

The western part of the SNG includes most of the prairie chicken leks. This area included 3433 ha of private land and 8984 ha of SNG administered lands. We calculated the HSI for this analysis unit to show estimated contributions to the HSI for prairie chickens from adjacent private lands. VOR class information was available for only 5738 ha (64 percent) of the SNG lands in this analysis unit. We assumed the mapped VOR classes were representative of the remaining of the western SNG and used these data for HSI calculations in this analysis unit. For private lands in the western SNG analysis unit we assumed: 1) CRP land had VOR class >2.0 dm; 2) hay and alfalfa had VOR cover classes <0.5 dm because of mowing approximately the third week of June that destroys existing nests and most young hatched birds; and 3) grazed pasture had VOR cover class 0.51-1.0 dm.

Durler/Venlo Management Unit

The Durler/Venlo management unit includes 3645 ha in nine range management allotments in the western SNG. The Durler/Venlo unit is a subset of the prairie chicken range in the western portion of the SNG. It includes the larger leks, highest prairie chicken numbers, and the greatest number of prairie chicken leks not shared by sharp-tailed grouse (*Tympanuchus phasianellus jamesi*). Most of the Durler/Venlo management unit is ≤1.6 km from a prairie chicken lek. This portion of SNG has complete vegetation classification and mapping.

We excluded vegetation communities that were not available for nesting by greater prairie chickens from the HSI for the Durler/Venlo management unit. This HSI analysis presents a complete picture of the nesting habitat for this area. We assigned vegetation types to mapped polygons using the dominant vegetation community in the polygons. Within these polygons, vegetation communities not capable of producing 1.5 dm VOR measurements or that are usually flooded (Manske and Barker 1987, Newell et al. 1987) were considered unavailable for nesting by greater prairie chickens. The area in each polygon assigned to a VOR class did not include unsuitable areas. For example, lowland vegetation communities dominated by species such as *Carex lanulosa* were considered unavailable because in most years the ground is flooded. Upland vegetation communities dominated by species such as *Boutelou gracilis* were considered unavailable for prairie chicken nesting because they are not capable of producing at least 1.5 dm VOR in most years.

Area Surrounding 14 Active Leks

The area within 1.6 km of active leks includes most of the nesting habitat of greater prairie chickens. This scale of analysis allowed us to evaluate HSI for areas of known greater prairie chicken occurrences. This level of analysis included the area surrounding active greater prairie chicken leks and we expected HSI from this analysis should equal or exceed the HSI's from the blocks of SNG that included areas >1.6 km from leks and unused areas.

RESULTS

Western Sheyenne National Grassland

The 12,445 ha in the western SNG had 24 percent EONH (table 1), less than the minimum considered necessary for the HSI to be greater than zero using fall VOR estimates. When over-winter VOR losses were included, the EONH in the spring declined to 21 percent, with an HSI remaining zero.

Durler/Venlo Management Unit

EONH in the Durler/Venlo unit was lower that the western SNG. EONH was reduced by eliminating the lowlands that are usually flooded in the spring from the HSI calculations. The net result was 12 percent fall EONH and 9 percent EONH in the spring. The subsequent HSI for the Durler/Venlo unit was also zero.

Table 1. Percent equivalent optimal nesting habitat and nesting HSI for three analysis areas with and without winter VOR loss on the Sheyenne National Grassland.

Analysis area	Percent EONH[1]	HSI	Percent EONH with overwinter VOR loss	HSI
Western SNG	23.8	0	19.8	0
Durler/Venlo	11.7	0	9.3	0
≤1.6 km leks	25.7	0	21.1	0

[1] *EONH = equivalent optimum nesting habitat as defined in HSI model by Prose (1985).*

Area Surrounding 14 Active Leks

The area within 1.6 km of the 14 active leks had a larger EONH (26 percent) in the fall than the other analysis units. However, the nesting HSI was zero for this area as well. Four of the lek areas provided sufficient EONH for HSI's greater than zero. However HSI estimates for spring showed that only two of these leks still provided sufficient EONH for HSI's greater than zero.

DISCUSSION

Nesting HSI

Our data suggests that nesting cover limits greater prairie chicken populations on the SNG. HSI's were zero for all the analysis units we compared. Four leks had sufficient nesting cover in the surrounding 1.6 km for HSI's greater than zero based on the fall measurements. HSI for these lek areas were less than 0.2 Only two leks had HSI's greater than zero for the area within 1.6 km from leks after over winter VOR losses were considered. HSI's for these two leks were ≤ 0.1.

VOR measurements in grassland vegetation that are 2 to 3 dm are considered optimal nest cover for greater prairie chickens (Prose 1985). VOR measurements >1.5 dm provide $SI_{VOR} \geq 0.7$. Only 16 percent of the western SNG was in the VOR class >1.5 dm. In the Durler/Venlo management unit, only 7 percent of the suitable nesting area provided vegetation >1.5 dm. For areas ≤ 1.6 km of leks, only 14 percent of the area had vegetation in the >1.5 dm VOR classes. Suitable nesting cover for prairie chickens may increase during drought years because lowlands that are usually flooded are drier and usable for nesting by hens.

Most of the nesting habitat for greater prairie chickens in the SNG is the midland community type in the humocky sandhills (Manske and Barker 1981, Manske and Barker 1987). Switchgrass (*Panicum virgatum*) communities found on the toe slopes surrounding lowland meadows provide the primary prairie chicken nesting cover on the SNG (Manske and Barker 1987, Newell 1987). Although lowlands are not considered suitable for nesting in most years, the lowland/midland interface is used for nesting by prairie chickens (Newell 1987). The lack of adequate cover for nesting in upland communities was attributed to heavy livestock utilization (Newell 1987). Historically, upland communities were likely tall grass prairie (Burgess 1964), but currently have limited capacity to provide nesting cover because they are dominated by short cool season and warm season grasses such as Kentucky bluegrass and blue grama.

The HSI model (Prose 1985) assumes that optimum nesting habitat conditions exist when 80 percent of the area supports herbaceous vegetation with a VOR of 2 - 3 dm. However, lingering populations of greater prairie chickens can exist in areas with 10-15 percent permanent grassland (Hamerstrom et al. 1957, Prose 1985). Topfer et al. (1990) considers a spring population of 200 birds (100 males) as a minimum number to insure perpetuation of the population. Greater prairie chickens probably persist on the SNG because natural variation provides small limited areas with adequate nesting cover. These areas exist at the lowland/midland community interface, in lowlands during drought years, and in limited quantity surrounding some leks. Limited nesting also occurs in alfalfa on private lands (Newell 1987). Small populations, such as the greater prairie chicken on the SNG, are highly susceptible to extinction due to catastrophic natural events (Ruggiero et al. 1994).

Robustness of Analyses to Assumptions

Because the HSI in our evaluation were based on ocular estimates of VOR classes, we conducted analyses to estimate HSI for systematic errors in estimating the VOR classes. If we over estimated the VOR classes (e.g.,VOR was actually lower), then HSI would decline further. Because, the lower limit on HSI is zero, our conclusion of limited nesting habitat remained unchanged.

If we systematically underestimated VOR classes by one class (0.5 dm), HSI for the Western SNG increased to 0.1 for fall VOR estimates and remained zero for estimates of spring nesting cover. HSI in the Durler/Venlo unit remained zero for both spring and fall VOR estimates. HSI for the areas around active leks increased to 0.3 for fall VOR estimates, but declined to 0.1 for spring estimates of nesting cover. Because the area surrounding leks included lowlands that are flooded in most years, the HSI was probably lower. None-the-less, analyses that assume we underestimated nesting cover, still show that nesting habitat is limited on the SNG.

The VOR estimates we used for the 3433 ha private lands in western SNG analysis unit were made subjectively post hoc. Because, these post hoc estimates of private land VOR may have influenced the HSI, we conducted an analysis that would present the best possible HSI for this analysis unit. HSI for the western SNG was recalculated assigning all private lands with suitable vegetation types (hay and alfalfa, pastures, and CRP) for nesting, a SI_{VOR} of 1.0 (this analysis does not change the HSI for nest cover on lands managed by the SNG). The resulting HSI for nest cover increased for the western SNG analysis unit to 0.33. This HSI represents the upper limit for the western SNG analysis unit, but it is not realistic. Most of the area considered to have SI_{VOR} of 1.0 are grazed or mowed annually. Hay and alfalfa is usually cut by the third week of June, destroying existing nests and young broods unable to escape the mowers. Only the 251 ha of CRP in the analysis unit maintained its structural integrity throughout the nesting and brood rearing periods. None-the-less, this analysis still indicated that regional nesting habitat for greater prairie chickens is limited in the vicinity of the SNG.

Contributing Factors

The encroachment of woody and exotic plant species, changes in adjacent agricultural/land use changes, and livestock grazing practices are three human induced factors that directly or and indirectly influence nesting cover for prairie chickens on the SNG. Quaking aspen (*Populus tremuloides*), willow (*Salix* spp.) and Russian olive (*Elaeagnus angustifolia*) have encroached into prairie reducing nesting cover on the SNG (Kobriger et al. 1987, Jensen 1992). Leafy spurge (*Euphorbia esula*) has expanded from 7 percent to over 17 percent of the SNG since 1985 (unpubl. data, SNG). Encroachment of woody plants reduces and fragments suitable nesting, brood rearing and roosting cover (Svedarsky 1979); provides travel corridors and perch sites for predators (Burhnerkempe et al. (1984) and creates habitat more suitable for closely related sharp-tailed grouse (Prose 1987).

Agricultural development on private lands adjacent to the SNG over the past 10-15 years shows that remnant prairie habitats on private lands have been largely converted to croplands (unpubl. data, Nat. Res. Conserv. Serv., Lisbon, ND). Our analysis of the western SNG unit, showed that most of the suitable nesting habitat on private lands was Conservation Reserve Program comprising 250 ha in the analysis unit. No privately owed parcels of native prairie were identified in our analysis of the western SNG.

Grazing by livestock is the predominant use of the SNG. Livestock stocking rates have fluctuated between 50,000 and 60,000 AUMs over the past 10 - 15 years on the SNG. However, the size of livestock has increased approximately 40 percent during a comparable period (L. Potts, pers. commun., SNG, Lisbon, ND). These heavier animals require approximately 30 percent more forage (National Research Council 1984) than the standard AUM established for a 454 kg animal.

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Black-Tailed Prairie Dog Status and Future Conservation Planning

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Abstract.—The black-tailed prairie dog is one of five prairie dog species estimated to have once occupied up to 100 million ha or more in North America. The area occupied by black-tailed prairie dogs has declined to approximately 2% of its former range. Conversion of habitat to other land uses and widespread prairie dog eradication efforts combined with sylvatic plague, *Yersinia pestis*, have caused significant reductions. Although, the species itself is not in imminent jeopardy of extinction, its unique ecosystem is jeopardized by continuing fragmentation and isolation.

INTRODUCTION

The black-tailed prairie dog, *Cynomys ludovicianus* Ord, is the most widespread and abundant of five species of prairie dog in North America. Two species, the Utah prairie dog, *C. parvidens* J.A. Allen and the Mexican prairie dog, *C. mexicanus*, are currently listed as threatened and endangered, respectively, under the Endangered Species Act of 1973. The two other widespread species are the white-tailed prairie dog, *C. leucurus* Merriam and the Gunnison's prairie dog, *C. gunnisoni* Baird.

The black-tailed prairie dog is native to the short and midgrass prairies of North America. Its historic range stretches from southern Canada to northern Mexico and includes portions of Arizona, Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, and Wyoming (Hall and Kelson 1959). The eastern boundary of prairie dog range is approximately the western edge of the zone of tallgrass prairie, from which prairie dogs are ecologically excluded. The western boundary of this species is roughly the Rocky Mountains. Its range is contiguous with, but generally does not overlap, ranges of other prairie dog species.

With the exception of Arizona, from which it has been extirpated, the species still occurs in all the states (including Canada and Mexico) within its historic range. Yet, widespread reductions have occurred in population numbers and occupied areas throughout this broad range. Historic evidence suggests that the total area occupied by all species of prairie dogs may have declined by as much as 98% during the first half of this century (Miller et al. 1994).

METHODS

We sent letters of inquiry to state and federal conservation and land management agencies and consulted published reports. This information was augmented by telephone interviews with individuals knowledgeable about prairie dog management. The area surveyed included all states within the original range of the black-tailed prairie dog. Although responses were received from all states and agencies queried, the quality of survey information varied. Therefore, this report is a picture of prairie dogs in the mid-1980s rather than an accurate assessment of 1995 populations.

Prairie dog abundance and distribution is probably better documented at present than at any previous time due to improved mapping techniques and greater interest in prairie dogs by land management agencies. Yet, prairie dog occupied acreage can still only be grossly estimated. A primary factor contributing to this uncertainty is that much of the mapping effort is temporally distributed over a decade or more and there is no method available to assess prairie dog abundance over a broad area within a short span of time. Typically, prairie dog populations change substantially within a few years due to the threats discussed below and to climatic factors and prairie dog reproductive ecology. Another factor contributing to errors in determining prairie dog abundance is a lack of information from private and state lands.

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THREATS TO THE PRAIRIE DOG

A number of causes have been identified or proposed to account for the reductions in the acreage occupied by black-tailed and other prairie dog species. We believe that four areas of threat warrant further discussion: 1) loss of habitat due to conversion of prairie to other land uses; 2) intentional poisoning or other eradication or control efforts, primarily prompted by the livestock industry; 3) shooting for recreation or as a control effort; and 4) sylvatic plague, *Yersinia pestis*.

LOSS OF PRAIRIE

Prairie dominated by blue grama, *Bouteloua gracilis* (H.B.K.) Lag. ex Griffiths, and buffalograss, *Buchloe dactyloides* (Nutt.) Engelm., possibly due to its relatively flat topography, is among the first grassland converted to agriculture (Dinsmore 1983). As a result, Graul (1980) noted that as much as 45% of this prairie type has been lost to other land uses. Reductions in all shortgrass and midgrass prairies is expected to be similar or possibly greater in some midgrass regions where precipitation may be more suitable for agriculture. Although National Grassland acreage in the northcentral region of the Forest Service represents only about 5% of that agency's land base, it also represents the majority of the native prairie remaining in this region of North and South Dakota (Knowles and Knowles 1994).

Currently, with the exception of some areas of the northwestern portion of the black-tailed prairie dog's range, conversion of prairie to agricultural cropland has lessened. This is because much of the arable land is already in cultivation or has been converted to nonnative grasses for forage. Municipal and industrial development probably account for most of the present losses to native prairies in the United States. While these losses are minor compared with those that occurred during settlement of this country, they continue to reduce habitat availability for prairie dogs and other species.

ERADICATION OR CONTROL EFFORTS

Eradication efforts have been carried out against prairie dogs on a very large scale, affecting several million ha of land (Anderson et al. 1986; Bell 1921). Clark (1979) reported that in some years prairie dogs were intentionally poisoned on more than 8 million ha in the United States. During the early 1980s, 185,600 ha of prairie dogs were eradicated on the Pine Ridge Indian Reservation in South Dakota (Hanson 1988; Sharps 1988). In 1986 and 1987, a South Dakota black-tailed prairie dog complex of 110,000 ha was destroyed, eliminating the largest remaining complex in the United States (Tschetter 1988).

Virtually every federal land management agency has been involved in this effort. The U.S. Fish and Wildlife Service used compound 1080 until its ban in 1972. In 1976, this agency approved the use of zinc phosphide as a prairie dog control agent, hoping to avoid secondary poisoning of nontarget species while maintaining its prairie dog poisoning program. It is estimated that permitting activities by both the Environmental Protection Agency and the Animal and Plant Health Inspection Service account for the annual poisoning of 80,000 ha of prairie dogs in the United States (Captive Breeding Specialist Group 1992). Much of this effort occurs on federally-owned and managed land, despite the fact that less than 5% of the United States beef weight is produced on these lands (United States General Accounting Office 1988). Most poisoning on federal land is due to private land concerns, not necessarily federal forage concerns.

The legal designation indicating the regulatory status of the black-tailed prairie dog varies among the 10 states in which it still occurs. In four states the species is designated a legal agricultural pest, with some level of either state or local mandatory controls in effect. This includes statewide legislation mandating control of prairie dogs in Wyoming. In Colorado, Kansas, and South Dakota, state legislation allows counties or townships to mandate controls on landowners. In 1995, Nebraska repealed their long-standing legislation that mandated statewide control, thereby joining the states of Montana, New Mexico, North Dakota, Oklahoma, and Texas, where control is not mandatory but assistance may be provided to landowners who believe they have a prairie dog population problem that requires control.

PRAIRIE DOG SHOOTING

Shooting of prairie dogs, either for recreation or to reduce or control their numbers, is widespread across the range of all species in the United States.

The impact this activity has on overall populations remains unclear, but preliminary monitoring results by the Bureau of Land Management (BLM) in Montana indicate that some level of shooting might impact the growth and expansion of prairie dog colonies (Reading et al. 1989). Fox and Knowles (1995) suggested that persistent unregulated shooting over a broad area of the Fort Belknap Indian Reservation in Montana might have significantly influenced prairie dog populations. However, they further concluded that it would require approximately one recreational day of shooting for every 6 ha of prairie dogs to result in such an impact. This level of shooting pressure is unlikely over the hundreds of thousands of ha of currently occupied range.

SYLVATIC PLAGUE

Prairie dogs have coexisted with a variety of predators for many centuries on the plains and have adapted means of persisting in spite of this predation. However, a more recent threat has arrived to which the prairie dog has no adaptive protection. A flea-borne bacterium, the sylvatic plague, was introduced into North America just before the turn of the century. First discovered in black-tailed prairie dogs in Texas in the 1940s (Cully 1989), small rodents such as prairie dogs apparently have no natural immunity to the plague, which now occurs virtually throughout the range of the black-tailed prairie dog.

The impacts of plague are more adverse than just the killing of many individuals. The plague persists in a colony resulting in a longer population recovery time than is common in colonies that have been poisoned (figure 1). Four years following impact, plague-killed colonies on the Rocky Mountain Arsenal National Wildlife Refuge had recovered to only 40%, while poisoned colonies had recovered to over 90% (Knowles 1986). Knowles and Knowles (1994) suggested that prairie dogs have survived the introduction of this disease simply due to their large, highly dispersed populations. Further reductions in these populations could make prairie dogs much more susceptible to local or regional extirpations due to the plague.

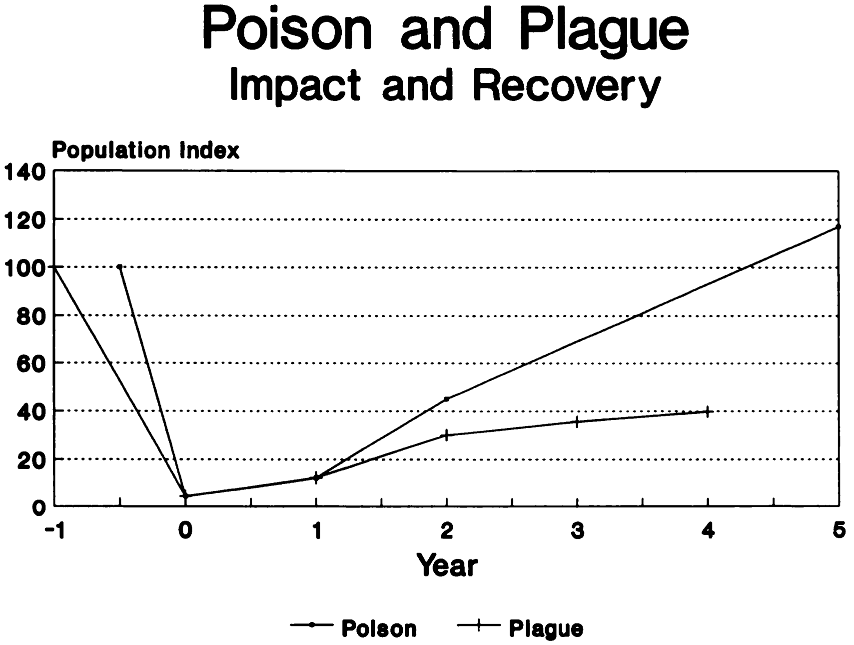

Figure 1. Comparison of prairie dog population recovery at the Rocky Mountain Arsenal National Wildlife Refuge following plague and at two colonies following control with zinc phosphide (Knowles 1986).

HISTORIC AND CURRENT STATUS

Rangewide

Seton (1929) estimated that in the early part of this century, there may have been 5 billion prairie dogs in North America. Around that time, prairie dog colonies were estimated to occupy 40 million to 100 million ha of prairie in North America, but by 1960 this area was reduced to approximately 600,000 ha (Anderson et al. 1986; Marsh 1984). These estimates result in the often-cited figure of a 98% decline in population among the five species of prairie dog. So, while the black-tailed prairie dog still occurs in all but one of the states in its historic range, significant reductions in its total colony area have taken place rangewide.

Table 1. Historic (pre-1920) and recent (post-1980) estimates of total area (ha) occupied by black-tailed prairie dogs in the United States.

State	Historic	Recent	% Change
AZ	[1]	extirpated	-100
CO	2,833,000	[1]	[1]
KS	810,000	18,845	-98
MT	595,000	35,545	-94
NE	[1]	24,415	[1]
NM[2]	4,838,460	201,220	-96
ND	85,000	8,500	-90
OK	[1]	3,850	[1]
SD	711,000	100,000	-86
TX	23,000,000	12,145	-99.9
WY	[1]	82,590	-75
United States	40,000,000 to 100,000,000	550,000	-98 to -99

[1] *Reliable data unavailable for analysis.*

[2] *Includes black-tailed and Gunnison's prairie dogs.*

PRAIRIE DOG STATUS IN EACH STATE

Current status information was solicited from state and federal agencies and from tribal authorities in all eleven states in the historic range of the black-tailed prairie dog (table 1). The following summary provides updated status and population data for those states.

Arizona

The Arizona Game and Fish Department (Duane L. Shroufe, Director, *in litt.* 1995) confirms that the black-tailed prairie dog, in the form of the Arizona subspecies *C. ludovicianus arizonensis*, is extirpated from the state. However, it still occurs nearby in Mexico and New Mexico. Arizona still supports populations of Gunnison's prairie dogs.

Colorado

On the Comanche and Pawnee National Grasslands, the Forest Service (*in litt.*) currently estimates a total of 2,455 ha of active prairie dogs, compared with 910 ha from 1978 to 1980 (Schenbeck 1982). This represents more than a doubling in area, but also represents only 0.5% of the area available on these public lands. Bent's Old Fort National Historic Site contains 325 ha of black-tailed prairie dogs (NPS, *in litt.*). Fort Carson and surrounding private lands contain approximately 1,620 ha, Pinyon Canyon less than 810 ha of prairie dogs (FWS, *in litt.*). The Rocky Mountain Arsenal NWR (FWS, *in litt.*) prairie dog population declined from 1,850 ha to 100 ha between 1988 and 1989, due to plague. Burnett (1918) estimated that three combined species of prairie dog occupied 5,665,720 ha in Colorado in the early 1900s. Based on geographic distribution of black-tailed, white-tailed, and Gunnison's prairie dogs in the state, it may be assumed that black-tailed prairie dogs accounted for approximately half this figure. There is no reliable estimate of the total area occupied by black-tailed prairie dogs statewide at this time.

Kansas

The National Park Service (*in litt.*) reports approximately 16 ha of prairie dogs at the Fort Larned National Historic Site. On the Cimarron National Grassland, the Forest Service (*in litt.*) currently estimates 440 ha of active prairie dog colonies compared with 20 ha estimated from 1978 to 1980 (Schenbeck 1982). This represents more than a twenty-fold increase on this 44,000-ha area, yet still only 1% of the total area of the Grassland. Both Lee and Henderson (1988) and Powell and Robel (1994) reported that selected counties had reductions of 84% since the beginning of the century (Lantz 1903, cited in Lee and Henderson 1988). A survey completed in 1992

(Vanderhoof et al. 1994) estimates 18,845 ha of prairie dogs in Kansas, just over 2% of the 810,000 ha estimated by Lantz (1903) some 90 years ago.

Montana

Flath and Clark (1986) estimated that black-tailed prairie dogs occupied 595,000 ha of land in Montana from 1908 to 1914. Estimated prairie dog occupied area by the early 1980s had declined to 50,600 ha (Flath and Clark 1986) and subsequent estimates show further declines in prairie dogs (40,500 ha, Campbell 1986; 35,545 ha, FaunaWest Wildlife Consultants 1995). This most recent estimate indicates a statewide reduction in occupied area of approximately 94% since the early 1900s.

Nebraska

On the Oglala National Grassland and Nebraska National Forest, the Forest Service (*in litt.*) currently estimates 105 ha of active prairie dog colonies, compared with 145 ha estimated from 1978 to 1980 (Schenbeck 1982). Current estimates represent 1.4% of land available. In 1973, prairie dog occupied area in Nebraska was estimated at 6,075 ha (Lock 1973). By 1982, this figure had increased to an estimated 32,400 ha (Frank Andelt, Nebraska Game and Parks Commission, cited in FaunaWest Wildlife Consultants 1995). By 1989, prairie dogs statewide occupied approximately 24,415 ha (Kevin Church, Nebraska Game and Parks Commission, *in litt.*). Plague and increased eradication efforts, resulting from state legislation mandating prairie dog control, have reduced this figure significantly since the 1980s, with less than 0.22% of the Nebraska landscape currently occupied by the species (FaunaWest Wildlife Consultants 1995). Historic estimates are unavailable.

New Mexico

The BLM (*in litt.*) reports that prairie dogs may be extirpated from several sites, with only 140 ha remaining on BLM land in the state. The White Sands Missile Range (Department of Army, *in litt.*) contains just over 300 ha of prairie dogs. Around 1919 the area in New Mexico occupied by prairie dogs, both Gunnison's and black-tailed (including *C. l. arizonensis*), was approximately 4,838,460 ha, but was estimated to have been reduced to 201,220 ha by 1980 (Hubbards and Schmitt 1984). This is a 96% reduction. Hubbards and Schmitt (1984) further estimated that the range of the black-tailed prairie dog in New Mexico has been reduced by one-fourth, primarily from the range of *arizonensis*.

North Dakota

Theodore Roosevelt National Park reportedly contains less than 360 ha of prairie dogs (NPS, *in litt.*), approximately 1% of the total Park land area. There are believed to be currently 2,690 ha of prairie dogs on the 660,435 ha of Custer National Forest in North and South Dakota (Forest Service, *in litt.*). This represents 0.4% prairie dog occupancy of these lands. The Forest management plan calls for an occupancy level at or around 2,225 ha. The North Dakota Game and Fish Department (*in litt.*) reports approximately 8,300 ha of prairie dogs statewide, which may be a reduction of 90% or more from historic levels. In 1992, only six complexes of over 400 ha were identified.

Oklahoma

The Department of the Army (*in litt.*) has no current estimate of prairie dog areas on Fort Sill, but report that they have declined markedly in the past 10 years. Shackford et al. (1990) reported a statewide estimate of 3,850 ha in 1967, increasing by 93% to 7,440 ha in 1989.

South Dakota

On the Buffalo Gap and Fort Pierre National Grasslands, the Forest Service (*in litt.*) estimates 3,025 ha of active prairie dog colonies and an additional 2,600 ha of colonies are subject to periodic rodenticide treatments. This compares to 17,600 ha estimated from 1978 to 1980 (Schenbeck 1982). The 500,285 ha Black Hills National Forest and Custer and Elk Mountain Ranger Districts currently support 53 ha of prairie dogs. In the early 1920s there may have been 711,000 ha of prairie dogs statewide (FaunaWest Wildlife Consultants 1995). The South Dakota Animal Damage Control office currently estimates 80,000 to 100,000 ha of active prairie dog colonies in the state; the Bureau of Indian Affairs estimates 65,000 ha of these on tribal lands (Cheyenne River Sioux Tribe, *in litt.*). These estimates suggest at least an 86% decline in prairie dog occupied area across the state. Badlands and Wind Cave National Parks currently contain 1,660 and 3,085 ha of prairie dogs, respectively (NPS, *in litt.*). These numbers represent 2 and 4%, respectively, of the area available on these public lands.

Texas

There were an estimated 31,385 ha of prairie dogs in northwest Texas in 1973 (Cheatham 1973). In 1991, there were at least 12,145 ha of prairie dogs estimated in Texas (Peggy Horner, Texas Parks and Wildlife, *in litt.*). Comparing this with a statewide historic estimate of 23,000,000 ha (Merriam 1902) results in a decline of over 99% in this century.

Wyoming

On Thunder Basin National Grassland, the Forest Service (*in litt.*) currently estimates 1,500 ha of active prairie dog colonies, with an additional 4,900 ha subject to periodic rodenticide treatment. Colony area for the period 1978 to 1980 was reported to be 2,550 ha (Schenbeck 1982). These numbers represent 0.6% of this 231,500 ha public grassland area. Devil's Tower National Monument contains approximately 16 ha of black-tailed prairie dogs (NPS, *in litt.*); 3% of the area available. Black-tailed prairie dogs in Wyoming may have increased in abundance near the turn of the century as a result of sheep and cattle grazing, with an estimated 53,650 ha by 1971 (Clark 1973). However, Campbell and Clark (1981) estimated a 75% reduction in prairie dog occupied areas since 1915. Current estimates indicate between 53,000 and 82,590 ha statewide (Wyoming Game and Fish Department, cited in FaunaWest Wildlife Consultants 1995).

SUMMARY OF PRAIRIE DOG STATUS IN EACH STATE

FaunaWest Wildlife Consultants (1995) attempted to estimate the amount of land area within the range of the black-tailed prairie dog that is currently occupied by the species. They included seven Great Plains states in their analysis and concluded that the states have less than a 1% occupancy of land surface within the species' range. The states included in this assessment and the percent of prairie dog occupancy within available area are Colorado (0.35%), Kansas (0.14%), Montana (0.17%), Nebraska (0.22%), North Dakota (0.17%), South Dakota (0.80%), and Wyoming (0.60 to 0.88%).

While these individual state accounts do not represent an exhaustive rangewide status review, they unfortunately provide the best information available. Significant reductions in occupied area have and continue to occur throughout the species' range; losses in some places exceeded 95%. Although the species still occurs in all but one state in its historic range, the eastern boundary of this distribution may be receding to the west. Figures indicate that there may be more than 550,000 ha of occupied black-tailed prairie dog range remaining in the United States, which is consistent with the estimate of 600,000 ha (Marsh 1984) cited previously. Over half the known prairie dog acreage in the central and northern Great Plains occurs on private land, almost 30% is on Indian reservations, and about 6% each occurs on Forest Service and Bureau of Land Management property (figure 2, FaunaWest Wildlife Consultants 1995). Neither Park Service nor Fish and Wildlife Service lands support significant acreage of any prairie dog species.

There is a need to develop a standardized survey technique for assessing prairie dog status. Presently, two methods are commonly employed and both involve mapping of individual prairie dog colonies either by ground reconnaissance or from aerial photo interpretation. Both methods are time consuming and expensive, making it unreasonable to expect a survey of over 500,000 ha of prairie dog colonies on the Great Plains within a short time period. Prairie dog colonies represent clumped patches on a broad landscape and there already exist nonmapping techniques that might be capable of statistical sampling of this distribution (Marcum and Loftsgaarden 1980). A statistical approach to monitoring prairie dog colony acreage may be a more appropriate technique than trying to map all prairie dog colonies.

PRAIRIE DOGS AND LIVESTOCK

Efforts to eradicate the prairie dog by the livestock and agricultural industry have existed for most of this century. Merriam (1902) estimated that prairie dogs caused a 50 to 75% reduction in range productivity. Taylor and Loftfield (1924) concluded that the prairie dog is "one of the most injurious rodents of the

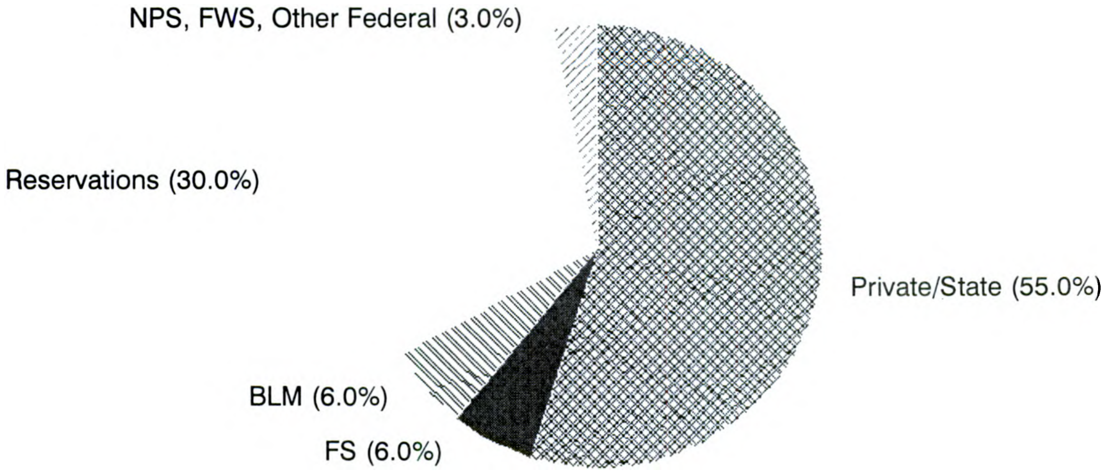

Figure 2. Distribution of black-tailed prairie dog colonies by land ownership in seven states in the northern and central Great Plains.

southwest and plains regions," and results in "the removal of vegetation in its entirety from the vicinity." Reports such as these were largely responsible for the escalating effort by range managers on the Great Plains to eradicate the prairie dog.

The conflict between the livestock industry and the prairie dog will likely not end easily or quickly, despite reports that prairie dog foraging does not significantly affect weight gain of cattle (O'Meilia et al. 1982; Hansen and Gold 1977). Others have reported the beneficial effects of prairie dogs on long-term range condition, including increased plant species diversity, richness, and overall plant production in prairie dog colonies (Archer et al. 1987; Uresk and Bjugstad 1983; Bonham and Lerwick 1976; Gold 1976). Uresk (1985) demonstrated that up to four years following prairie dog control, plant production was not increased whether the range was grazed or ungrazed by cattle.

Conversely, Hanson and Gold (1977) reported dietary overlap between cattle and prairie dogs, suggesting there may be some competition for the same species of forage plants. An estimation of true competition would be dependent on a variety of factors, including density of prairie dogs, stocking rate of cattle, ground cover, forage species present, and others (Uresk and Paulson 1988). Collins et al. (1984) reported that the annual cost of prairie dog poisoning was higher than the annual value of the forage gained by these measures. This issue requires more study, with input from both sides of the debate.

PRAIRIE DOGS AND BIODIVERSITY

The prairie dog, an integral component of the shortgrass prairie biotic community, is capable of transforming its own landscape and creating habitat alterations on a scale surpassed only by humans on the Great Plains. The ecosystem that is maintained by the prairie dog is valuable to many other species, with over 100 species of vertebrate wildlife reportedly using prairie dog colonies as habitat (Sharps and Uresk 1990; Clark et al. 1989; Reading et al. 1989). While few of these species are critically dependent on prairie dogs for all their life requisites, the increased biodiversity associated with prairie dog colonies indicates the importance of this habitat. Agnew et al. (1986) reported greater avian densities and species richness on prairie dog colonies. Also, numerous researchers have documented the preferential feeding of wild and domestic ungulates on prairie dog colonies (Coppock et al. 1983; Detling and Whicker 1987; Knowles 1986; Krueger 1986; Wydeven and Dahlgren 1985).

A number of rare and declining species are associated with prairie dogs and the habitat they provide. The black-footed ferret, *Mustela nigripes* Audubon and Bachman, 1851, is considered a true prairie dog obligate because it requires the prairie dog ecosystem for its survival. As one of the most endangered mammals in North America, this species has come to symbolize the decline in native grassland biodiversity. At least two species that are candidates for listing under the Endangered Species Act are also associated to a lesser degree with prairie dogs. The mountain plover, *Charadrius montanus* Townsend, 1837, and the swift fox, *Vulpes velox* Say, 1823, are attracted to the vegetative changes and possibly increased food availability in prairie dog colonies. The association of other species that are either declining or vulnerable indicate the problems facing this habitat.

CONSERVATION EFFORTS

Prairie dogs are managed either directly or indirectly within the survey area by at least six federal agencies, 11 state wildlife departments, state agriculture departments, departments of state lands, and numerous weed and pest districts, counties and private landowners. Prairie dog management goals and objectives vary significantly among these entities. Even management within agencies but between areas varies significantly. This variation can range from total protection of prairie dogs to a legal mandate to exterminate. All states have simultaneously classified the prairie dog as a pest and as wildlife, often with opposing management goals. Federal policy regarding prairie dogs has been inconsistent over time and across geographic regions. The legal mechanisms responsible for the decline of prairie dogs during this century are still intact. Restoration of the prairie dog ecosystem may not be possible without major changes in management policy.

At least two federal agencies have taken the initiative to begin to address the problems associated with declining prairie dog occupied areas and to involve other interested parties. The Forest Service initiated a working group comprised of various federal land and resource agencies throughout the northern states in the Great Plains, involving the Bureau of Land Management, Park Service, Bureau of Indian Affairs, and Fish and Wildlife Service. The function of this group is to encourage development of conservation assessments and strategies for the species across broad landscapes.

In January 1995, the Fish and Wildlife Service convened a meeting of federal, state, and nongovernmental entities to discuss problems facing the shortgrass prairie ecosystem, including the prairie dog as a focal species. Consensus recommendations were: 1) Fish and Wildlife Service will develop conservation strategies to keep prairie species from becoming listed under the Endangered Species Act and to recover declining species before a listing occurs; and 2) work with the Western Governor's Association to investigate ways to coordinate and communicate with all involved parties on prairie issues. The Fish and Wildlife Service recognizes that prairie dog management remains within the jurisdiction of the various state and federal land management agencies. Therefore, this agency is particularly interested in participating in cooperative agreements with other agencies so that the prairie dog may be managed as a wildlife species rather than simply controlled as a pest.

CONCLUSION

The black-tailed prairie dog does not appear to be in danger of becoming extinct in the foreseeable future, given current management. However, the additional negative impacts resulting from habitat fragmentation (Wilcox and Murphy 1985) could seriously impact the ability of some prairie dog populations to persist or become re-established. Habitat fragmentation adversely quickly affects highly specialized species (Miller et al. 1994) and the myriad of species associated with prairie dog colonies recover from habitat or population losses at different rates. This could result in a significant disruption of the ecosystem overall functioning, further delaying its recovery. Such effects are already evident for the endangered black-footed ferret. The future recovery or extinction of this species is inextricably entwined with the decisions resource managers make today regarding the conservation of the prairie dog ecosystem.

Management of the black-tailed prairie dog must give greater consideration to developing an abundance and distribution of prairie dogs that will ensure long-term population persistence of associated species. As a minimum, we believe that broad areas of suitable grasslands should have from 1 to 3% of the area occupied by prairie dogs. Federally-owned lands should assume a greater share of this responsibility, with a goal of from 5 to 10% occupancy by prairie dogs. Maintaining this level of occupancy may allow resource managers to determine what actually constitutes a functioning prairie dog ecosystem, so attempts may be made to preserve this system into the future.

ACKNOWLEDGMENTS

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The Role of Fire in Managing for Biological Diversity on Native Rangelands of the Northern Great Plains

Carolyn Hull Sieg[1]

Abstract.—A strategy for using fire to manage for biological diversity on native rangelands in the Northern Great Plains incorporates an understanding of its past frequency, timing and intensity. Historically, lightning and humans were the major fire setters, and the role of fire varied both in space and time. A burning regime that includes fires at various intervals, seasons and intensities, including midsummer burns, should be reinstated. However, burning to enhance rare systems and species and to discourage exotic species is also needed. The goal is to base plans on an understanding of historic processes and ecosystem interactions, and resist techniques that rely on unexamined conventions.

INTRODUCTION

"A common thread runs through the many definitions of biological diversity: variety of life and its processes in a given area" (Salwasser 1990). A management strategy for conserving biological diversity of any natural ecosystem must focus on saving all the components, including the structure, composition (including genetic diversity), and processes that characterize these systems (Kaufmann et al. 1994). Biological diversity is more than just the identifiable parts; it also includes the symbioses and synergisms that make nature work (Salwasser 1990).

The importance of disturbances in shaping native communities has recently received more attention. Ecosystems are dynamic entities whose patterns and processes are shaped and sustained on the landscape by successional processes and by abiotic disturbances such as fire, drought, and wind. To sustain these ecosystems, processes that characterize the variability found in native ecosystems should be present and functioning, and management activities should conserve or restore historic disturbance patterns (Kaufmann et al. 1994). This paper describes a strategy for managing biological diversity of rangelands on the Northern Great Plains. The approach is based on restoring historical disturbance processes given the significantly altered landscape patterns of today. Plant nomenclature follows Great Plains Flora Association (1986) (table 1).

SETTING

The Northern Great Plains region includes North Dakota, South Dakota and Nebraska, plus the eastern portions of Montana and Wyoming, and extends northward into Manitoba, Saskatchewan and Alberta. The climate of the region is characterized by an increase in precipitation and humidity and a decrease in periodic droughts during the summer from west to east (Risser 1990). This climate range influences not only the potential native vegetation but also the fire regime and effects. The shortgrass prairie on the Western and Southern portions of the region is the most arid type; the mixed-grass prairie occurs in the midsection of the region; and the tallgrass prairie on the Eastern edge receives the most precipitation (Risser et al. 1981).

The variation in precipitation across the region greatly influences the growth and expansion of woody plants. In the most Western portion of the region, big sagebrush occupies uplands; in the absence of fire it persists or expands (Wright and Bailey 1982). In the remainder of the shortgrass and mixed-grass portions of the region, woody plants are restricted to areas of increased elevation, such as the Black Hills, or to areas of increased moisture such as riparian zones, draws, and north-facing slopes. Escarpments, ridges, and outcrops in the Western portion support ponderosa pine and Rocky Mountain juniper (Wells 1965).

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Table 1. Common and scientific names used in this report. Nomenclature follows Great Plains Flora Association (1986).

Common name	Scientific name
Graminoids	
big bluestem	*Andropogon gerardii*
smooth brome	*Bromus inermis*
cheatgrass	*Bromus tectorum*
Japanese brome	*Bromus japonicus*
buffalo grass	*Buchloe dactyloides*
threadleaf sedge	*Carex filifolia*
sand dropseed	*Sporobolus cryptandrus*
green needlegrass	*Stipa viridula*
Forbs	
leafy spurge	*Euphorbia esula*
western prairie fringed orchid	*Platanthera praeclara*
Shrubs and trees	
sagebrush	*Artemisia* spp.
dwarf sagebrush	*Artemisia cana*
big sagebrush	*Artemisia tridentata*
green ash	*Fraxinus pennsylvanica*
Rocky Mountain juniper	*Juniperus scopulorum*
Eastern red cedar	*Juniperus virginianus*
cactus	*Opuntia* spp.
ponderosa pine	*Pinus ponderosa*
plains cottonwood	*Populus deltoides*
aspen	*Populus tremuloides*
chokecherry	*Prunus virginiana*
bur oak	*Quercus macrocarpa*
willows	*Salix* spp.
snowberry	*Symphoricarpos occidentalis*

Woody draws (narrow woodlands occurring in ravines) are examples of communities in more arid portions of the region that are restricted to sites with greater soil moisture. The most common woody plants in these draws are green ash and chokecherry. Riparian zones along streams and rivers support plains cottonwood, willows, and dwarf sagebrush (Severson and Boldt 1978). These woodlands may also expand in the absence of fire, but the expansion is restricted to sites with adequate moisture and the expansion rate is slower than in the tallgrass region. Further, many deciduous species, such as chokecherry and willows, sprout vigorously following burning (Wright and Bailey 1982). Only very frequent fires (i.e., every 1 to 5 years) would favor grasses over these species.

In contrast to more arid portions of the region, mesic prairies in the Northern, Eastern and Southeastern portions of the region are characterized by precipitation amounts high enough to support the expansion of woody plants onto uplands. It is in these areas that frequent fires slow the expansion of woody plants on uplands (Bragg and Hulbert 1976). In the Northern portion of the region, aspen replaces ponderosa pine on outcrops and expands into the Canadian prairies (Wright and Bailey 1982). Eastern red cedar replaces Rocky Mountain juniper in the Southeastern part of the region where it readily expands onto uplands (Gehring and Bragg 1992). In the eastern tallgrass prairies, woody species, such as willows and bur oak, invade grasslands, and only frequent fires slow their expansion (Anderson 1990). Plains cottonwood and willow dominate floodplains in the more mesic portions of the Northern Great Plains; green ash and bur oak are common on higher terraces along major rivers (Johnson et al. 1976).

In addition to climatic factors, herbivores also influence the region's vegetation and fire regimes. However, it is difficult to distinguish the particular influence each force has on vegetation (Henderson and Statz 1995). Fire is often associated with periodic drought, and fire and grazing are sometimes interrelated. For example, recently burned grasslands often attract grazers; yet, heavily grazed areas usually resist fire until dead litter reaccumulates (Steuter et al. 1990, Vinton et al. 1993). Therefore, the influences of grazing and drought must be a part of a discussion of historical fire effects (Henderson and Statz 1995).

FIRE HISTORY

An understanding of the frequency, timing, and intensities of past fires is necessary before fire can be incorporated into a strategy to conserve prairie systems. Based on data from adjoining ponderosa pine forests, which indicated that fire frequency varied from 2 to 25 years, Wright and Bailey (1982) estimate that on level-to-rolling topography, a fire frequency of 5 to 10 years in the Northern Great Plains is reasonable. On topography more dissected with breaks and rivers, they estimate a fire frequency of 20 to 30 years. Wendtland and Dodd (1992) agree with this range, based on their examination of historical documents and fire records from the Scotts Bluff National Monument area in northwestern Nebraska. Dendrochronology data in the Devils Tower region northwest of the Black Hills reveal that before 1770 the mean interval between fires was 27 years; from 1770 to 1900 the fire return interval was 14 years (Fisher et al. 1987). Brown and Sieg (1996) report a mean fire frequency in the south-central Black Hills of 16 years for the period 1388 to 1918.

In the more mesic portions of the Northern Great Plains, the average fire return interval was shorter. Collins and Gibson (1990) estimate a frequency of every 1 to 5 years in the tallgrass portions of this region. In northcentral Nebraska, the fire return interval averaged 3.5 years between 1851 and 1900 (Bragg 1985).

Historically, the major ignition sources for prairie fires were lightning and American Indians. Lightning was, and is, an important ignition source in the Northern Great Plains. In northwestern South Dakota, lightning-set fires occur an average of 6 to 25 times per year, and most commonly occur in July and August (Higgins 1984); fewer occur in April, May, June, and September. Wendtland and Dodd (1992) note that of 10 fires described in historical documents between 1824 and 1934, and of 26 fires officially recorded between 1934 and 1969 in the Scotts Bluff National Monument area, over 70 percent occurred in July and August.

Higgins' (1986) review of 300 historical accounts written between 1673 and 1920 reveals that fires accidentally or intentionally set by American Indians were common in the Northern Great Plains. He found that although Indians set fires in nearly every month of the year, April, September and October were their peak fire-setting times. The majority of the 97 fires described were scattered, single events of short duration and small extent; only 10 fires burned longer than 1 day.

American Indians had many uses for fire. These included attracting and herding wild animals, signaling threats and warnings, improving pasturage, masking and eliminating personal signs at camps and along trails, and for pleasure, warfare and ceremonies (Higgins 1986). During their 10,000-year occupation of this region, the timing of fires set by American Indians did not mirror lightning-set fires; therefore, these Indian-set fires can be considered additive to lightning fires (Higgins 1986).

A combination of periodic droughts, high temperatures and strong winds in the region provide the components necessary for fire spread (Collins 1990). The end result of the erratic climate, flammable fuels, topographic relief and other factors, such as grazing animals, was that the role of fire was not constant in time or space (Anderson 1990).

With the arrival of non-native settlers came fire suppression policies and, in many areas, a shift in the timing of fires. Near Devils Tower, Wyoming, after 1900, the fire return interval increased to every 42 years, versus less than every 27 years previously (Fisher et al. 1987). In the south-central Black Hills, Brown and Sieg (1996) record a 104-year fire-free period in ponderosa pine stands between 1890 and 1994, and note that most of past fires occurred late in the growing season or after growth had ceased for the year. Higgins (1984) suggests that the recent extent and spread of lightning fires has been modified by cultural features such as roads; further, the fire regime has also been altered by differing patterns of grazing animals (first bison, then cattle). In contrast to the late summer ignitions that commonly burned before 1935 near Scotts Bluff, Nebraska, the 46 fires recorded since 1935 dramatically shifted to spring occurrences (Wendtland and Dodd 1992). Lengthening the interval between fires, shifting from summer to early spring burning, and/or reducing fire intensity by prescribing cooler fires may alter species composition to favor fire-intolerant species (Wendtland and Dodd 1992) such as cactus and non-sprouting woody species like sagebrush (Wright and Bailey 1982).

DEVELOPING A FIRE MANAGEMENT STRATEGY TO CONSERVE DIVERSITY

The fire strategy most likely to manage diversity on native rangelands of the Northern Great Plains is based on two premises: 1) processes that mimic, as much as possible, the variability found in native ecosystems should be present and functioning; and 2) management activities should conserve or restore historical disturbance patterns (Kaufmann et al. 1994). This management strategy should reflect the differing roles that fire historically played in the various portions of the region. However, this strategy must also address the fundamental changes that have occurred in the landscape such as drastically different landscape patterns imposed by species changes and management unit boundaries.

Wendtland and Dodd (1992) recommend a scenario that mimics the presettlement fire history. For the Scotts Bluff, Nebraska area, they infer this strategy including high intensity summer fires on a return interval of 5 to 30 years. Shifting burning programs from all spring or fall burns to include some midsummer burns should favor some species not enhanced by spring or fall burns (Howe 1994). For example, an April fire burns early foliage critical for root production of cool-season plants, leaving late-season plants unscathed; an August fire burns the largely inactive foliage of cool-season species, while consuming foliage and reproductive stems of warm-season species (Howe 1994). However, historically, fires occurring after fuels have cured in the fall or in the early spring before green-up may have been more significant than summer fires. High fuel moisture in July and August and concurrent slow rates of spread result in a smaller area being burned by an individual fire, compared to those fires occurring when fuels are cured in the fall (Steuter 1988). Given the highly variable fire regime in the past, burns of varying intensities at differing seasons are appropriate. Further, the interval between fires should be varied to best restore fire disturbance patterns of the Northern Great Plains. The strategy should avoid a uniformity in timing of burns or in intervals between burns that artificially simplifies what was probably a more complex system (Howe 1994).

SPECIAL HABITATS AND SENSITIVE SPECIES

Reinstituting a fire regime based on historical processes that includes burning at varying intervals and in differing seasons is the first step in developing a strategy for using fire to manage biological diversity on native rangelands in this region. The second step involves assessing the direct and indirect impacts of fire on special habitats and sensitive species. Special habitats are native biological communities or ecosystems that are rare, unique, or highly productive elements of regional landscapes (Salwasser 1990). Sensitive species include those native species currently in danger of extinction or those whose population trends are negatively affected by human actions (Salwasser 1990). The burning strategy should also consider the potentially different historical fire disturbance regimes in these sensitive ecosystems, minimize potential negative influences of fire, and maximize conditions favorable to the expansion of these systems and species.

The special habitats in the Northern Great Plains (wetlands, lowlands, and riparian areas) contain high numbers of listed vulnerable species (Finch 1992, Finch and Ruggiero 1993). Although each of these habitats constitutes a relatively small percentage of the total land area, each contributes disproportionately to the diversity of native rangelands in this region (Finch and Ruggiero 1993). If sensitive communities such as these occur within a management unit, burning programs should be examined relative to their impacts on these habitats. The range in frequency, timing, and intensity of burns suitable to upland habitats may not provide optimum conditions for sustaining these distinctive systems.

Wetlands, lowlands, and riparian woodlands in this region are examples of communities that, because of higher moisture, likely burned less frequently than uplands. Riparian zones throughout the region, and woody draws in the more arid portions, tend to be green throughout most of the growing season, have higher relative humidities than adjacent grasslands, and often have running water or moist soils that slow the spread of fire into these communities. In most years, prairie fires would skip over or only burn lightly through these narrow woodlands (Severson and Boldt 1978). However, the narrow configuration and close contact of these woodlands with flammable grassland fuels suggest that historically they were exposed to a high number of grassland fires. Fire inevitably entered these woodlands, especially in dry years on hot and windy days.

Given that the species composition in woody draws includes a number of deciduous species, such as snowberry and chokecherry, that sprout following burning (Wright and Bailey 1982), and that several woody species establish best in mineral soils, fire probably functioned as a regeneration mechanism in these systems. Further, since these communities stay green longer than uplands, fires probably burned late in the growing season when there were adequate levels of cured, fine fuel. Repeated, annual fires, especially during droughts, tend to favor the growth of grasses over woody plants (Wright and Bailey 1982). Fires occurring infrequently when plants are dormant, followed by high precipitation, may enhance woody plant growth (Wright and Bailey 1982, Sieg 1991). If the goal is to regenerate woody plants in woody draws and/or to mimic historical fires, prescriptions should be set to achieve high intensities (Sieg 1996).

Rocky Mountain juniper woodlands are an example of a relatively uncommon community in the Western portion of the Northern Great Plains that rarely burned. In this region, Rocky Mountain juniper grows best on steep barren slopes (Noble 1990) where the sparse understory vegetation is rarely adequate to sustain a fire. In areas where fine fuels are sufficient to carry a fire, the high volatile oil content of the foliage combined with Rocky Mountain juniper's inability to sprout following topkilling, results in high mortality rates (Wright and Bailey 1982).

Threatened or endangered species are examples of sensitive species whose needs cannot be ignored. Because they are the first species to drop out of ecosystems, they are considered the weakest link in the conservation of native biological diversity (Finch and Ruggiero 1993). Providing habitats in an appropriate spatial and temporal arrangement is necessary to maintain viable populations of sensitive species. Thus, vegetation management is a major tool for maintaining and restoring biodiversity, and for delisting or avoiding listing of threatened and endangered species (Kaufmann et al. 1994).

Adjusting fire management programs to meet the needs of threatened and endangered species requires an understanding of the role of fire in the long-term sustainability of the ecosystems supporting these species, and in the life history and habitat needs of individual species. For example, the western prairie fringed orchid is a federally listed threatened plant species associated with swales (low-lying often wet land) of the tallgrass prairie (U.S. Fish and Wildlife Service 1989). Although the tallgrass prairie is prone to burn every 1 to 5 years (Collins and Gibson 1990), it is unlikely that swales supporting orchids burned as often, especially during years when they were flooded. Vogl (1969) describes a "quasi-equilibrium" of a Wisconsin lowland maintained by floods during wet periods and fires during droughts. Lowlands supporting orchid populations likely burned throughout the growing season during prolonged droughts; however, fires that occur when orchids are actively growing are apt to injure or kill them. Since fall burning allows orchids to complete their life cycle, and dry conditions and lightning are inclined to occur late in the growing season, fall fires are a better choice than spring burning to sustain orchid populations and their associated habitat (Bjugstad-Porter 1993).

MANAGE INTRODUCED SPECIES

The introduction of exotic species to new environments without their associated parasites and pests may be humankind's greatest environmental manipulation (Young and Evans 1976). Many invasive exotic species have characteristics that enable them to vigorously compete with native plants and to exploit disturbed areas (Parker et al. 1993). In addition to reviewing impacts of existing non-native species and preventing the introduction of new ones (Kaufmann et al. 1994), management plans should address how to manage these species; fire is a useful tool in this arena. Problem species include those purposely planted, such as smooth brome, and a variety of species accidentally introduced, such as cheatgrass, Japanese brome, and leafy spurge (Lym 1991).

Although burning is not a panacea for discouraging introduced species, with careful planning it can be a useful tool, especially if native species are not adversely affected. Burning at a time when plants are most vulnerable is useful for suppressing undesirable species. For example, burning in mid-or late May, when smooth brome tillers are either elongating or heading, reduces tiller density of smooth brome by 50 percent when compared to unburned plots in Nebraska (Willson 1992). Burning in May also enhances production of flowering culms of some native warm-season grasses such as big bluestem (Willson 1992). However, burning is not a cure-all for reducing persistent species such as smooth brome, and the outcome is strongly dependent on other factors such as climate and precipitation patterns. Subsequent burning in Pipestone, Minnesota failed to significantly reduce smooth tiller density (Willson and Stubbendieck 1996).

In addition to killing or injuring individual exotic plants, burning can be used to make the habitat less conducive to a species expansion. Spring burning in western South Dakota killed Japanese brome seedlings for one growing season, and by reducing litter accumulations, decreased future germination rates (Whisenant and Uresk 1990). In this case, spring burning was detrimental to the production of one native species, green needlegrass; enhanced production of two others, buffalo grass and sand dropseed; and did not change the production of a fourth, threadleaf sedge (Whisenant and Uresk 1990).

A combination of burning and other management tools may be valuable in managing invasive species. For example, picloram plus 2,4-D applied in the fall followed by spring burning reduced the stem density and germination rates of leafy spurge in North Dakota more than any other treatment tested (Wolters et al. 1994). The key to success in managing invasive species is to begin treatment before expansive spread occurs and to focus as much as possible on the invaded ecosystem rather than on the invader (Hobbs and Humphries 1995).

SUMMARY

A strategy for using fire to manage native biological diversity on rangelands in the Northern Great Plains should consider natural disturbance patterns. Fires historically occurred as often as every 1 to 5 years in the more mesic portions of the region, but less frequently in areas of rough topography and in lowlands. Lightning, a major ignition source in this region, caused fires most often in July and August. American Indians accidentally or intentionally set fires in nearly every month of the year; however, the greatest number were set in April, September, and October. The end result of the erratic climate, fuels, topographic relief and factors such as grazing animals, was that the role of fire was not constant in time or space.

Reinstituting a fire regime based on historical processes, including burning at varying intervals (to reflect climatic patterns) and in differing seasons, is the first step in developing a strategy for using fire to manage for biological diversity on native rangelands in this region. Including mid-summer burns, rather than concentrating all prescribed burning in the spring and fall, would better mimic natural disturbance patterns. The second step involves adjusting fire regimes to best sustain special habitats, such as wetlands and riparian zones, and sensitive species, especially threatened and endangered ones. Third, fire prescriptions should be planned so that burning does not enhance the spread of invasive species. The overall goal is to base the fire management strategy on an understanding of historic processes and ecosystem interactions, and resist techniques that rely on unexamined conventions (Howe 1994).

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Rocky Mountain Forest and Range Experiment Station

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Southwest

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Great Plains

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United States Department of the Interior

FISH AND WILDLIFE SERVICE
Washington, D.C. 20240

SEP 8 2009

In Response Reply to:
FWS/AFHC-DEQ/042031

Debbie Edwards, Ph.D.
U.S. Environmental Protection Agency
Office of Pesticide Programs
Ariel Rios Building
1200 Pennsylvania Avenue, NW
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Dear Dr. Edwards:

Thank you for the opportunity to comment on the Environmental Protection Agency's (EPA) approval to use two rodenticides to control black-tailed prairie dogs. As communicated previously, the U.S. Fish and Wildlife Service (Service) has strong concerns about the potential impacts of these products on nontarget wildlife protected under the Endangered Species Act and the Migratory Bird Treaty Act. Specifically, the Service's comments address the conditional registration under Section 3 of the Federal Insecticide, Fungicide, and Rodenticide Act (FIFRA) for Rozol Prairie Dog Bait (active ingredient: chlorophacinone) to control black-tailed prairie dogs (*Cynomys ludovicianus*) in Colorado, Kansas, Montana, Nebraska, New Mexico, North Dakota, Oklahoma, South Dakota, Texas, and Wyoming, and the anticipation of a similar registration for the rodenticide Kaput (active ingredient: diphacinone). We recommend that EPA withdraw the registration for Rozol and not issue a registration for prairie dog control for Kaput until EPA completes a formal consultation with the Service on the use of these rodenticides to control black-tailed prairie dogs.

Service Field Offices provided letters to EPA expressing our concerns regarding special local needs registrations under FIFRA Section 24(c) for both Rozol and Kaput on May 5, 2006 and December 21, 2007, respectively. In addition, our Wyoming Field Office provided comments on this registration of Rozol under separate cover (June 19, 2009). The Western Association of Fish & Wildlife Agencies expressed similar concerns to EPA in a letter dated August 19, 2008. The issues raised in these communications have not been addressed sufficiently by EPA to warrant registration of these products under Section 3 of FIFRA. Our specific concerns include the documented risk from the use of these products to non-target species for which the Service is a federal trustee, including federally listed threatened and endangered species such as the black-footed ferret *(Mustela nigripes)* and migratory birds such as bald eagles *(Haliaeetus leucocephalus)* and golden eagles *(Aquila chrysaeos)*, hawks, and other avian predators and scavengers.

The black-tailed prairie dog occupies an estimated 2.4 million acres in the western U.S. Their colonies are used by many wildlife species that prey on or scavenge prairie dogs and/or use their burrows for shelter. The high availability of prey at these colonies can result in a disproportionate use by avian and mammalian predators and scavengers. Therefore, the use of rodenticides, with known secondary toxicity to animals that consume poisoned prairie dogs, can have significant impacts to animal populations far beyond the footprint of the colony.

The risk of secondary poisoning to non-target wildlife from anticoagulants such as Rozol and Kaput is much higher than from zinc phosphide, the traditional choice for prairie dog control (Colvin *et al*. 1988, Erickson and Urban 2004). Several EPA documents note the risk from Rozol (EPA 2004, EPA 2006, Erickson and Urban 2004). The most recent document (EPA 2006) repeats a conclusion from Erickson and Urban (2004) that *use of chlorophacinone bait to control prairie dogs has a considerable potential for both primary and secondary risks to birds and nontarget mammals and possibly reptiles. Secondary risks, especially to mammalian predators and scavengers, are likely to be much greater for chlorophacinone than for zinc phosphide.*

The secondary poisoning risks from Kaput are even greater than those from Rozol (Erickson and Urban 2004). Colvin *et al*. (1988) noted that anticoagulants can pose a substantial hazard to raptors. A study that evaluated the risks of 11 vertebrate pesticides (Littrell 1990) ranked both Rozol and Kaput as the second most hazardous pesticides. Strychnine was ranked as the most hazardous; zinc phosphide was ranked fifth.

Anticoagulants cause a more prolonged period of distress for the target animal prior to mortality than zinc phosphide. Anticoagulants act as blood thinners, with poisoned animals losing blood through various orifices, including eventually the skin membranes, over a period of weeks. During this period, poisoned prairie dogs may wander around on the surface becoming increasingly debilitated and susceptible to predation. For example, two weeks after an illegal application of Rozol on 160 acres in South Dakota in 2005, Service biologists found over 50 dead, dying, and scavenged prairie dogs. This information was shared with EPA law enforcement. On a follow-up visit by both the Service and EPA four weeks after application, it was noted that 400-500 prairie dogs had been retrieved from the Rozol treated site during the previous two weeks. Anticoagulants also have a longer persistence in the body tissues of the poisoned prairie dogs than zinc phosphide (Erickson and Urban 2004, Mendenhall and Pank 1980). Consequently, contaminated prey are available to non-target species for a period of weeks versus hours for zinc phosphide. The disoriented, dead, and dying prairie dogs likely attract even more predators and scavengers to the site than might typically occur, further increasing impacts from secondary poisoning.

There appears to be a significant data gap regarding the potential impact of residues of these anticoagulants in prairie dog carcasses. We have received anecdotal information indicating that anticoagulant concentrations in prairie dog tissues are higher than residue levels in other treated rodent species. If so, higher concentrations of the anticoagulants, compounded by the larger body size of prairie dogs compared to many other rodents (ground squirrels, mice, pocket gophers, voles) that are typically poisoned with anticoagulant, would deliver a substantially larger dose of poison to prairie dog predators and scavengers than would consuming other prey species.

Though laboratory trials have been conducted where poisoned prairie dog carcasses were fed to non-target species, this study did not provide information regarding anticoagulant concentrations in prairie dog tissue either before or after death (Fisher and Timm 1987). In a field efficacy study for Rozol that was sponsored by the manufacturer, LiphaTech, and carried out in conjunction with the National Wildlife Research Center/Animal and Plant Health Inspection Service (NWRC/APHIS), carcasses of black-tailed prairie dogs collected from treated areas were to be analyzed to measure residue levels in whole-body and liver tissue samples (Lee and Hygnstrom 2007). We request that EPA provide information from that study to the Service. Similarly, the Service will provide EPA the results of a study, when completed, with NWRC/APHIS to test tissue residues in prairie dogs at incremental time periods post-exposure.

Threatened and Endangered Species

In 1993 when about 650 species were listed under the Federal Endangered Species Act (ESA), the Service completed a Biological Opinion on 16 vertebrate control agents including chlorophachinone and diphacinone. At that time, the registered uses for these anticoagulants did not include prairie dogs. Consequently, impacts from poisonings at prairie dog colonies were not part of the review. The 1993 Biological Opinion determined that the registered uses for chlorophacinone would jeopardize the continued existence of 21 Federally listed species. With the 2009 registration by EPA to expand the use of Rozol and potentially Kaput, we expect that the list of adversely affected species would be greater because there are over twice as many species now listed under the Act and the new registration greatly expands the likelihood to non-target species exposures. EPA noted in their 1998 Reregistration Eligibility Decision for these rodenticides that additional consultation with the Service may be necessary if new uses of these pesticides are proposed. We consider the use of Rozol and Kaput for the control of prairie dogs to be a new use. We asked EPA to consider reinitiating Section 7 consultation in both a letter to EPA dated May 5, 2006 and in a conference call with EPA on May 19, 2006, however this has not occurred.

Of particular concern are effects to the Federally-listed black-footed ferret. Black-footed ferrets are highly dependent upon black-tailed prairie dogs, both for food and for the utilization of their burrows. In November 2008, the Service issued a 5-Year Review of the ferret, citing the poisoning of prairie dogs as a major factor in the decline of ferrets, through both decline of prairie dogs and inadvertent poisoning of ferrets (USFWS 2008). The report recommended that Federal agencies more fully embrace ESA Section 7 (a)(1) responsibilities to restore and manage viable prairie dog complexes to support ferret recovery, and specifically cites the need for EPA to re-address the use of anticoagulants for control of prairie dogs.

Migratory Birds and Other Non-target Species

The Migratory Bird Treaty Act prohibits the take of migratory birds, including avian mortality resulting from exposure to pesticides registered under FIFRA [U.S. v. Corbin Farm Services, 444 F. Supp. 510 (1978)]. We are especially concerned about potential mortality of migratory raptors due to the use of Rozol and Kaput. The ferruginous hawk *(Bueto regalis)*, in particular, is very closely linked to prairie dogs and often occurs in large numbers where prairie dogs concentrate (Seery and Matiatos 2000). The ferruginous hawk is a Species of Conservation Concern (U.S. Fish and Wildlife Service 2008) in Service Region 6, where most of the proposed use of Rozol and Kaput would occur. In addition, bald eagles are known kleptoparasitic associates of ferruginous hawks (Jorde and Lingle 1988). Accordingly, we believe that potential violations of the Migratory Bird Treaty Act, and Bald and Golden Eagle Protection Act may be occurring via use of these products.

Take of Federally protected migratory birds also would be inconsistent with Federal Agency responsibilities stipulated in Executive Order (EO) 13186, which required federal agencies proposing actions that may have measurable effects on migratory birds to develop a Memorandum of Understanding (MOU) with the Service to demonstrate how conservation of migratory birds will be promoted (66 FR 3853). EPA has not completed this MOU. We believe authorization of Rozol and Kaput for prairie dog control has a high likelihood of adversely affecting ferruginous hawks and other raptors at a measurable level. Accordingly, we request that EPA undertake development of the MOU outlined in EO 13186.

Mortalities of badgers *(Taxidea taxus,* Klataske 2009 and Lydick 2006) and a bald eagle (USFWS 2007) were reported to EPA from secondary poisoning by the legal application of chlorophacinone in prairie dog colonies. We believe that the actual number of non-target species impacted is much greater. However, the ability to verify impacts to non-target species is quite limited. Carcass searches to assess hazards to non-target wildlife are of minimal value because of cryptic coloration, vegetative cover, consumption by other scavengers, the ranging ability of many scavengers and predators, and, in the case of anticoagulants, the delayed action of the rodenticide (Colvin *et al.* 1988). Therefore, only a very small percentage of animals that die from secondary poisoning are ever located.

Black-tailed Prairie Dog Conservation

In 2000, the black-tailed prairie dog was designated a candidate species for listing under the ESA. Though candidate status was removed following the discovery of additional colonies, many states subsequently developed black-tailed prairie dog management plans to keep populations stable and prevent future listing. For example, in 2005, the Service and the Texas Parks and Wildlife Department signed a conservation agreement for planning and implementation of the Black-tailed Prairie Dog Conservation and Management Plan. The Texas management plan cites specific acreage needed to support stable prairie dog populations and is part of a larger overall effort by the western states to conserve prairie dogs. Since local registration of Rozol and Kaput in Texas, the Service has observed an increase in prairie dog control. The Service is concerned that the widespread use of Rozol and Kaput on prairie dog colonies in Texas, as compared with other methods of prairie dog control, may result in the Department failing to achieve its prairie dog conservation goals.

Comments Specific to Current Rozol Label

The Service also has specific concerns and comments with regard to the Rozol label that accompanies the May 13, 2009 registration for this rodenticide. We are concerned that the label requirements needed to ensure non-target exposure are so cumbersome that they will be ignored, especially regarding the retrieval of dead and dying prairie dogs (recommendation #7 below). We have received first hand verbal reports from applicators regarding this issue. A document produced by LiphaTech quoted a County Pest Control Supervisor as stating that *zp* [zinc phosphide] *requires two trips based on the need to pre-bait. That adds up quickly. With an anticoagulant, I can cut the labor costs in half when compared with zinc* (Bruesch undated). If the current requirements for retrieval of dead and dying prairie dogs, which fall short of adequate protection, are being side-stepped, it is unlikely that the actions truly needed to protect nontarget species will be taken. Hence our recommendation that EPA withdraw the registration of Rozol until completion of a formal consultation with the Service. Nonetheless, short of immediate withdrawal of registration, we suggest the following interim modifications to these labels (**Rozol and Kaput**) to minimize potential impacts to non-target species pending consultation with the Service:

- The Notice of Pesticide Registration states that the product is conditionally registered provided certain actions are completed by LiphaTech. Among those actions is a requirement that LiphaTech conduct an Avian Reproduction Study within three years. We suggest all necessary studies be completed before registration.
- There is a lack of field studies designed to assess secondary risks to mammals (Erickson and Urban 2004). We suggest that secondary risk studies also be completed before registration.
- In the Precautionary Statements section of the label, under Environmental Hazards, we suggest that the following statement be added after the second sentence. *Do not apply in prairie dog towns where raptors or other predatory or scavenging migratory birds may occur.*
- In the Storage and Disposal section of the label, specify that only empty pesticide containers be placed in the trash, not waste products that may include pesticide product.
- In the Directions for Use section of the label, under Endangered Species considerations, we suggest that the third sentence be replaced with the following sentence. *Do not use this product within prairie dog towns in the range of the black-footed ferret.* The Service will provide information on the location and range of the ferret to EPA for use in the creation of county bulletins for its Bulletins Live Web site.
- In the Directions for Use section of the label, under Application, change "6 inches down active prairie dog burrows" to 12 inches.
- In the Directions for Use section of the label, under Follow-up, the label instructs applicators to return to the site 5-10 days after bait application and again 14-21 days after bait application to collect and properly dispose of any bait or dead or dying prairie dogs that may have come to the surface. This relaxes requirements of the previous 24 (c) labels for Colorado, Nebraska, Oklahoma, and Texas, which instruct applicators to return

at 1-2 day intervals to collect and properly dispose of bait and dead or dying prairie dogs. Leaving aside the question of how closely this label requirement is adhered to in the field, we suggest that in order to be truly protective of non-target species, the label should require at least twice daily trips at dawn and dusk to retrieve carcasses and bait. This should be done for a minimum of one month or until no more carcasses are found.

- In the Directions for Use section of the label, under Follow-up, eliminate inactive prairie dog burrow as a burial site.
- EPA should request documentation of the collection of dead and dying prairie dogs, including reports of any non-target mortality associated with the application, and involve the Service in the design of any studies that document or investigate any such effects.

In conclusion, we are very concerned about this registration and encourage EPA not to finalize any registration of chlorophacinone or diphacinone for prairie dog control due to the risks of secondary poisoning to predatory and scavenging wildlife. In summary, we find that:

- The labels for both of these products have been issued without the appropriate studies to assess risks to non-target wildlife and to provide adequate protective recommendations.
- The cost-benefit studies have not been realistically evaluated inasmuch as post-application surveys have been inadequate.
- The protections offered to nontarget wildlife under the current labels are insufficient in light of the concerns and evidence to date brought to EPA's attention by federal and state wildlife agencies.

Therefore we recommend that EPA withdraw the registration for Rozol and not issue a registration for prairie dog control for Kaput until EPA completes a formal consultation with the Service on the use of these rodenticides to control black-tailed prairie dogs. We also request that EPA undertake development of the MOU outlined in EO 13186 regarding migratory birds.

Please contact Dr. Roger C. Helm, Division of Environmental Quality, at (703) 358-2148 if you have any questions about these comments or to arrange for consultation.

Sincerely,

Assistant Director for Fisheries
and Habitat Conservation

cc: Donald Koch
President WAFWA
5400 Bishop Blouvard
Cheyenne, WY 82006

Bill Van Pelt
WAFWA Grasslands Coordinator
5000 W. Carefree Highway
Phoenix, AZ 85086

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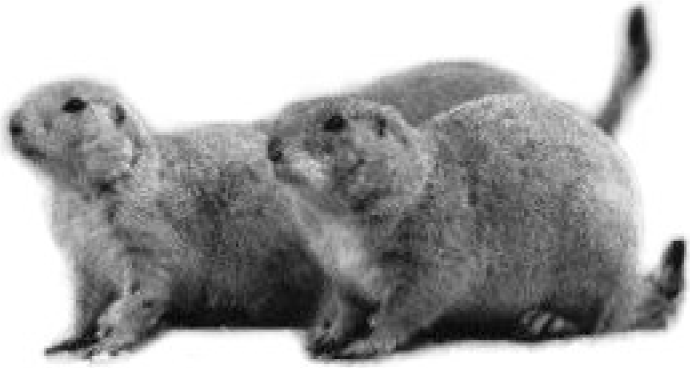
THE
BLACK-TAILED PRAIRIE DOG
CONSERVATION ASSESSMENT AND STRATEGY

Edited by:

William E. Van Pelt, Nongame Mammals Program Manager
Wildlife Management Division
Arizona Game and Fish Department



Technical Report 159
Nongame and Endangered Wildlife Program
Program Chief: Terry B. Johnson
Arizona Game and Fish Department
2221 West Greenway Road
Phoenix, Arizona 85023-4399

November 3, 1999

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Arizona Game and Fish Department
Office of the Deputy Director, DOHQ
2221 West Greenway Road
Phoenix, Arizona 85023-4399

and

The Office for Diversity and Civil Rights
U.S. Fish and Wildlife Service
4040 North Fairfax Drive, Room 300
Arlington, Virginia 22203

AMERICANS WITH DISABILITIES ACT COMPLIANCE

The Arizona Game and Fish Department complies with all provisions of the Americans with Disabilities Act. This document is available in alternative format by contacting the Arizona Game and Fish Department, Office of the Deputy Director at the address listed above or by calling (602) 789-3290 or TTY 1-800-367-8939.

MEMORANDUM OF UNDERSTANDING

AMONG

STATE FISH AND WILDLIFE AGENCIES WITHIN BLACK-TAILED PRAIRIE DOG RANGE

Conservation and Management of Black-tailed prairie dog in North America

I. Purpose

The purpose of this Memorandum of Understanding (MOU) is to provide guidance for conservation and management of the black-tailed prairie dog (*Cynomys ludovicianus*) and the short to mid-grass habitats upon which the species depends. Black-tailed prairie dogs are an obligate short to mid-grass species that require large tracts of grasslands for their survival and viability. Black-tailed prairie dogs historically occurred in at least 11 states, one Canadian province, and two Mexican states. However, this species has been extirpated from Arizona. The current black-tailed prairie dog distribution has been reduced throughout the species' historic range. Habitat loss and fragmentation, inadequate protection from regulatory mechanisms, plague outbreaks, and control in the form of poisoning, have all been identified as factors in the reduction of the species' occupied range. The long-term trend for black-tailed prairie dog abundance rangewide is downward. The affected State Fish and Wildlife Agencies agree that cooperative efforts are necessary to collect and analyze data on black-tailed prairie dogs and their habitats so that comprehensive state plans may be formulated and implemented to maintain the broadest distribution and greatest abundance possible within the fiscal realities of the state agencies and cooperating partners.

II. Objectives

All affected State Fish and Wildlife agencies agree that black-tailed prairie dogs are an important natural component of the short to mid-grass ecosystem. As such, black-tailed prairie dogs serve as an indicator of the overall health of this important habitat type. Furthermore, the presence and abundance of black-tailed prairie dogs reflects humankind's commitment to maintaining all natural components of the short to mid-grass ecosystem so that all uses of this habitat type are sustainable over time.

The primary purpose of this MOU is to implement the Conservation Assessment and Strategy (Appendix) for the black-tailed prairie dog, thus establishing an open process by which to identify and carry out such actions that will conserve the species through participation of public and private partners. Specific conservation objectives are:

1. Maintain and increase where possible the present distribution of the black-tailed prairie dogs.

2. Maintain and increase where possible the present abundance of the black-tailed prairie dogs.
3. Develop strategies using cooperative partnerships to maintain and enhance suitable and occupied black-tailed prairie dog habitats.
4. Conduct management experiments of a sufficient scale to demonstrate that population management can stabilize and enhance black-tailed prairie dog distribution and abundance.
5. Collect and analyze population and habitat data throughout the range of the black-tailed prairie dog for use in preparation of state management plans.
6. Develop partnerships with communities, industry, interested entities, and private landowners to accomplish conservation objectives.

III. Actions

It is the intent of the members of the affected State Fish and Wildlife Agencies to sustain and enhance the distribution and abundance of black-tailed prairie dogs through responsible collective management programs. These programs will include:

1. Identification of the present distribution of black-tailed prairie dog in each member state.
2. Collection of black-tailed prairie dog population data following standardized protocols throughout the range of the species.
3. Continuation of development of State Management Plans based on the local working group concept.
4. Validation of habitat evaluation and population viability models.
5. Completion of genetic analyses across the range of the black-tailed prairie dog to more effectively define and manage individual populations.
6. Development of cooperative partnerships with interested individuals, and private, state, tribal, and federal land managers.
7. Support and implement the revised black-tailed prairie dog population and habitat management guidelines developed through this conservation effort.
8. Further develop, implement, and amend as necessary, the objectives, strategies, and tasks in the Conservation Assessment and Strategy for black-tailed prairie dogs as information becomes available.
9. As needed for this conservation effort, and as available, provide personnel with facilities, equipment, logistical support to implement the conservation strategies.
10. Designate a member to the Black-tailed Prairie dog Conservation Team.
11. Participate regularly in conservation team and work group meetings to enhance communication and cooperation, and help develop annual and other work plans.
12. Develop and distribute educational material on this conservation effort.
13. Provide ongoing review of, and feedback on this conservation effort.
14. Cooperate in developing major media releases and media projects.
15. Keep local governments, communities, private citizens, and other interested and affected parties informed on the status of this conservation effort, including ways that might provide local economic benefits.
16. Assist in generating the funds necessary to fully implement this conservation effort.

IV. Responsibilities

1. Each state will collect data as recommended by the Black-tailed Prairie Dog Conservation Team within the constraints of their budgetary process.
2. All State Fish and Wildlife agencies will work cooperatively to maintain and enhance black-tailed prairie dog populations and their habitats.
3. Any State Fish and Wildlife Agencies deciding to terminate their participation in this MOU will provide 60-days written notice to the other cooperators.
4. This MOU shall have a term of five years from the last date written below. At the end of this period, this MOU will expire unless it is canceled, extended, or renewed.

V. Approval

We, the undersigned designated officials, do hereby approve this Memorandum of Understanding and execute it as of the last date written below.

Approved Steve K. Ferrell (for) Date 11/3/99
Arizona Game and Fish Department Duane L. Shroufe, Director

Approved ______ Date ______
Colorado Division of Wildlife

Approved Steve Williams Kansas execution subject to DA-146a (Attach A) Date 10/28/99
Kansas Department of Wildlife and Parks

Approved Patrick Graham Date 10-24-99
Montana Department of Fish, Wildlife, and Parks

Approved Rex Amack (rec for) Date 14 Oct 99
Nebraska Game and Parks Commission

Approved ✓ Subject to Attach.B Date 2-1-2000
New Mexico Game and Fish Department

Approved ______ Date ______
North Dakota Game and Fish Department

Approved ______ Date 10-17-99
Oklahoma Department of Wildlife Conservation

Approved John L Cooper Date 10/26/99
South Dakota Department of Game, Fish and Parks

Approved Andrew Sansom Date 11/3/99
Texas Parks and Wildlife Department

Approved Bill Wichers Date 10/21/99
Wyoming Game and Fish Department

STATE OF ARIZONA
SPECIAL CONDITIONS

1. All cooperators agree to comply with the Governor's Executive Order No. 75-5, entitled "Prohibition of Discrimination in State Contracts - Discrimination in Employment by Government Contractors and Subcontractors."

2. All cooperators hereby are put on notice that this MOA is subject to cancellation by the Governor of the State of Arizona, pursuant to Arizona Revised Statutes Section 38-511.

3. To the extent required pursuant to Arizona Revised Statutes Section 12-1518 and any successor statutes, the cooperators agree to use arbitration, after exhausting all applicable administrative remedies, to resolve any dispute arising out of this agreement, where not in conflict with Federal Law.

4. Pursuant to Arizona Revised Statutes Sections 35-214 and 35-215, and Section 41-1179.04 as amended, all books, accounts, reports, files, and other records relating to any contracts issued under the umbrella of the MOA shall be subject at all reasonable times to inspection and audit by the State for five years after completion of the contract. Such records shall be reproduced as designated by the State of Arizona.

:bvp

State of Kansas
Department of Administration
DA-146a (Rev. 6-96)

Attachment A

CONTRACTUAL PROVISIONS ATTACHMENT

Important: This form contains mandatory contract provisions and must be attached to or incorporated in all copies of any contractual agreement. If it is attached to the vendor/contractor's standard contract form, then that form must be altered to contain the following provision:

"The Provisions found in Contractual Provisions Attachment (Form DA-146a, Rev. 6-96), which is attached hereto, are hereby incorporated in this contract and made a part thereof."

The parties agree that the following provisions are hereby incorporated into the contract to which it is attached and made a part thereof, said contract being the _____ day of ___________________, 19___.

1. TERMS HEREIN CONTROLLING PROVISIONS
It is expressly agreed that the terms of each and every provision in this attachment shall prevail and control over the terms of any other conflicting provision in any other document relating to and a part of the contract in which this attachment is incorporated.

2. AGREEMENT WITH KANSAS LAW
All contractual agreements shall be subject to, governed by, and construed according to the laws of the State of Kansas.

3. TERMINATION DUE TO LACK OF FUNDING APPROPRIATION
If, in the judgment of the Director of Accounts and Reports, Department of Administration, sufficient funds are not appropriated to continue the function performed in this agreement and for the payment of the charges hereunder, State may terminate this agreement at the end of its current fiscal year. State agrees to give written notice of termination to contractor at least 30 days prior to the end of its current fiscal year, and shall give such notice for a greater period prior to the end of such fiscal year as may be provided in this contract, except that such notice shall not be required prior to 90 days before the end of such fiscal year. Contractor shall have the right, at the end of such fiscal year, to take possession of any equipment provided State under the contract. State will pay to the contractor all regular contractual payments incurred through the end of such fiscal year, plus contractual charges incidental to the return of any such equipment. Upon termination of the agreement by State, title to any such equipment shall revert to contractor at the end of State's current fiscal year. The termination of the contract pursuant to this paragraph shall not cause any penalty to be charged to the agency or the contractor.

4. DISCLAIMER OF LIABILITY
Neither the State of Kansas nor any agency thereof shall hold harmless or indemnify any contractor beyond that liability incurred under the Kansas Tort Claims Act (K.S.A. 75-6101 et seq.).

5. ANTI-DISCRIMINATION CLAUSE
The contractor agrees: (a) to comply with the Kansas Act Against Discrimination (K.S.A. 44-1001 et seq.) and the Kansas Age Discrimination in Employment Act (K.S.A. 44-1111 et seq.) and the applicable provisions of the Americans With Disabilities Act (42 U.S.C. 12101 et seq.) (ADA) and to not discriminate against any person because of race, religion, color, sex, disability, national origin or ancestry, or age in the admission or access to, or treatment or employment in, its programs or activities; (b) to include in all solicitations or advertisements for employees, the phrase "equal opportunity employer"; (c) to comply with the reporting requirements set out at K.S.A. 44-1031 and K.S.A. 44-1116; (d) to include those provisions in every subcontract or purchase order so that they are binding upon such subcontractor or vendor; (e) that a failure to comply with the reporting requirements of (c) above or if the contractor is found guilty of any violation of such acts by the Kansas Human Rights Commission, such violation shall constitute a breach of contract and the contract may be cancelled, terminated or suspended, in whole or in part, by the contracting state agency or the Kansas Department of Administration; (f) if it is determined that the contractor has violated applicable provisions of ADA, such violation shall constitute a breach of contract and the contract may be cancelled, terminated or suspended, in whole or in part, by the contracting state agency or the Kansas Department of Administration.

Parties to this contract understand that the provisions of this paragraph number 5 (with the exception of those provisions relating to the ADA) are not applicable to a contractor who employs fewer than four employees during the term of such contract or whose contracts with the contracting state agency cumulatively total $5,000 or less during the fiscal year of such agency.

6. ACCEPTANCE OF CONTRACT
This contract shall not be considered accepted, approved or otherwise effective until the statutorily required approvals and certifications have been given.

7. ARBITRATION, DAMAGES, WARRANTIES
Notwithstanding any language to the contrary, no interpretation shall be allowed to find the State or any agency thereof has agreed to binding arbitration, or the payment of damages or penalties upon the occurrence of a contingency. Further, the State of Kansas shall not agree to pay attorney fees and late payment charges beyond those available under the Kansas Prompt Payment Act (K.S.A. 75-6403), and no provision will be given effect which attempts to exclude, modify, disclaim or otherwise attempt to limit implied warranties of merchantability and fitness for a particular purpose.

8. REPRESENTATIVE'S AUTHORITY TO CONTRACT
By signing this contract, the representative of the contractor thereby represents that such person is duly authorized by the contractor to execute this contract on behalf of the contractor and that the contract agrees to be bound by the provisions thereof.

9. RESPONSIBILITY FOR TAXES
The State of Kansas shall not be responsible for, nor indemnify a contractor for, any federal, state or local taxes which may be imposed or levied upon the subject matter of this contract.

10. INSURANCE
The State of Kansas shall not be required to purchase, any insurance against loss or damage to any personal property to which this contract relates, nor shall this contract require the State to establish a "self-insurance" fund to protect against any such loss of damage. Subject to the provisions of the Kansas Tort Claims Act (K.S.A. 75-6101 et seq.), the vendor or lessor shall bear the risk of any loss or damage to any personal property in which vendor or lessor holds title.

11. INFORMATION
No provision of this contract shall be construed as limiting the Legislative Division of Post Audit from having access to information pursuant to K.S.A. 46-1101 et seq.

ATTACHMENT B

STATE OF NEW MEXICO

SPECIAL CONDITIONS

PERTAINING TO MEMORANDUM OF UNDERSTANDING REGARDING BLACK-TAILED PRAIRIE DOG

The following conditions apply to the Memorandum of Understanding (Agreement) among State Fish and Wildlife Agencies within Black-Tailed Prairie Dog Range.

1. The New Mexico Department of Game and Fish (Department) will participate in the above Agreement to the extent authorized under New Mexico's Wildlife Conservation Act [17-2-37 NMSA through 17-2-46 NMSA 1978]. The Department will attempt to undertake only those actions within this Agreement that are in compliance with the existing laws of the State of New Mexico.

2. The terms of this Agreement are contingent upon sufficient appropriations being available to the Department for the performance of this Agreement. The Department's decision as the whether sufficient appropriations are available shall be accepted by all cooperators in this Agreement, and shall be final.

3. This Agreement does not confer or imply any support or opposition from the Department for the proposal to list the black-tailed prairie dog as "threatened" under the Endangered Species Act, nor to any of the assertions made within that proposal.

RECOMMENDED CITATION

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, Arizona.

ACKNOWLEDGMENTS

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THE BLACK-TAILED PRAIRIE DOG CONSERVATION ASSESSMENT AND STRATEGY

William E. Van Pelt

INTRODUCTION

On July 30, 1998 the National Wildlife Federation (NWF) petitioned the U.S. Fish and Wildlife Service (Service or USFWS) to emergency list the black-tailed prairie dog (*Cynomys ludovicianus)* as threatened throughout its range. The NWF stated the emergency need was due to unregulated shooting and poisoning of prairie dogs that would occur during the Service's 12-month listing evaluation process. By law, the Service was compelled to respond to the petition within 90 calendar days.

In September 1998, the Service responded to the NWF that although it did not believe the threshold had been met for emergency listing the black-tailed prairie dog, listing the species might be warranted and they would further evaluate the petition. On March 23, 1999 a positive 90-day finding for the petition was announced (USFWS 1999). This action initiated a 9-month review process for the petition. A status review decision is expected sometime by January 2000.

Starting in November 1998, state wildlife agencies and departments of agriculture in Wyoming, Montana, and South Dakota held a series of meetings with the Service and NWF to discuss the petition and the options the states have in regard to the petition. Based on discussions at these meetings, it was determined that involvement by all states, other management agencies, and tribal interest within the historic range of the black-tailed prairie dog was warranted and a meeting should be convened to begin developing an interstate effort to conserve the species.

On March 17, 1999 the Colorado Division of Wildlife (CDOW) invited various state, federal, tribal, and other entities with an interest in black-tailed prairie dogs to a meeting to assess the feasibility of a range wide conservation agreement. Meeting participants agreed that pursuing a conservation agreement was the most reasonable approach for black-tailed prairie dog conservation. They believed that if strong partnerships could be developed under this approach, it would be a significant step forward in bringing local governments, private landowners, and nongovernmental organizations directly into black-tailed prairie dog management.

The purpose of this Conservation Agreement is to manage, maintain, and enhance habitat and populations of black-tailed prairie dogs across its historic range and reduce the number of threats impacting their viability through the cooperation of private, tribal, federal, and state landowners. The Conservation Agreement has many elements that provide actions, opportunities, and incentives for interested parties to become involved with conservation. By implementing management actions such as eliminating mandatory control, regulating seasons or possession limits, maintaining and conserving their habitat and ecosystem needs, and establishing core populations on public lands to provide animals for dispersal to uninhabited areas or individuals for recolonization, the cooperators of this conservation agreement contribute greatly toward the conservation of the species.

The Conservation Agreement embraces two main components. The first is a Conservation Assessment, which describes the current status of the black-tailed prairie dog in the United States, Mexico, and Canada and identifies the threats limiting its conservation. The second component, the

Conservation Strategy focuses on reducing or eliminating threats limiting black-tailed prairie dog viability, as defined in the conservation assessment, and thus contributes to its conservation when implemented.

CONSERVATION ASSESSMENT

The following subsections provide life history, status, and management information on the black-tailed prairie dog.

DESCRIPTION

The black-tailed prairie dog is a diurnal, burrowing rodent, almost 15 inches in length, including a 2½-inch, black-tipped tail. It is yellowish buff in color and weighs up to three pounds. Albinism and melanism occur in black-tailed prairie dogs but are considered rare. Historically, the black-tailed prairie dog ranged from Canada to Mexico throughout the Great Plains states and west to southeastern Arizona (Foster and Hygnstrom 1990), but the species is now considered uncommon or extirpated in many areas of its former range (Hoogland 1996).

LIFE HISTORY

Black-tailed prairie dogs are highly social animals. They live in colonies or towns, which cover from one acre to thousands of acres of grassland habitat. A family group, or coterie, is made up of an adult male, one to four breeding females and their offspring younger than two years of age. With the emergence of young, coteries can number as many as 40 individuals (Hoogland 1996). Black-tailed prairie dogs are active all year long, but during extremely cold weather will remain underground for several consecutive days.

Black-tailed prairie dogs become sexually mature in the second February or March following birth (Hoogland 1996). Breeding season varies with latitude, starting in January in the southern parts of its range and continuing into April in the northern part (Hoogland 1996). They normally have one litter per year and sizes range from one to eight young. However, due to mortalities, on the average, only three individuals survive and come above ground. Pups emerge at about 41 days and will stay with their natal coteries for a minimum of two years (Hoogland 1996). Prairie dogs have been documented to live up to eight years in the wild (Foster and Hygnstrom 1990).

Black-tailed prairie dogs are herbivores and feed on a variety of vegetation including grasses and forbs (Koford 1958), and to a lesser extent seeds and insects (Foster and Hygnstrom 1990). Short-grass species commonly eaten by prairie dogs include buffalograss (*Buchloe dactyloides*) and blue grama (*Bouteloua gracilis*). It has been estimated that it takes 256 prairie dogs to eat as much as one cow eats in one month (Koford 1958). Grasses and other vegetation are clipped close to the ground to allow for a greater range of sight. The digging actions of prairie dogs contribute to enhancing soil structure, water filtration, and forb growth.

Ungulate species seek out and take advantage of the highly nutritional vegetation created by prairie dogs continuously clipping it (Foster and Hygnstrom 1990). Besides attracting ungulates, prairie dogs and their colonies also are used by a wide variety of wildlife species. A number of species prey on prairie dogs, and in the case of the black-footed ferret, have become very specialized in killing this communal rodent (Koford 1958). Because the black-tailed prairie dog influences ecosystem functions through its activities in unique and significant ways, it is considered by some as a keystone species of the prairie grasslands (USFWS 1999).

However, the same activities some consider as a necessity to the grassland ecosystem, others consider them as a nuisance. In a study by Conover and Decker (1991), prairie dogs, and their activities were identified by some as causing the worst damage by any wildlife species in their state and contribute hundreds of thousands of dollars worth of damage to agriculture crops, earthen dams, airports, and golf courses annually. In addition to damages, prairie dog species can be a health hazard. Cases of human death due to plague contracted from handling Gunnison's prairie dog have been documented in Arizona (ADHS 1993).

TAXONOMY

Taxonomists recognize two subspecies of black-tailed prairie dogs: *Cynomys ludovicianus ludovicianus* and *C. l. arizonensis* (Hall 1981). Black-tailed prairie dogs that occurred in Arizona, southern New Mexico, western Texas and northern Mexico are typically considered Arizona black-tailed prairie dogs, while others elsewhere are considered plains black-tailed prairie dogs. These two subspecies have been the subject of several investigations including those of Hollister (1916), Pizzimenti (1975), Hansen (1977), and Chesser (1981). Regardless of conclusions made during these and other investigations, it is generally recognized that *arizonensis* is only slightly differentiated from the nominant form *ludovicianus*. For purposes of nomenclatural convenience, regarding this species as monotypic may be adequate. However, from the standpoint of evolution, the uniqueness of populations throughout their range must be given serious consideration. This Conservation Agreement covers all black-tailed prairie dogs.

DISTRIBUTION

Early accounts about prairie dogs, although anecdotal at times, indicate they occurred in large numbers. Naturalist Ernest Thompson Seton estimated that five billion black-tailed prairie dogs inhabited the North America prairies in the early 1900s (Seton 1953). However, since that time prairie dog numbers and distribution have been greatly reduced across their range. This reduction resulted from a number of factors including intensive control programs, conversion of habitat to croplands, disease epizootic, and urbanization. The historic and current distributions of black tailed prairie dogs throughout their range are as follows:

Arizona-In the 1800s, black-tailed prairie dogs were considered quite abundant throughout their range in southeastern Arizona. In 1907, Mearns (cited in Hoffmeister 1986) reported that "For miles the burrows of these animals are thickly scattered over the plains south of the Pinaleno range or Sierra Bonito, where the soil is clayey and better suited to the habits of this animal than the loose sand of most of Arizona." Black-tails ranged from the Sulphur Springs Valley north of Bonito, south to the Mexican border, and west to the Sonoita grasslands, on the west side of the Huachuca Mountains. Although Alexander (1932) considered black-tailed prairie dogs extirpated by 1932, Charles Vorhies collected two animals six miles southeast of Fort Huachuca in 1938 (Hoffmeister 1986). In 1962, in a memorandum to the Bureau of Sports Fisheries and Wildlife Regional Director, Everett M. Mercer documents the persistence of a small black-tailed prairie dog colony near Apache, Arizona until 1959-1960. Cockrum (1960) considered black-tailed prairie dogs extirpated from Arizona in 1960 and the species is still considered extirpated by the Arizona Game and Fish Department (AGFD)(AGFD 1988).

Colorado-In the 1800s, black-tailed prairie dog towns covered large portions of the eastern 1/3 of Colorado. Cary (1911) stated "[t]here is probably not a county east of the foothills in which it is not present in considerable numbers, and colonies are found in some of the broader foothill valleys to an elevation of 6,000 feet." Lechleitner (1969) cites Hollister (1916) as a source that indicated "...this species was very abundant on the plains of Colorado and often occurred in towns covering several square miles." However, no early estimates on the acreage inhabited by prairie dogs are available for Colorado.

Historical estimates suggest that 20 percent of the short- and mid- grass prairies may once have been inhabited by prairie dogs (Laurenroth 1979). If it is assumed lands used for dry-land and irrigated crops within the black-tailed prairie dog range were once suitable habitat, and that a 20% occupation rate is reasonable, then historically, black-tailed prairie dogs occupied approximately 4.6 million acres in Colorado.

Colorado has no current statewide, scientifically based estimate of habitat occupied by black-tailed prairie dogs. Prior to 1979, most reports of prairie dogs in Colorado were anecdotal in nature. A 1978 and 1979 survey of 12 counties in eastern Colorado mapped 24,600 acres of black-tailed prairie dog towns (Bissell et al. 1979). The counties surveyed represent approximately 48% of the land area of the counties in eastern Colorado within the species range. This survey did not include the rapidly developing counties along Colorado's Front Range, where as much as 39,000 acres were occupied by prairie dogs. Extrapolating the acreage yields an estimate of approximately 50,800 acres, and with the addition of 39,000 acres of prairie dog towns along the Front Range yields a total estimate of approximately 89,000 acres occupied by black-tailed prairie dogs in eastern Colorado at that time. In contrast, Colorado Agricultural Statistics Service estimated approximately 1,553,000 acres being occupied by prairie dogs in Colorado. However, this survey included all prairie dog species, and landowners were asked to estimate occupied acreage. However, due to prairie dog species distribution the Colorado Department of Agriculture interprets the results to over 930,000 of the acres identified in the survey were black-tailed prairie dogs. In 1998, Knowles (1998) estimated 44,000 acres were occupied in areas outside agricultural and private lands in eastern Colorado.

Regardless of the lack of complete information, it is clear the black-tailed prairie dog in Colorado has undergone a substantial reduction in population size (number and size of towns) since the early 1900s; however, they are still abundant in many localities (Fitzgerald et al. 1994). Limited acres of small, scattered black-tailed prairie dogs colonies exist on parcels of public lands administered by the Bureau of Land Management (BLM) in eastern Colorado. Few colonies exceeded 49 acres

(Lechleitner 1969), with a mean colony size of 43 acres (Bissell et al. 1979).

Kansas-The first description of the prairie dog in Kansas occurred in 1806-07 by Pike and he designated it by its Indian name, Wishtonwish. The historic range of the prairie dog was the western two-thirds of Kansas, west of the tall grass prairie of the Flint Hills. In 1859, J.R. Mead (1899) indicated that prairie dogs were innumerable and the divide between the Saline and Solomon rivers in Ellsworth County (north central Kansas) and west was a continuous dog town for miles. Lantz (1903) reported that 68 counties in Kansas were occupied with prairie dogs totaling about 1,250,000 acres and estimated a statewide population of 2,000,000 acres.

The decline of the black-tailed prairie dog was primarily due to poisoning efforts (Smith 1958) and changes in land use practices after settlement in western Kansas. Nearly two-thirds of the 33 million acres of range and pasture land within the geographic range of the prairie dog in Kansas were converted to cropland and other uses after settlement. Because prairie dogs prefer deep, relatively level soils, much of this agricultural development probably occurred in areas inhabited by prairie dogs, with resultant destruction or fragmentation of many of the larger colonies (Choate et al. 1982). Furthermore, legislative action directed at extermination of prairie dogs in Kansas was initiated in 1901 (Lantz 1903).

Numerous methods have been used to collect population information on prairie dogs in Kansas. Methods include questionnaires to landowners, on-the-ground surveys by Natural Resource Conservation Services and Kansas Department of Wildlife and Parks (KDWP) personnel, and counting towns from aerial photos. In 1956, Smith (1958) indicated a total of 57,045 acres of prairie dog towns remaining in Kansas, about one-thirtieth of the number reported by Lantz in 1903. Henderson and Little (1973) indicated approximately 35,881 acres of prairie dog towns. In 1977 and 1988, the KDWP conducted a ground count survey of prairie dog towns (unpublished data) evaluating acreage of prairie dogs at 57,407 and 24,094 respectively. Finally, Vanderhoof and Robel (1994) reported 46,542 acres of prairie dogs in 1990-1992.

Recent studies have documented drastic prairie dog declines in areas of Kansas. Lee and Henderson (1989) compared their 1986 data with 1902 data (Lantz 1903) on eight Kansas counties and found an 86% decline in prairie dog occupied area. Powell (1992) found an 84% decline in prairie dog area from 1902 (Lantz 1903) to 1990 for eight Kansas counties and a 17% decline from 1986 (Lee and Henderson 1988) to 1990 for three Kansas Counties.

Montana-Although the original abundance of prairie dogs in Montana is unknown, early accounts indicate they were abundant and widely distributed east of the Continental Divide (FaunaWest 1999). Lewis and Clark reported prairie dog colonies along the Missouri River were common and some were three to seven miles long (FaunaWest 1999). There are anecdotal accounts of prairie dog towns stretching from the Little Rocky Mountains to the Larb Hills (FaunaWest 1999). Flath and Clark (1986) estimated prairie dog acreage in southeastern Montana at 117,492 acres based on railroad survey notes recorded from 1908-1914.

Prairie dogs were intensely controlled with toxicants in Montana starting at the time of settlement.

Control efforts peaked during the 1920s and 30s resulting in a substantial decline in prairie dogs. For example, over 172,000 acres were poisoned in Phillips County during this period. Declines in prairie dog numbers continued until 1972 when the use of Compound 1080 was banned on Federal lands. Plague and conversion of habitat to agricultural use continue to impact prairie dogs in Montana.

The first attempt to estimate prairie dog acreage occurred in the late 1980s. Campbell (1989) estimated over 100,000 acres located in about 1,000 colonies east of the 110 meridian. However, much of the information was not based on actual field surveys and the degrees of certainty for this estimate is low (FaunaWest 1999). In 1995, Knowles and Knowles updated the Campbell information and estimated 80,000 acres. FaunaWest (1999) estimated 1,353 colonies covering 66,139 acres. Colony size average was 49 acres.

Nebraska-Historically, black-tailed prairie dogs were found throughout most of Nebraska, nearly to the Missouri River on the eastern edge of the state (Jones 1964). Colonies in the early 1900's were noted as far east as Cuming and Washington counties (Jones 1964). Merriam (1901) suggested that prairie dogs might have increased with the arrival of white settlers on the plains, due to an increase in the food supply through cultivation and by reducing the natural enemies of prairie dogs.

Prairie dogs were once found through a large portion of the tall-grass prairie in Nebraska, in habitat made suitable by the grazing of vast herds of bison (Jones 1964). At present, prairie dogs occur in short and mid-grass prairies of the panhandle, Sandhill region, and southwestern Nebraska. Prairie dog occurrence in the Sandhills of north central Nebraska is limited primarily to river valleys and other areas where the substrate will support the burrow systems.

Black-tailed prairie dog numbers in Nebraska have undoubtedly declined substantially from historic levels. Most of the decline occurred in the early 1900s with the conversion of grassland to crops and poisoning campaigns. Although numbers declined substantially in the early 1900s, surveys conducted in Nebraska since the 1970s have shown populations to be fairly stable in recent years.

In 1975 and 1976, Nebraska Game and Parks Commission (NGPC) reviewed the status and distribution of black-tailed prairie dogs through analysis of aerial photographs for 52 of Nebraska's 93 counties that were known to contain most of the prairie dogs in the state. Although the scale of some of the photos was small, resulting in problems with colony identification, the survey has served as a baseline for subsequent surveys. This initial survey showed 2,018 prairie dog colonies totaling 41,197 acres. Twenty-one counties surveyed in 1975-76 were surveyed again in 1982, using larger scale aerial photos. These counties contained 1,395 prairie dog colonies totaling 29,066 acres in the 1975-76 survey while they showed 1,604 colonies totaling 46,245 acres in the 1982 survey. The mean photograph date for these counties in the 1975-76 survey was 1965, while the mean date for the 1982 survey was 1975. Seven of the counties that were surveyed in 1975-76 and again in 1982 were surveyed again in 1997, using 1993 photographs. These seven counties showed 563 colonies totaling 12,554 acres on the 1975-76 survey, 697 colonies totaling 21,265 acres on the 1982 survey and 484 colonies totaling 18,723 acres on the 1997 survey.

Using information from the surveys conducted since 1975, an estimate was made for the total statewide prairie dog acreage in Nebraska. Using photographs from the early 1980's, prairie dog acreage in Nebraska was estimated at about 80,000 acres.

In general, the NGPC feels prairie dog numbers appear to be fairly stable in recent years for the state. Recreational shooting is thought to have little impact on overall numbers. Plague has been documented in the state, but only in a few areas. Impact by plague on the statewide prairie dog population is unknown but thought to be insignificant. Of all the human control activities in Nebraska poisoning is thought to have the most impact on the statewide prairie dog population at the present time. Prairie dogs occur primarily on private land in Nebraska, and landowners appear to be quite interested in prairie dog control. Control activities are implemented by landowners directly, by private pest control agents or with the assistance of U.S. Department of Agriculture Animal and Plant Health Inspection Service Wildlife Services (APHIS-WS), which is active in counties that provide partial funding.

New Mexico-The first detailed accounts of prairie dogs in the state began around the mid 1850s. C. B. Kennerly (Baird 1859) observed prairie dogs near the San Luis Mountains in what is now Hidalgo County (Hubbard and Schmitt 1984). Proof that Kennerly observed prairie dogs is verified by a specimen taken at San Luis Spring, Hidalgo County by J. H. Clarke in May 1855 (Baird 1859). Bailey (1932) described the distribution of black-tailed prairie dogs as, although irregularly distributed, "they may be said to occupy practically all of it" in the area east of the Pecos River Valley and the Sangre de Cristo Mountains. Bailey (1932) further described prairie dogs as occurring over southern New Mexico, west of the Pecos Valley. Bailey reported that in 1899 at the Pecos River Valley they were "abundant at frequent intervals" from Portales to Roswell, south to Carlsbad and the Texas border, and from Roswell west to the Capitan Mountains "in numerous and extensive colonies." Bailey (1932) also mentioned the presence of black-tailed prairie dogs in southwestern New Mexico northward to Cliff and Silver City in Grant County during 1892-1908 and Lake Valley in Sierra County in 1909.

There is no evidence of black-tailed prairie dogs in Luna County (Findley et al. 1975) or in adjacent northern Chihuahua (Anderson 1972). Mearns (1907) crossed the area from El Paso to Hidalgo County and indicated that after leaving El Paso, the first prairie dogs encountered were at Dog Spring in southern Hidalgo County near where the species was noted by Kennerly. Hubbard and Schmitt (1984) concluded that black-tailed prairie dogs were absent between El Paso and the eastern portion of southern Hidalgo County. Perhaps colonies of black-tailed prairie dogs in Hidalgo County were connected eastward through Grant, northern Luna, Sierra, and Doña Ana counties to populations in the Tularosa Basin and beyond (Hubbard and Schmitt 1984). This assumption is verified in Bailey's (1932) description of black-tailed prairie dogs in the Animas Valley in 1908 as "an almost continuous prairie dog town for its whole length and breadth." Bailey estimated that as many as 6,400,000 prairie dogs occupied 1,000 square miles in that part of southwestern New Mexico.

Nonetheless, the range of this species in New Mexico has been significantly reduced since the mid 1800s (Hubbard and Schmitt 1984). In contrast to Bailey's 1908 observations, Alexander (1932) reported seeing prairie dogs totaling only about 50 acres in the Animas Valley and she had heard of only one other colony in the Playas Valley. By 1955, black-tailed prairie dogs were scarce south of the Mogollon Plateau (Findley et al. 1975). Small numbers of prairie dogs persisted into the late 1950s and early 1960s in the Summit area of Hidalgo County and the Separ to White Signal areas of Grant County (A. Bayne et al. pers. comm. in Hubbard and Schmitt 1984). These few known populations were soon thereafter extirpated, with no populations of black-tailed prairie dogs existing in New Mexico west of the Rio Grande.

In 1984, Hubbard and Schmitt reported that the estimated overall range of the black-tailed prairie dog in New Mexico had been reduced by 25% by 1981. Bodenchuk (1981) estimated acreage of prairie dogs per county using questionnaires mailed to agricultural producers statewide. Based on this statewide survey, Bodenchuk reported a total of 500,000 acres of prairie dog colonies in the state, of which black-tailed prairie dogs comprised 27.5%. Using Bodenchuk's estimate, there were an estimated 137,500 acres of remaining black-tailed prairie dog colonies in New Mexico in 1981. These data revealed prairie dogs were not present in Hidalgo, Grant, Luna, Doña Ana, Sierra, Otero, Lincoln, Eddy, and Union counties. Absence of records of prairie dogs reported by Bodenchuk (1981) for Hidalgo, Grant, Luna, and Doña Ana Counties are consistent with conclusions made by Findley et al. (1975) and Hubbard and Schmitt (1984). However, the absence of records of prairie dogs in Sierra County may reflect a failure in his survey to reach all agricultural producers because Gunnison's prairie dogs (*C. gunnisoni*) are known to occur. The absence of reports from Union County may be explained by the same reasons because black-tailed prairie dogs are rather widespread inhabitants of Union County (Hubbard and Schmitt 1983) and their presence was recently reconfirmed in 1996 (Sager 1996). The examples of no reports of prairie dogs for Lincoln and Otero counties and inclusion of these counties in the area of probable extirpation by Findley et al. (1975) were premature. Black-tailed prairie dogs are known to occur in each of these counties (e.g., Hansen 1977; Hubbard and Schmitt 1984).

Additional investigations on black-tailed prairie dogs, including surveys in Colfax, Union, Harding, and Mora Counties (covering about 11,500 square miles), were conducted in 1996 (Sager). These surveys revealed the presence of a total of 1,191 black-tailed prairie dog individuals in over 41 colonies in Union County, 11 colonies in Colfax County, two colonies in Mora County, and 10 colonies in Harding County. Similar surveys were conducted in 1997 by Paternoster, revealing the presence of 33 colonies of black-tailed prairie dogs in Roosevelt County and 40 colonies in Curry County together totaling about 3,174 occupied acres. Although these two surveys revealed a total of 137 colonies of black-tailed prairie dogs in six counties, current systematic surveys such as these are lacking in the remaining counties of New Mexico.

Although efforts to control prairie dogs continue in New Mexico, the New Mexico Department of Game and Fish (NMDGF) believes these control activities are now more localized in application and on a smaller scale than in the recent past. Control of prairie dogs is still done for the purpose of protecting grazing lands, agricultural crops, and farming developments. Other control activities, usually in close proximity to human developments, include eradication or control of prairie dogs for their presumed role in transmission of sylvatic plague to humans. Management of black-tailed prairie dogs has not been limited to control. Black-tailed prairie dogs have recently been reintroduced in two areas in Sierra County, and two areas in Hidalgo County are being discussed for possible reintroduction in areas of private ownership on the Gray Ranch.

Given some gaps in current information concerning their distribution, numbers, viability of isolated populations, impacts of habitat fragmentation, amount and extent of efforts to control (or eradicate) them, population impacts from plague, and other biological factors, the overall status of black-tailed prairie dogs in New Mexico needs further verification. However, there are no data available that would suggest populations in New Mexico are stable and/or improving.

North Dakota-The black-tailed prairie dog range extended across the southwestern portion of the state and occupied an estimated two million acres. Settlers viewed prairie dogs as vermin and there were extensive efforts to exterminate or substantially reduce their numbers. These efforts were initiated in the 1920s by various entities, and between 1920 and 1961, occupied prairie dog habitat was reduced by more than 99 percent. In 1961, the Bureau of Sport Fisheries and Wildlife estimated 19,750 acres of occupied habitat in North Dakota. Bishop and Culbertson (1976) also documented historical declines of prairie dogs in North Dakota. They examined aerial photographs of western North Dakota from 1939-1972 to evaluate the impact of control programs and land use practices on prairie dogs within the Little Missouri National Grassland. Results showed an 89% reduction in the number of towns. The Regional Environmental Assessment Program (REAP) conducted a census from 1975-1978 covering all areas of North Dakota with active prairie dog towns. Results indicated 9,231 acres of active prairie dog towns, and a tentative conclusion was that prairie dogs were increasing during this time period.

The most recent survey of prairie dogs in North Dakota was conducted in the late 1980s. Results showed approximately 20,000 acres of prairie dog towns, which is roughly double the acres found by the REAP report and supports their conclusion on increasing numbers. Approximately half of the acreage is on private land while the other half is on state, federal, or tribal land. Although there have been no additional surveys since the late 1980s, the prairie dog population appears to have remained fairly stable based on anecdotal information and observations from various natural resource agencies. A current survey for occupied habitat by the U.S. Geological Survey (USGS) Northern Prairie Wildlife Research Center estimates population levels at about 30,000 acres.

Oklahoma-In the 1800s, black-tailed prairie dogs covered a vast portion of Oklahoma. It has been reported that millions of acres were present at that time within the state (Lewis and Hassien 1974). Shackford (1989) cites an 1898 colony near Fort Reno in Canadian County that stretched northward for 22 miles. Prior to 1967, however, most reports of prairie dogs in Oklahoma were anecdotal in nature. Because of a lack of data the degree to which black-tailed prairie dog numbers have been reduced since pre-settlement times cannot be accurately determined.

It is generally accepted that the black-tailed prairie dog in Oklahoma has undergone a reduction in population size (number and size of towns) over the past 150 years. However, the geographic limits of the species within the state have remained unchanged from historical records. Much of the decline in prairie dogs numbers in Oklahoma probably occurred during the early 1900s. This decline in numbers was a direct result of control programs. Though extremely diminished in numbers compared to the mid 1800s, the black-tailed prairie dog has been able to survive on smaller patches of habitat widely scattered over the western part of the state (Shackford 1989).

In 1967, Tyler (1968) made an extensive survey of prairie dogs and associated species throughout the state. Tyler (1968) found 280 active black-tailed prairie dog towns in 34 counties, totaling 9,522 acres and 34,452 prairie dogs. Of this acreage, 42% occurred in the three panhandle counties: Cimarron, Texas, and Beaver (Tyler 1968). Lewis and Hassien (1974) noted an increase to 15,000 acres seven years later. In 1988, Shackford (1989) conducted a second comprehensive prairie dog survey and discovered 399 towns within 33 counties, incorporating 18,382 acres and 66,656 prairie dogs. Total acreage and number of towns increased in the three panhandle counties to 242 (61%) towns, covering 14,479 (79%) acres in 1989.

During 1998 and 1999, the Oklahoma Department of Wildlife Conservation (ODWC) verified the presence or absence of 315 (78%) of the 1989 towns statewide. Of these 313 towns, 192 (61%) are still in existence today. Additionally, 111 new towns were identified while verifying the 1989 town status, totaling 303 towns documented. ODWC considers the 111 new towns to be a conservative number, since they did not systematically survey the state for new prairie dog towns. Other new towns may be present but were not detected because ODWC concentrated on examining the 1989 survey data. Without conducting a systematic survey, however, the 24 counties for which they have current data show a net loss of only nine towns, representing a 3.81% change in the number of towns throughout the prairie dog's range in Oklahoma. Full verification within ten counties remains to be completed.

The greatest loss of prairie dog towns since 1989 occurred in Cimarron County, in the western 1/3 of the panhandle, where the majority of these losses were the result of plague (confirmed outbreak 1991; suspected outbreak 1994). In the panhandle region, ODWC verified the presence/absence of 193 (80%) of the 242 towns surveyed in 1989. Of these 193 towns, 109 (56%) still exist nearly 10 years later. Eighty new towns were observed, resulting in 189 confirmed prairie dog towns in the panhandle. This represents a net loss of only four towns or -2.07% change in prairie dog towns in the Oklahoma panhandle.

In a letter to Jamie Clark, USFWS Director, Mark Lomolino, Oklahoma Biological Survey, cautioned looking at only town numbers. Although the number of towns may not or may decrease, town size (occupied area) and prairie dog numbers may decrease at greater rates. For example, in Cimarron, County the mean town size decreased from 84 acres to 25 acres. Contributing to a lower average is the loss of a town greater than 600 acres.

South Dakota- Presettlement estimates of South Dakota's prairie dog acreage are anecdotal, as are many such wildlife population estimates. In 1923, it was estimated approximately 1,756,720 acres of occupied black-tailed prairie dog habitat existed in South Dakota, following the initiation of control efforts in 1918. Estimates for prairie dogs in the 1960s ranged from 33,000 acres to 60,000 acres in 1968. Hansen (1988) reported statewide acreage for 1968 as 61,000 acres. Tschetter (1988) reported results of a prairie dog survey questionnaire, estimating 184,000 acres in 1987, with more than 75% of this acreage on tribal lands. In 1996, South Dakota Department of Game, Fish and Parks (SDGFP) completed a similar survey questionnaire, resulting in a statewide prairie dog acreage estimate of 264,000 acres (SDGFP 1996), with 58% reported on tribal lands, 43% on private lands, 9% on federal lands, and 4% on state lands. A recent report, based on a interview with a state agency representative, estimates 244,520 acres of occupied habitat in South Dakota, which is 36% of the habitat in the United States (Knowles 1998).

No comprehensive statewide prairie dog acreage survey has been conducted in South Dakota. Recent statewide estimates are based on questionnaires of land management agency representatives, with varying levels of ground-truthing associated with the estimates. However, the Cheyenne River Sioux Tribe and several federal land management agencies, such as Wind Cave and Badlands National Parks and Nebraska National Forest, have implemented prairie dog acreage monitoring programs (USDA-Forest Service 1988).

Texas-Field notes from early explorers, museum specimens, and turn-of-the-century accounts in the literature provide the information upon which the historical range of the black-tailed prairie dog in Texas is based. While these accounts provide useful information about the original distribution and abundance of the species, it does not allow for scientifically accurate estimates of pre-settlement population densities or the total number of acres inhabited. Nonetheless, there has been an overall, dramatic decrease in the total number of prairie dogs and occupied habitat in Texas. This decrease is primarily due to conversion of grasslands to agriculture but disease and poisoning have also contributed to the losses. However, the geographic limits of the species within the State have remained practically unchanged from the earliest recorded accounts.

Bailey (1905) described the range of the prairie dog in Texas as extending from Henrietta, Fort Belknap, Baird, and Mason west to near the Rio Grande River, north through the Panhandle and south to Devil's River, to 10 miles south of Marathon and 25 miles south of Marfa. This equates to approximately the northwest 1/2 of the state and includes all or portions of the High and Rolling Plains, Edwards Plateau, and the Trans Pecos Ecological Regions. Bailey estimated 800,000,000 prairie dogs covering an area of 90,000 square miles (57,600,000 acres). Although these historical numbers are the most reliable estimates for Texas, caution should be exercised in using these numbers because they were based on rough estimations and extrapolations.

Only two modern studies have been conducted to determine the status of black-tailed prairie dogs in Texas, and only one included the entire historical range. In Cheatheam's study (1977), aerial photographs of 108 central and western Texas counties were studied to determine size and distribution of prairie dog towns. Ninety-nine of the 108 counties were within the historical distribution described by Bailey (1905). Cheatheam (1977) found 1,336 colonies covering 90,023 acres in 89 counties. He estimated the average colony size at 67.38 acres.

The second and most recent attempt to determine black-tailed prairie dog status in Texas was made by Lair and Mecham (1991) in an effort to evaluate and identify potential black-footed ferret reintroduction areas. They examined aerial photos (dated from 1978 to 1985) from 29 counties in the panhandle to determine the existence, distribution, and status of prairie dog towns greater than 100 acres. These particular counties were selected because Cheatheam’s work indicated that they had the highest density of prairie dogs. Prairie dog towns in those counties were mapped and town sizes were measured using a compensating polar planimeter. The map work was supplemented by the use of ASCS crop slides for eight counties (a subset of the 29) taken during the spring of 1990. In total, they recorded more than 800 prairie dog towns in the 29 counties and 298 towns in 22 counties were larger than 100 acres, with the largest being 2,200 acres. The total coverage was 67,907 acres, with an average of 228 acres. They noted that many towns of less than 100 acres existed in close proximity to one another and probably acted as a complex, but these were not considered in their total. In addition, several large towns were located by casual ground surveys in 1990, but were not documented in their study because they were not on the older photographs, nor included in the area covered by the crop slides.

Without reliable baseline or current information regarding distribution and status, it is impossible to accurately determine declines in population density or distribution. Although they have been compared to show evidence of declines, use of the results from the Cheatheam (1977) and Lair and Mecham (1991) studies for this purpose do not provide useful data on population trends because the studies do not cover the same number of counties nor do they use the same criteria for assessing population status. Cheatheam's 1977 total of 90,023 acres included all prairie dog towns in 89 counties, whereas Lair and Mecham’s 1991 total of 67,907 acres included towns in only a portion of 29 counties, and towns of less than 100 acres were not considered. Cheatheam's results are an estimated total from the mid 1970s, whereas Lair and Mecham's results estimate a minimum number of acres of prairie dogs known from 1978 to 1990.

Wyoming-The historical range of the black-tailed prairie dog includes approximately the eastern third of the state and was contiguous with the range of the species on the Great Plains. Elevation (approximately 5,500 feet) and vegetation define the western edge of the range. The habitat changes from Great Plains to the Intermountain West. The western range boundary follows a line from the Wyoming-Montana state line along the east slope of the Bighorn Mountain Range, then southeast along the east slope of the Laramie Mountains to the Wyoming-Colorado state line.

The black-tailed prairie dog has undergone severe reduction in occupied range and population in Wyoming since settlement and the advent of farming and ranching. Occupied range has been reduced by over 80% from pre-settlement (Campbell and Clark 1981). Similar to other parts of the historical range, the major reduction in prairie dog populations probably occurred in the early 1900s when poisoning programs began in earnest.

The Wyoming Game and Fish Department (WGFD) conducted prairie dog colony mapping between 1982 and 1987 to identify potential black-footed ferret populations and/or reintroduction sites. Mapping was concentrated in the primary range of the species in Wyoming. Small, scattered colonies were thought to occur in the Bighorn Basin but were not mapped.

In 1987, estimates indicated that within the primary range 73 townships supported between 1,000 and 2,000 acres of prairie dog colonies, and 29 townships supported over 2,000 acres of prairie dog colonies. The data indicated a minimum of 131,000 acres and a maximum of 204,000 acres. In 1998, the Wyoming Department of Agriculture (WDOA) estimated 362,284 acres of occupied black-tailed prairie dog habitat in their Weed and Pest Districts and Conservation Districts (pers. comm. Reichenbach 1999).

Conversion of native rangeland to cropland is occurring at a very negligible rate in eastern Wyoming. Poisoning of black-tailed prairie dogs continues, and estimates indicate that acreage remaining decreases a few percent annually in localized areas. Data have not been collected in such a way that annual or long-term increases or decreases by colony, complex or county could be monitored. The five-year Objective in the WGFD Nongame Bird and Mammal Plan is to maintain black-tailed prairie dog distribution in a minimum of 102 townships, and all counties, within the range and at a level of 167,500 acres.

Canada-Historically, it is estimated that there were 1,500-2,000 acres of black-tailed prairie dog occupied habitat in Canada (Knowles 1998). Currently, the species is found in a small area along the Frenchman River Valley in extreme southern Saskatchewan. Many of these colonies are in Canada's Grasslands National Park. Millson (1976) mapped 15 colonies in this area totaling 1,242 acres (503 hectares) in 1970; and in 1975, 16 colonies were mapped totaling 1,885 acres (763 hectares). Laing (1986) later mapped 14 colonies totaling 1,691 acres (684.5 hectares). Surveys conducted between 1993 and 1996 found 25 colonies totaling 2,318 acres (938 hectares), with 13 colonies totaling 1,353 acres (548 hectares) located within current park holdings (USFWS 1999). Colonies ranged from 3.9 acres (1.57 hectares) to 328 acres (132.9 hectares).

Mexico-Historically, black-tailed prairie dog occupied habitat in Mexico was estimated at 1,384,000 acres (Mearns 1907 and others in Ceballos et al. 1993). However, two studies have documented historic and recent declines. Ceballos et al. (1993) mapped 136,000 acres of occupied habitat in Chihuahua, Mexico, in 1988. Included in this estimate was one colony within the Janos-Nuevo Casas Grandes Complex, which totaled 86,450 acres. List (1997) reported the total amount of occupied habitat as 90,000 acres in 1996. Colony fragmentation had occurred in prairie dog colonies previously surveyed, reducing the size of towns and increasing their isolation. The average town size decreased from 6,320 acres in 1988 to 417 acres in 1996. List indicated that reduction was due to increased agricultural conversion, poisoning, and drought.

MANAGEMENT STATUS

The black-tailed prairie dog's management status varies across its range. During the 1980s and early 1990s, the Service maintained a three tiered list of species (and subspecies) that were considered "candidates" for federal listing as threatened or endangered, pending more information on status, threats, and other factors relevant to listing determinations under the federal Endangered Species Act of 1973, as amended. The Arizona black-tailed prairie dog was added to the C-2 list in 1985, because of its presumed range-wide extirpation from Arizona and reductions in numbers in Texas and New Mexico. The Service discontinued the use of the three categories on the candidate list in 1996 and maintains a list of candidates where listing may be warrant listing, but is precluded by other higher priority listing actions. In addition, the U.S. Forest Service (USFS) and BLM maintain lists that identify the black-tailed prairie dog as a sensitive species.

The current state management or legal status for black-tailed prairie dogs throughout their range is as follows:

Arizona-The black-tailed prairie dog is classified as extirpated on the AGFD's list of *Threatened Native Wildlife in Arizona* (AGFD 1988). The Arizona Game and Fish Commission in July 1988 approved this list, in public session, after comment was solicited and considered from government agencies, professional and academic biologists, and the public. It provides policy guidance to state and federal agencies and the public on AGFD priorities. It does not provide specific legal or regulatory protection for listed species. However, the general provisions of Arizona Revised Statutes, Title 17, protect federally listed species, as well as all native wildlife.

In Arizona, the AGFD classifies all prairie dog species as nongame mammals. In 1999, the hunting season for black-tailed prairie dogs was closed.

Colorado-The black-tailed prairie dog is classified under Colorado Wildlife Commission regulation #300 A.2 as a small game species. Regulation #302.B sets method of take, which includes rifles, handguns, shotguns, handheld bows and crossbows, pellet guns and slingshots, hawking, and toxicants. The season is year-round, with no bag or possession limit (regulation #308). However, for hunt contests, no participant may take more than five prairie dogs during the entire event (regulation #302-1.a.1).

A small game license is required to take prairie dogs, except that landowners, their immediate family members and designees may take prairie dogs causing damage on their lands without a license with the above methods of take. Some toxicants may be used only by licensed applicators regulated by the CDOA or the U.S. Environmental Protection Service but gas cartridges can be applied without a license. The CDOW does not promote prairie dog shooting or poisoning.

Translocation has been used in the recent past, particularly in the rapidly developing Front Range counties, to move prairie dogs from development sites. However, Senate Bill 99-111, which was passed by the Colorado State Legislature in its 1999 session, prohibits the translocation of prairie dogs and other species between counties without the consent of the county’s commissioners.

Kansas-The black-tailed prairie dog is classified as wildlife (KSA 32-701). Therefore a hunting license is required to hunt them (KSA 32-919) with specified legal equipment and taking methods (KAR 115-20-2). The season is open year round with no limits.

In 1901 and 1903, the Kansas legislature passed laws (KSA 80-1201,1203) authorizing townships to conduct prairie dog eradication programs and provide funds for Kansas State Agricultural College to hire a field agent to direct and conduct experiments for the purpose of destroying prairie dogs and gophers (Lantz 1903). In recent years some counties have invoked "Home Rule" to take over authority for prairie dog control from the townships and impose mandatory control requirements on landowners. The landowner is first given the opportunity to control prairie dogs on their land and if they fail to do so it is done by the county at the landowner's expense (Lee and Henderson 1989). A prairie dog control permit (KAR 115-16-2) is required to use any poisonous gas or smoke to control prairie dogs, except toxicants labeled and registered for above ground use. Each permit needs to be approved by the Secretary of the KDWP and the extension specialist in wildlife damage control.

Montana-Prairie dogs are legally categorized as rodents and vertebrate pests (Mont. Code Ann. 7-22-2207), subjecting them to systematic suppression by the Department of Agriculture.

Nebraska-The black-tailed prairie dog is currently considered an unprotected nongame species in Nebraska. This allows them to be taken by any manner, without restrictions, including shooting or control activities. Permits are not required for residents to take prairie dogs; nonresidents must have a small-game hunting permit to take prairie dogs in the state. Most prairie dogs occur on private land in Nebraska and permission of the landowner is required before entering private property. A statute dating back to the early 1900's, requiring extermination of prairie dogs on private and state-owned lands in the state was repealed in 1995.

In 1996, the NGPC adopted a policy on the shooting of prairie dogs. The agency recognized prairie dog shooting as a legitimate recreational activity while also recognizing the importance of prairie dog communities to a variety of interdependent wildlife species. The NGPC does not actively promote prairie dog shooting. With the location of Nebraska on the eastern edge of the prairie dog range and on Interstate 80, the agency receives numerous requests for information on shooting prairie dogs. Providing general maps and other information fulfills these requests. Specific locations of prairie dog colonies are not provided.

New Mexico-Black-tailed prairie dogs receive no specific legal protection from regulations administered by the NMDGF (NMSA 1978 (1988 Repl.)). Statutes under which the New Mexico State Department of Agriculture (NMSA 1978) operates offer no protection to this species. Portions in the latter statutes direct the State of New Mexico to cooperate with the federal government to destroy predatory wild animals and rodent pests in the interest of the protection of crops and livestock and the improvement of range conditions. The Arizona black-tailed prairie dog (i.e., *C.l. arizonensis*) was included on the NMDGF listing of threatened and endangered species from 24 January 1975 until its delisting on 10 February 1978 (Jones and Schmitt 1997). From 10 February 1978 until 9 January 1988, black-tailed prairie dogs in the Tularosa Basin of south central New Mexico were included on the same listing of threatened and endangered species (Jones and Schmitt 1997). Presently, no populations of black-tailed prairie dogs are listed as threatened or endangered under authority of the Wildlife Conservation Act (17-2-37 to 17-2-46 NMSA [1995 Repl]) by the NMDGF.

North Dakota-The black-tailed prairie dog is considered a nongame wildlife species by the North Dakota Game and Fish Department (NDGFD). A resident is not required to purchase a hunting license to shoot prairie dogs but nonresidents are required. North Dakota does not have a bag limit or season for prairie dogs.

Under state law the black-tailed prairie dog is listed as a pest and two pest laws apply to them. The first, passed in 1913, allowed for a bounty to be placed on prairie dogs. The second, passed in 1995, identified prairie dogs as a pest species under the law, which generally applies to noxious weed control. A pest means any invertebrate, animal, pathogen, parasitic plant, or similar organism, which can cause damage to a plant or part thereof or any processed, manufactured, or other product of plants.

The State Department of Agriculture has the statutory authority and responsibilities of enforcing this statute. However, county weed boards will have jurisdiction on all lands within the county and make the on-the-ground decision of whether or not to initiate a suppression/eradication effort based on recommendations from county commissioners.

Oklahoma-The black-tailed prairie dog is classified under Title 800, ODWC Commission Regulation, as a Category II Mammal Species of Special Concern. This classification involves those species in which there is a concern over the long-term survival indicated by technical experts and insufficient documentation to adequately assess the population status/trend in the state.

Although the prairie dog is not designated a game species in Oklahoma, Subchapter 17 of Chapter 25, Title 800 outlines the legal means in which prairie dogs may be controlled in Oklahoma. Prairie dogs may not be killed by any means except rifle, shotguns, handguns, and bows and arrows. Prairie dogs may be controlled with the use of poisons subject to the provisions of Subchapter 17. A permit is required of all landowners and operators in Oklahoma prior to any prairie dog control work involving the use of poisons, including solid chemicals and gases. The permit must be obtained from the ODWC and can be issued for periods up to 90 days. Permit restrictions for the use of poisons in prairie dog control include: 1) permits may not be issued by the ODWC to reduce prairie dogs in any county to fewer than 1000 prairie dogs, and 2) The killing of prairie dogs with poisons shall not be permitted on public lands.

The Director of the ODWC may issue permits for the total or partial control of prairie dogs on the State School Lands. Prior to issuing such permits, the Commissioners of the Land office shall advise the ODWC of the sites to be included in their program. Each site shall be evaluated for the presence of endangered, threatened or otherwise unique or uncommon wildlife species and the potential adverse impact that might be caused by a control program. Permits will be conditioned, as necessary, to assure that the control efforts do not threaten the continued existence of other species of concern that may be found in association with prairie dog towns.

While poisoning and recreational shooting of black-tailed prairie dogs can occur on private land, the ODWC does not promote either activity. Prairie dog eradication is no longer mandatory in Oklahoma. In order to hunt prairie dogs in Oklahoma, one must have a resident or nonresident hunting license or proof of exemption. Because most of the prairie dogs in the state occur on private land, hunters must seek permission from the landowners. The ODWC does not coordinate hunters looking for prairie dog shooting access with landowners. Inquiries about access to prairie dogs for recreational purposes are referred to the local chamber of commerce.

The ODWC does not actively translocate black-tailed prairie dogs, but restorations of prairie dog towns have been conducted on the Wichita Mountains National Wildlife Refuge, Canton Wildlife Management Area, Darlington Game Farms near El Reno, and other locations (Caire et al. 1989). In

1998, the ODWC did assist the Oklahoma Department of Transportation with the relocation of 52 prairie dogs from a highway project right-of-way to ODWC property in north central Oklahoma. These translocated prairie dog towns are closed to prairie dog hunting.

South Dakota-The black-tailed prairie dog currently has state designations under two different authorities in South Dakota. This species is a game species regulated by the SDGFP (South Dakota Codified Law 41-1-1). Since January 1, 1999, the species is further designated as a predator/varmint, a statutory action taken primarily for hunting license purposes. Residents must possess a Game and Fish or Sportsman's License to shoot prairie dogs; nonresidents must possess a Predator, Small Game, Waterfowl, or Big Game License. Aside from license requirements, the black-tailed prairie dog is unregulated by the SDGFP; i.e., no limits exist on times, places, or quantities, aside from closures or other limitations on federal, tribal, or state park lands.

As part of its Systematic Approach to Management planning effort, the SDGFP released a strategic plan for the black-tailed prairie dog in March 1994 (SDGFP 1994). This plan contains objectives and strategies designed to accomplish the following goal in South Dakota:

> "To achieve and maintain populations of prairie dogs that will preserve this unique ecosystem, help buffer predatory losses to livestock and provide increased recreational opportunity consistent with economic, ecological, social, and aesthetic values for the people of South Dakota and its visitors."

The black-tailed prairie dog has been designated as a statewide pest since 1984, an action taken by the South Dakota State Weed and Pest Control Commission (SDWPCC). South Dakota Codified Law (SDCL) Chapter 38-22 provides for the control of noxious weeds and declared pests. Control operations may be directed at those populations considered threats to neighboring property. The costs of such control must be borne by the landowner. The SDWPCC supports control efforts that are legal, biologically sound, and economically feasible (South Dakota Department of Agriculture, no date).

This species is also statutorily addressed in South Dakota's threatened and endangered species law, which became effective in 1978. SDCL Chapter 34A-8-7 directs the secretaries of South Dakota Department of Agriculture and SDGFP to "establish and conduct control programs at state expense on private lands that are encroached upon by prairie dogs from contiguous public lands."

Texas-Several agencies have statutory responsibilities for prairie dogs in Texas. The Texas Parks & Wildlife Department (TPWD) designates prairie dogs as a nongame species (TPW Code 67.001), and is prohibited from listing them as an endangered species (TPW Code 68.020). A hunting license is required to hunt prairie dogs (TPW Code 42.002) and there is no season or bag limit. Because most prairie dogs in the state occur on private land, hunters must seek permission from the landowners. There is no program within TPWD that coordinates hunters looking for access to private lands for shooting. TPWD has the authority to establish regulations on the taking, possession, propagation, transportation, importation, exportation, and sale of prairie dogs (TPW Code 67.004), and in January 1999, a new regulation for the collection and sale of nongame wildlife was established. This new regulation requires a nongame collection or dealer's permit to possess more than 10 prairie dogs or to sell any number of prairie dogs.

Under Chapter 825 of the 1989 Texas Health and Safety Code, (Predatory Animals and Animal Pests), authority is given for the state to cooperate with appropriate federal officers and agencies in controlling predators and rodents to protect livestock, food and feed supplies, crops, and ranges. It further authorizes the Commissioner's Court of a county to purchase poisons to destroy animal pests and authorizes landowners, lessees, and tenants to apply poisons on their lands. Texas Department of Agriculture (TDA) is given responsibility to provide commissioner's courts who request it, information on controlling predators and rodents as defined under Section 825.021. To be interpreted consistently with TDA's mandates under Chapter 76 of the Texas Agricultural Code and the Federal Insecticide, Fungicide and Rodenticide Act (FIFRA), this effectively means that TDA can provide information in response to a request to identify registered products labeled for controlling prairie dogs. TDA currently registers a number of restricted use rodenticides labeled for control of prairie dogs. These can be legally applied only by a licensed applicator.

Wyoming-The black-tailed prairie dog is a nongame wildlife species in Wyoming and is listed by the WGFD in the Nongame Bird and Mammal Plan (Oakleaf et al. 1996) as a Species of Special Concern. The black-tailed prairie dog is also covered by Chapter 52 (Nongame Wildlife) of the Wyoming Game and Fish Commission Regulations. Under Section 6 of the Regulation the species may be taken during the calendar year without securing a permit.

The WDOA classifies the black-tailed prairie dog as a pest under Statute W.S. 11-5-101 through 11-5-119 (Weed and Pest Control Act of 1973), allowing uncontrolled take.

With the exception of approximately 20,000 acres on Thunder Basin National Grassland and small or parts of colonies, which occur on BLM lands, most prairie dogs occur on private land.

Recreational shooting of black-tailed prairie dogs takes place throughout the range in Wyoming. No license is required and there is no restriction on take. Any weapon may be used. The WGFD does not provide recreational shooters locations of black-tailed prairie dog colonies and does not encourage recreational shooting. Thunder Basin National Grassland uses recreational shooting, along with poisoning, to prevent expansion of prairie dogs beyond designated protection and management areas on the Grasslands. The WGFD has not relocated black-tailed prairie dogs.

Canada-the Committee on Endangered Species and Wildlife lists the species as vulnerable.

Mexico-the black-tailed prairie dog is listed as threatened. The other species of prairie dog found in Mexico, the Mexican prairie dog (*C. mexicanus*) is listed as endangered. It is in the same subgenus as the black-tailed prairie dog.

RISK ASSESSMENT

For the 90-day finding, the Service assessed real and/or potential problems identified in the petition that face the black-tailed prairie dog, based on one or more of the following five factors, as required by Section 4(a)(1) of the Act. In their 90-day finding, the Service concluded that the following factors act both alone, and in concert, to affect the status of the black-tailed prairie dog and a complete status review was needed for the species. The cooperators to this agreement acknowledge that more aggressive management for black-tailed prairie dogs is needed at this time to ensure the viability of the species rangewide and this management can be accomplished at a coordinated state level. The factors identified by the Service in their 90-day finding are presented in the first part of this risk assessment. The wording is almost verbatim as to how it appeared in the Federal Register. The cooperator's evaluation and corrective solutions for these factors are the second part. In some cases, parts of the solution may already be implemented. The risk assessment is as follows:

1. Present or threatened destruction, modification, or curtailment of its habitat or range.

The petitioners asserted that conversion of prairie habitat to farmland was one of the primary causes of the decline in occupied habitat of the black-tailed prairie dog. Between 1880 and 1899, 104 million ac (42 million ha) of the western plains surface area were converted to crop productions (Laycock 1987). Native grasslands have been reduced by approximately 60 percent (Burke in prep.) resulting in significant destruction of black-tailed prairie dog habitat. Some agricultural conversion of native grasslands continues today, and could accelerate with the increase of dry land cropping and use of genetically engineered drought resistant crop strains. Hexem and Krupa (1987) identified 57,700,000 ac (23,400,000 ha) of unplowed land in the western Great Plains with potential for cropland conversion. Such conversion could significantly reduce the remaining native prairie and black-tailed prairie dog habitat.

Urbanization also presents a significant loss of black-tailed prairie dog habitat in local areas near metropolitan areas throughout the Great Plains such as Helena, Montana (Knowles 1995); and the Front Range of Colorado near Denver (USFWS 1999). Habitat loss also occurs through degradation of burrows and vegetation changes in areas where black-tailed prairie dogs have been removed. Once underground burrows collapse or there is an increase in woody or taller vegetation, the species is less likely to reestablish itself in the area. At the Rocky Mountain Arsenal National Wildlife Refuge in Colorado, reintroduced black-tailed prairie dogs quickly reestablished themselves where intact burrows constructed by previous prairie dogs (extirpated by sylvatic plague) had not deteriorated (Seery, USFWS, pers. comm. 1998). Where burrows had deteriorated, prairie dogs established themselves slowly and with little success.

Weltzin et al. (1997) determined historically, black-tailed prairie dogs, and the herbivores and granivores associated with their colonies probably maintained grassland and savanna by preventing woody species from establishing or attaining dominance. List (1997) reported that poisoning of black-tailed prairie dogs in Mexico resulted in the invasion of mesquite shrubs that rendered the landscape unsuitable for reoccupation by the species; moreover, fire suppression would likely maintain this situation. Davis (1974) also noted that removal of the species from some sites in Texas resulted in the invasion of brush. Thus, when degradation of burrows or vegetation changes occur, the amount of habitat suitable for recolonization may be reduced. Current levels of conversion of rangeland to farmland or urban development may not be as important to the species' numbers and viability as are direct losses caused by poisoning or disease. These direct losses of individuals or local populations may result in habitat loss for the species through the deterioration of burrows and the alteration of vegetative communities.

Evaluation: It is difficult to determine the degree of destruction, modification, or curtailment of the species habitat or range. Although there are estimates of occupied black-tailed prairie dog habitat from the turn of the century, these estimates are most likely exaggerated and extrapolated from partial data sets. While it is true occupied prairie dog habitat has been reduced and fragmented by conversion of grasslands to agriculture, urbanization, invasion of woody plants, and poisoning black-tailed prairie dogs are still relatively abundant and widespread with opportunities for management and significant recovery (Knowles 1998). For example, Hoogland (1995) states that prairie dogs typically have unused suitable habitat at their disposal. Suitable unoccupied habitat has been identified in New Mexico and Montana and translocation efforts have been initiated with some degree of success (Matchett 1997, Truett and Savage 1998). Other unoccupied habitat is still present across the range of the species. In 1995, the AGFD identified 10,989 acres of habitat on Fort Huachuca exhibiting characteristics that would be considered moderate or excellent for prairie dogs (Van Pelt and Belitsky 1995). In 1992, based on the Natural Resources Conservation Service's National Resources Inventory (NRI), a statistically based sample of land use and natural resource conditions and trends on nonfederal lands in the United States showed a majority of the nonfederal land within the black-tailed prairie dog range was in rangeland. The lands within the High Plains as a whole have less than a five-percent high potential for conversion to cropland in the next 10-15 years.

Solution: Current conservation actions are focused on identifying and conserving unoccupied habitat, and at a minimum, maintaining the current level of occupied habitat on federal and tribal lands until the population viability analysis (PVA) funded by the USFWS can be completed. Poisoning restrictions and other land management actions on USFS and BLM lands and current management practices of Native American tribes conserve significant core areas of black-tailed prairie dogs. Once the PVA is completed, land protection efforts under federal, state, and tribal land management programs working through the Conservation Agreement can then focus conservation efforts on additional habitat important to black-tailed prairie dog conservation. Existing federal laws and policies are presently in place and are adequate to provide for such actions, especially in regard to lands under management jurisdiction of the BLM, National Park Service (NPS), USFWS, and USFS. Some of the Native American nations have already developed plans to manage for sustainable occupied prairie dog habitat on their lands. On private lands, the potential for habitat conservation measures is limited by the extent to which the landowners wish to cooperate in such programs. However, in some states such as New Mexico, private landowners are already reintroducing black-tailed prairie dogs. Before such proposals are made in other areas, better information is needed on what are suitable prairie dog habitat, and the extent to which dispersal or recolonization is likely. Incentive programs need to be developed to increase private landowner interest in prairie dog conservation.

2. <u>Overutilization for commercial, recreational, scientific, or educational purposes</u>.

One activity impacting black-tailed prairie dog populations, in some local areas, is unregulated recreational (sport or varmint) shooting. Shooting has increased appreciably in popularity in recent years. An example of this is the Buffalo Gap National Grassland in South Dakota where the number of annual shooter days has increased from a few hundred in the mid-1990's to an estimated 6,500 in 1998 (Perry, USFS, pers. comm., 1998). High-powered rifles with high-quality scopes enable the modern varmint shooter to be consistently accurate at distances of 400 yards or greater, and an individual shooter may shoot a considerable number of animals each day (Kayser 1998). Only three states do not require a hunting license for taking prairie dogs. Prairie dog density may decrease with increased shooting pressure and prairie dogs may spend more time on alert and less time foraging (Vosberg 1996). Shooting also may contribute to population reduction and fragmentation, reduce colony productivity and health, contribute to the loss of non-target species, and preclude or delay recovery of colonies reduced by other factors such as sylvatic plague. Recreational shooting may significantly impact colonies in local areas where shooting is most intense or colony numbers are already reduced from other losses.

Evaluation: It is recognized that shooting did not contribute as much as habitat conversion and poisoning to historical prairie dog declines. However, it has been demonstrated that shooting can reduce or suppress local populations of prairie dogs, which could make them more susceptible to catastrophic events such as a disease epizootic. Fox and Knowles (1995) concluded it would require approximately one recreational day for every 15 acres of prairie dogs to significantly influence prairie dog populations. However, an example of a significant local impact exceeding the one recreational day per 15 acres threshold is the Conata Basin area of the Buffalo Gap National Grassland, one of the seven large black-tailed prairie dog complexes found in North America. In 1998, 6,500 shooter days occurred on 9,000 acres, which equals one shooter day for every 1.38 acres (Perry, USFS, pers. comm., 1998). Mulhern and Knowles (1995) stated that this level of shooting pressure is unlikely over the hundreds of thousands of acres of currently occupied black-tailed prairie dog range, which would not influence populations rangewide but could significantly affect local populations. On some tribal lands, prairie dog shooting is managed to generate revenue for the tribes, which creates an incentive to manage the species. Typically, it is the responsibility of the state wildlife agency to set bag limits and seasons for shooting prairie dogs. Some of the states have regulations in place for prairie dogs but protection is limited. For example, Arizona has closed the season on black-tailed prairie dogs. Colorado has a bag limit of five prairie dogs during shooting contests, and Texas limits the number of live prairie dogs one can possess. In some cases, regulations for the state agriculture and wildlife agencies conflict in regulating the level of take of prairie dogs which makes it difficult to determine and promote the viability of the species in a given area.

Solution: Current conservation actions are focused on evaluating current regulatory measures and determining if modifications are necessary to ensure the viability of the species. For example, modifications could include more restricted hunting seasons, areas closed or with limits on prairie dog shooting, bag limits, or more defined criteria for control actions. In addition, in states where prairie dogs can be collected live (vacuuming or flooding) and possessed for commercial or scientific use, impacts to the population will be monitored. If it is determined that these impacts are affecting the viability of the species, regulations will be modified to address these impacts.

3. Disease or predation.

Sylvatic plague is a disease caused by the bacterium, *Yersinia pestis*, which fleas harbor and transmit to rodents and other species (Cully 1989). The term ``sylvatic'' refers to the occurrence of the disease in the wild (Berkow 1982). Barnes (1993) recorded sylvatic plague in 76 species of six mammalian orders, although it is primarily a rodent disease. Rodent species vary in their susceptibility to plague, with some species acting as hosts or carriers of the disease or infected fleas and showing no symptoms (e.g., kangaroo rats, *Dipodomys* spp., and deer mice, *Peromyscus maniculatus*). Conversely, prairie dogs show nearly 100 percent mortality when exposed to sylvatic plague (Barnes 1993, Cully 1993). Scientists discovered the plague among wild rodents near San Francisco in 1908 and it has spread throughout much of the Great Plains over the past century (Eskey and Haas 1940, Miles et al. 1952 in Cully 1989, Ecke and Johnson 1952). Black-tailed prairie dogs show neither effective antibodies nor immunity to the disease. Generally for all prairie dog species, death occurs quickly for individuals that are exposed to plague; noticeable symptoms usually do not develop (Cully 1993). Data obtained from the Rocky Mountain Arsenal National Wildlife Refuge show that plague has the potential to severely depress black-tailed prairie dog populations and cause local extirpations (Seery and Matiatos, in press; USFWS 1998). Scientists have also observed long-term plague-related declines in white-tailed prairie dogs near Meeteetse, Wyoming (USFWS 1999).

Many mammals, snakes, and raptors prey on prairie dogs (Hoogland 1995) and the species has evolved resilience to natural levels of predation. Scientists do not generally see predation as a threat to the species but in unusual circumstances intense levels of predation may be problematic to individual small colonies, particularly if they are already reduced by other causes.

Evaluation: While plague occurs throughout the western United States, its prevalence and effect on prairie dog populations are greatest in Arizona, Utah, Colorado New Mexico, Montana, Wyoming, and Texas, but is less severe in the

Dakotas, Nebraska, Oklahoma, and other areas of the black-tailed prairie dog range. Plague epizootics affect localized populations of prairie dogs but because some areas in the United States are plague–free, or epizootics are sporadic in nature, black-tailed prairie dogs do not appear to be in any imminent threat of extinction due to plague. Knowles and Knowles (1994) suggested that prairie dogs have survived introduction of the plague simply due to their highly dispersed populations. Although further reductions in size and number of populations could make prairie dogs more susceptible to local and regional extirpation, progress of the disease has probably been slowed by the increasing isolation of small colonies as a result of past control efforts. The WGFD reported in their nongame annual report that the white-tailed prairie dog population in Shirley Basin has fluctuated annually in the presence of plague, but has not precipitously declined as happened at the Meeteetse Complex, and individual colonies have shown recovery.

Solutions: At this time, in association with black-footed ferret recovery, conservation measures are focused on studying how plague affects prairie dog populations, monitoring its presence in an area, and developing control measures or barriers that include nonlethal methods to limit its progression in a prairie dog complex.

4. Inadequacy of existing regulatory mechanisms.

All states within the historic range of the black-tailed prairie dog classify the species as a pest for agricultural purposes and either permit or require their eradication (Mulhern and Knowles 1995). Fish and wildlife agencies in many states classify black-tailed prairie dogs by categories such as unclassified game that permit licensed or unlicensed shooting with no limitations on take or season. Knowles (1995) reviewed federal regulatory management policies as they relate to the black-tailed prairie dog. Significant black-tailed prairie dog occupied habitat is found on tribal lands and public lands managed by the BLM, USFWS, USFS, and the NPS. The BLM manages prairie dogs to meet multiple-use resource objectives (Knowles 1995). Various National Forest Resource Management Plans address black-tailed prairie dog habitat on USFS-administered land; these plans reflect USFS policy, not regulation. Two tribes have voluntary prairie dog management plans in place (Knowles 1995). In some areas where black-footed ferrets are being reintroduced, programs are in place to manage prairie dog populations to preserve black-footed ferret habitat.

Evaluation: Across its range, the black-tailed prairie dog, has various classifications ranging from agricultural pest to nongame mammal. In four states, Colorado, Kansas, North and South Dakota, prairie dogs are classified as a legal agricultural pest with some level of either state or local mandatory controls in effect. Prairie dogs in Wyoming are classified as agricultural pests but detriment to other landowners has to be proven before control can be mandated, and eradication is not necessary. In Montana, New Mexico, Oklahoma, and Texas control is not mandatory, but assistance may be provided to landowners requesting prairie dog control. However, Arizona, Colorado, and Texas have regulations on hunting seasons, bag limits under certain conditions, or possession limits for commercial use of black-tailed prairie dogs, respectively. While classifications result in different management actions for the species, they are imbedded in state laws and state hunting regulations. In some cases, this may require legislative change, which can prove to be challenging when some state legislatures only meet biannually to address new or amendments to existing laws.

Solutions: At this point in time, states are reviewing and evaluating current laws and regulations to determine which regulations have precedence and their affect on black-tailed prairie dogs. States will implement actions for state laws and regulations that will contribute to the continued viability of the species.

5. Other natural or manmade factors affecting its continued existence.

Control (Poisoning)

Hanson (1993) cited poisoning as a major factor in the reduction of prairie dog populations. An extensive poisoning effort has occurred over most of the species' range (Bell 1921, Cain et al. 1971, Anderson et al. 1986, Roemer and Forrest 1996, and Forrest and Proctor in prep.). Organized prairie dog control gained momentum from 1916 to 1920, when property owners and federal agencies poisoned prairie dogs on millions of acres of western rangeland (Bell 1921). From 1937-1968, 30,447,355 ac (12,321,875 ha) of occupied prairie dog habitat were controlled (Cain et al. 1971). After the 1970's some toxicants previously used for prairie dog control were banned and although prairie dog control continued, it occurred at a reduced rate.

Federal agencies and private individuals are involved to varying degrees in active control of prairie dog colonies. The Environmental Protection Agency regulates use of prairie dog poisons. The APHIS-WS provides technical assistance and distributes prairie dog poison to state and federal agencies, tribes, and private landowners. Based on information obtained from the APHIS Freedom of Information Act web page (foia.aphis.usda.gov), the agency distributed or applied enough poison to control 95,076 acres of black-tailed prairie dog habitat from 1991-1996. Although this number could have included some acreage that was treated more than once, this number indicates that over a 5-year period, AHPIS-WS alone has conducted prairie dog control on 14 percent of the estimated remaining black-tailed prairie dog habitat.

Control programs have significantly reduced black-tailed prairie dog populations. These programs essentially remove all animals from the area treated and directly contribute to habitat fragmentation and vegetation changes that limit future recolonization by the black-tailed prairie dog. In particular, federal control programs may play a significant role in the continued decline of black-tailed prairie dog populations.

Habitat Fragmentation

The grassland biome in North America has arguably suffered the most extensive fragmentation and transformation of any biome on the continent (Groombridge 1992). More fragmented, more isolated, and less connected populations usually have higher extinction rates (MacArther and Wilson 1967, Wilcox and Murphy 1985, Clark 1989). Miller et al. (1996) described existing prairie dog populations as small, disjunct, and geographically isolated. They further describe the discontinuous nature of remaining populations as widely separated islands where habitat fragmentation has increased the likelihood of individual colony extinction due to genetic inbreeding and random demographic events. Lost genetic diversity is inherently detrimental to most species. Black-tailed prairie dog dispersal movements that previously offset these adverse effects likely are limited by short migration distances, as reported by Hoogland (1995) and Knowles (1985), and longer distances between remaining colonies.

Evaluation: Historically, it was estimated that black-tailed prairie dogs did not inhabit all of the available habitat, but only inhabited 3-20% of it (Knowles 1992). There is anecdotal evidence that black-tailed prairie dog numbers decreased following the extermination of the bison in the mid to late 1800s (Meade 1898 as in Knowles 1995), and an increase in numbers after the advent of homesteading (Merriam 1901 as in Knowles 1992). Fragmentation of the black-tailed prairie dog range began in the early part of the 1900s as a result of poisoning. While fragmentation from poisoning still occurs throughout the range of the black-tailed prairie dog, it does not occur in the same degree or intensity as past efforts. For example, there has been no organized control on BLM administered lands for over two decades and currently the USFS has banned poisoning on National Grasslands until the status review has been completed. On Native American lands, prairie dogs were controlled extensively up until the early 1990s. In 1992, the USFWS issued a jeopardy opinion for black-footed ferrets in regards to prairie dog control on the Cheyenne River and Rosebud Indian reservations in South Dakota. Since issuing that opinion, no funding for prairie dog control has been approved by Congress for distribution by the Bureau of Indian Affairs. Fragmentation may actually be beneficial to prairie dogs. As mentioned in the evaluation of Factor 3, *Disease and predation,* Knowles and Knowles (1994) recognized that fragmented and isolated prairie dog populations may actually be protected from a plague epizootic and may be a source of animals for future recolonization efforts. Management options exist to reduce the effect of control on the species (i.e. during control measures entire towns do not need to be eliminated). Depending on the type of rodenticide used to control prairie dogs and its efficiency at reducing numbers, population recovery can return to the same level as it was prior to treatment in as little as 10 months (Apa et al. 1990). Portions of prairie dog towns could be controlled or translocated to other areas where less conflict exists. Truett and Savage (1998) have successfully reintroduced black-tailed prairie dogs into portions of New Mexico where they were once extirpated for at least 30 years. Translocation efforts would occur in areas that would increase connectivity of populations, and thus contribute to the species viability. However, with great reductions in numbers, fragmentation, and translocation genetic variation can be lost using this management option.

Solutions: Control measures are being reviewed and other alternatives of control are being evaluated. For example, some Native American tribes have plans in place using alternative means such as pasture rotation to control prairie dogs. States with restrictions on translocation of wildlife species will review existing regulations, and if necessary, implement changes that will allow translocation of populations onto public lands or willing private landowners.

CONCLUSION

Historically, black-tailed prairie dogs occurred across a majority of the short and mid-grass habitats of North America, and in adjacent areas of Mexico and Canada. While the occupied range of the species has been greatly reduced, the species still occurs in great numbers and occupies hundreds of thousands of acres. As populations become localized and reduced in density from shooting, poisoning, and habitat conversion they can become more susceptible to local extirpation when a catastrophic event, such as a plague epizootic, occurs. Plague is an unknown factor in the equation for conserving the species. While work is currently being conducted on the ecology of the disease, humans have had trouble controlling epizootics over large areas. Although past control activities fragmented prairie dog towns, which may have assisted with the restriction of a plague epizootic, effects of the disease can be catastrophic enough in an area to severely impact recovery of the species for years.

Although a variety of human factors are acting collectively in suppressing black-tailed prairie dog numbers throughout their range, these factors usually affect populations at a local level and not rangewide. Human factors affecting the viability of the black-tailed prairie dog can be modified, as has been done in the past with the elimination of certain poisons, to promote the continued persistence of the species in the United States. By implementing management actions which might include eliminating mandatory control, regulating seasons or possession limits, maintaining and conserving habitat, and establishing core populations on public lands to provide animals for dispersal to uninhabited areas or individuals for recolonization, the cooperators of this conservation agreement will significantly contribute toward the conservation of the species. In term of actions, this translates into providing sufficient habitat to maintain self-sustaining populations that are well distributed across the Great Plains grasslands. Abundance of available food and suitable soil for burrow construction may be more important than a particular grass type. Above all, a reasonable balance between preservation and control needs to be identified.

The mosaic of habitats in which black-tailed prairie dogs have occurred in the United States is mirrored by a complex pattern of land ownership. A patchwork of federal, state, tribal, and private lands overlays the habitat mosaic. A conservation program for prairie dogs must consider both mosaics and provide opportunities and incentives for involvement by all interested and affected parties. It must include the approaches noted by Weber and Rabinowitz (1996) as hallmarks of successful conservation projects: field research (to provide a sound scientific basis for decisions); consideration of relevant cultural, economic, and political factors; design and implementation of a comprehensive approach to conservation (including public education); and monitoring and feedback. Unlike other protective measures, which often alienate segments of the population or stakeholders, this conservation agreement approach provides a forum for local involvement, participation, and acceptance for an effort directed at conserving the black-tailed prairie dog and its ecosystem.

CONSERVATION STRATEGY

INTRODUCTION

The black-tailed prairie dog is a North American species that plays an important role in maintenance of the Great Plains grassland ecosystem and the associated fauna. For a variety of reasons, this species has declined dramatically in distribution and abundance. Factors also contributing to this decline include the absence of management policies, necessary staff, and financial commitments to assure prairie dogs and associated species will persist. Currently, many states and some federal agencies in the range of the black-tailed prairie dogs have administrative and regulatory structures that either ignore their declining trend or contribute to the decline. The objective of the signatories to this Agreement is to promote viable prairie dog populations and the grassland ecosystems associated with them. The purpose of this document is to provide a structure that provides management and administrative reforms that need to be made and implemented to protect and enhance the persistence of prairie dogs and their associated ecosystems and the continuation of local (state) or tribal authority to manage these species.

The management framework proposed below includes a core of essential elements needed to achieve appropriate levels of security for black-tailed prairie dogs and their associated ecosystems in each state. In addition to these core elements, other elements are listed that may be needed in individual state plans to effectively conserve prairie dogs. This framework also recognizes that circumstances exist where population control is appropriate and seeks to identify these circumstances to provide appropriate recommendations for such control.

Absent any changes in current management of all prairie dogs, these species as well as other associated grassland species are, according to recent status reports, exhibiting trends that may merit listing under the Endangered Species Act. States and tribes desire to maintain their management flexibility and decision-space through concerted efforts to conserve prairie dogs and other grassland species. State and tribal management flexibility will be reduced if the black-tailed prairie dog is listed under the Endangered Species Act.

This Conservation Strategy describes the goal, objectives, strategies, and activities that will be implemented to further conserve black-tailed prairie dogs in the United States. It reflects the metapopulation concept for species persistence and an ecosystem management approach for habitat conservation. Planning and management proposals and actions will be coordinated among the states, the Service, tribes, other government cooperators, and private entities.

A feature of this Strategy is an interstate/intergovernmental Black-tailed Prairie Dog Conservation Team (BTPDCT). The purpose of the BTPDCT is to assist with and coordinate the activities of the states and other team members. This coordination will include: 1) Developing protocols for compiling information from the states in categories that can be aggregated to depict conservation measures occurring throughout the species' range, 2) Encouraging review and dialogue regarding means for balancing legitimate needs for both protection and control, and; 3) identifying research needs and helping to obtain funds to implement projects. BTPDCT members may be assigned to various technical committees as information or other needs (e.g. review of materials) arise. Each state wildlife agency BTPDCT member is responsible for coordinating the Conservation Strategy activities within its respective state. Any member of the public may attend BTPDCT meetings, provide comments on documents and proposed actions, and attend state work group meetings, when they are established by the state.

Species restoration and habitat conservation are linked to key federal, state, tribal, and private land ownership patterns. This Strategy identifies both short and long-term objectives, and sets various time frames to complete activities. The state wildlife agencies will implement this Strategy and will aggressively seek new funds to enhance agreement implementation.

Effective conservation of the black-tailed prairie dog and its habitat under this Strategy will necessarily depend on cooperation of federal, state, tribal, and private landowners and stewards. Thus, all cooperators must, from the beginning, be aware of the importance of full involvement of private landowners to the extent they wish to be involved, and further recognize the importance of compatible rural livelihoods and activities, such as ranching and outdoor recreation (including hunting and wildlife watching), and voluntary participation by private landowners in habitat identification, enhancement, and conservation, as key to the Conservation Strategy.

GOAL

The goal of the Conservation Agreement is to conserve viable black-tailed prairie dog populations in the United States, while recognizing the legitimacy of control as well as preservation of the species, and to encourage parallel conservation actions in Mexico and Canada, by (a) gathering, sharing, and disseminating information on status, biology, habitat use, and management needs; (b) identifying and maintaining habitat suitable for population maintenance, expansion, translocation, and possible reintroduction in the United States; (c) allowing for innovative, active, and adaptive management; (d) creating strong private-public partnerships; (e) implementing any state regulations needed for population management, conservation, and control; and (f) identify and secure funding sources to mitigate landowner losses and promote prairie dog conservation.

The actions under this Agreement will: (a) promote conservation of the black-tailed prairie dog and its habitat; (b) reduce risk of overutilization of the black-tailed prairie dog for commercial, recreational, scientific, or educational purposes; (c) focus use of existing regulatory mechanisms to maintain species viability; (d) reduce risk of any other factors affecting continued existence of the black-tailed prairie dog in the United States; and (e) increase landowner participation in prairie dog conservation efforts by minimizing impacts from lost management options.

Although this Conservation Agreement focuses on black-tailed prairie dog conservation, participants recognize the risks identified for black-tailed prairie dogs also affect other species of prairie dogs and associated grassland species. Initially, participants agree to direct their conservation actions at black-tailed prairie dogs, but when applicable, will work toward the conservation of all prairie dog species and grassland associates.

CONSERVATION OBJECTIVES AND STRATEGIES

The Black-tailed Prairie Dog Conservation Agreement has nine objectives, with a varying number of activities under each objective, for conserving black-tailed prairie dogs across their range. These objectives allow cooperators to manage black-tailed prairie dog populations in a manner that preserves the long-term viability of the species while also maintaining management flexibility. The nine objectives are as follows:

1. Implement the Conservation Strategy

2. Establish a Black-tailed Prairie Dog Conservation Team and state working groups, which will develop, coordinate, and implement individual state management plans for black-tailed prairie dogs.

3. Determine and monitor species distribution and status.

4. Cooperate with Mexico and Canada.

5. Identify, maintain, and promote existing and additional suitable prairie dog habitats, which includes identifying landowner incentives, stewardship agreements, and manageable population levels.

6. Educate the public.

7. Identify, prioritize, and implement research needs.

8. Establish regulatory protection.

9. Evaluate progress and accomplishments.

CONSERVATION ACTIVITIES

1. Implementation of the Conservation Strategy.

    A. To initiate conservation efforts in a timely fashion, this Conservation Agreement will be signed, at a minimum, by all state wildlife agencies within the historic range of the black-tailed prairie dog by **October 29, 1999**. This does not preclude any other state, federal, tribal, or local entity that wishes to cooperate in this endeavor from signing. Those wishing to sign the Conservation Agreement need to notify, in writing, Bill Van Pelt of their interest. Having a minimum of all state wildlife agencies signing identifies an entity to coordinate on-the-ground conservation activities. Other elements of this Strategy will be developed and implemented through individual state management plans and through the cooperation from federal, state, tribal, and other government cooperators, and through partnerships with private landowners and organizations.

B. It is fundamental that the needs of the black-tailed prairie dog be met in the context of a wide spectrum of other wildlife needs and a variety of land uses on federal, state, tribal, and private lands. Thus, it follows that this Strategy be implemented in complete recognition of those factors, and through close coordination with other current or future planning and management efforts. These would include federal, state, and tribal management efforts, as well as private cooperative endeavors in ecosystem, wildlife, and land management. Any proposed changes to management plans or other land uses will be done in consultation, cooperation, and coordination with the lessees, permittees, other involved landowners, and any state or states having lands within the area covered by the proposal, per Section 8 of the Public Rangelands Improvement Act (PRIA) (Public Law 95-514/714/1978, U.S.C. Title 43 §1901).

C. Although this Strategy applies to the full historical range of the black-tailed prairie dog in the United States, implementation of elements will be focused at a state level. This restricted geographic approach will allow available resources to be focused in an area.

D. Participation in this Conservation Agreement is strictly voluntary. Parties are not legally bound to take actions that are prohibited by current laws and regulations. No party is committed to expend funds not otherwise available for the purposes set forth in this Agreement. In addition, parties of this agreement recognize the rights and legal authorities of all private, state, federal, and tribal entities for managing lands under their ownership or jurisdiction.

2. Establishment of a Black-tailed Prairie Dog Conservation Team (BTPDCT) and state working groups.

A. The BTPDCT will be comprised of one representative from each signatory to the Conservation Agreement. This is necessary to ensure that members have the authority to carry out the actions to which they voluntarily agree.

(1) The state wildlife agencies will be known as the lead in developing and implementing this Strategy. Each state is to ensure that individual state management plans support conservation measures identified in the Conservation Agreement. States will be required to assemble a state work group of interested entities and individuals to establish state prairie dog management plans. By **October 30, 1999** each state wildlife agency will identify an individual to coordinate prairie dog conservation measures.

(2) State work groups will be known as cooperators in developing and implementing this Strategy. They will be comprised of a balanced representation of state and federal agencies and programs, local and tribal governments, private landowners, and interested organizations. Work group meeting will be open to the public. Work groups will determine their decision making process within their work group charter. Each state is to hold its first working group meeting by **October 15, 1999**.

(3) Interested private citizens and organizations, state and federal agencies and programs, local and tribal governments will be encouraged to cooperate with the BTPDCT by attending its meetings and by participating in voluntary, action-specific agreements to promote black-tailed prairie dog conservation and education activities.

The BTPDCT will coordinate and assist in directing the activities outlined in this Strategy. It will review information provided by interested and affected parties, outline management guidelines, research, and education needs, ensure state prairie dog management plans contribute to the conservation of the species, and identify known and potential funding sources for carrying out prairie dog conservation work.

The BTPDCT will meet quarterly the first year either by conference call or in person. After the first year, cooperators will determine the necessary meeting schedule. BTPDCT meetings will be open to the public, with agendas available to the public and state working groups at least 30 calendar-days in advance, via a notice sent to each state wildlife agency where a state mailing list will be maintained. Arizona will host the first BTPDCT meeting in **December 1999**.

BTPDCT meetings will be hosted by each state within the range of the black-tailed prairie dog on a rotational basis. Each state will be responsible for setting up the meeting and ensuring information is distributed in a manner to allow for cooperators to process travel requests. The meeting should be planned in cooperation with the Swift Fox Conservation Team or another Great Plains species conservation team.

(4) At the first BTPDCT meeting, one of the state wildlife agency representatives will be chosen by the other BTPDCT members to chair the team. This will ensure appropriate administrative support for BTPDCT meetings. The chair's term of office will be one year, without limit on the number of terms served. Subsequent chairs will be BTPDCT members selected by the team. Chairpersons will assemble the agenda for BTPDCT meetings and coordinate completion of the year-end evaluation report.

B. Each State will establish a work group, to provide for direct public involvement in addressing specific black-tailed prairie dog conservation issues and reporting recommendations back to the BTPDCT.

(1) Participation in a state work group is strictly voluntary. By **October 29, 1999**, a list of participants from the first state work group meeting, an outline of a proposed state management plan as discussed at their meeting or a completed plan will be submitted to Bill Van Pelt. In addition, work groups need to provide any information regarding on-the-ground activities initiated to conserve the black-tailed prairie dog. This information will be provided to the USFWS for their consideration during their status review.

(2) Work group participation may be at the organizational, governmental, or tribal level. Participation by representatives should be maintained as much as possible to ensure group continuity.

(3) Work group participants will be informed of all meetings at least 30 calendar-days in advance by notice sent to them from the mailing list being maintained by the state. If possible, agendas for each meeting should be provided with the notification.

Work groups are to have an agreed upon state prairie dog management plan in place and initiated by **October 1, 2001**. Work groups should adopt a philosophy and formally recognize prairie dogs and the habitat their colonies provide as valuable, important, and desired components of the landscape, while also recognizing the economic and political realities that control of the species may be necessary in some instances. State plans should identify: 1) Funding, 2) Personnel, and; 3) Time frames for implementing elements of their state plans. Conservation strategies should be coordinated within the state to encompass other management efforts including tribal and federal land management agencies and private landowners. State plans will be flexible enough to allow for modifications, as new information becomes available. In addition, state work plans need not be in place to begin conservation actions. If measures are being implemented during the development of the state plan, it should be acknowledged within the plan.

3. Species distribution, status, and monitoring.

A. A body of recognized prairie dog and grassland ecosystem experts will be assembled for the purpose of advising the BTPDCT. With the assistance from these scientific experts in the fields of population genetics, population viability, prairie dog control, and wildlife diseases, the BTPDCT and state work groups will develop a long-term conservation goal for the entire range of the black-tailed prairie dog. This goal will be expressed in number of occupied acres and individual towns of minimum size rather than in number of individuals. This goal will be developed and distributed to the state work groups to include in their individual state management plans by **August 15, 2000**.

B. With assistance from the scientific experts mentioned above, the BTPDCT will develop a generalized rating system for prairie dog complexes to assist the states in identifying areas important to prairie dog conservation. Criteria may include, but are not limited to, the following:

(1) Land ownership. For example, does an entity or landowner own the land with a commitment to prairie dog conservation?

(2) Sylvatic plague history within the complex and distance to known plague-affected complexes.

(3) Size and continuity of complex. For example, is the complex large, continuous, and without potential conflict with adjoining landowners, or is the complex composed of small towns within a checkerboard land ownership pattern?

(4) Demonstrated dependence of rare or sensitive species on the complex.

(5) Age and condition of the complex. For example, is the complex an old, degraded site with few options for long-term viability, or can the life span of the complex be prolonged with more aggressive grazing rotational systems or other management techniques?

(6) Potential for the complex to serve as a meaningful research site or demonstration area for landowners and land managers.

(7) Compatibility of prairie dog management with other mandated or traditional uses of the complex that is not in direct conflict with prairie dog management.

(8) Quality of habitat. For example, describe the soil type, elevation, vegetation composition, quantity of woody material etc.

This rating system will incorporate other needs of grassland species and be distributed to state work groups for consideration in their individual state management plans by **August 15, 2000**.

C. Work groups will establish long-term state goals for total number of prairie dog-occupied acres and for the number of occupied acres on different lands owned by different entities and **include them in their state management plan**. Work groups will take into consideration the amount of available habitat, land ownership, colony sizes contributing to the complex, and disease history when establishing these goals.

D. The BTPDCT will evaluate and establish minimum survey methods, in concert with experts from the scientific advisory group, for estimating, in a statistically valid fashion, the total number of occupied prairie dog acres in each state. The methodology will be developed to allow for comparable analysis. Work groups should evaluate current monitoring techniques for accuracy, logistical ease, cost, and forward the results to the BTPDCT for consideration. Examples include the prairie dog inventory technique for black-footed ferret reintroduction, U.S. Forest Service aerial transect method, and landowner/land manager surveys with field verification of sample sites. Survey data should be updated every five years or less, **starting with the year 2000**. Occupied acres should be stratified and reported by land ownership categories (state, tribal, federal, and private). Population and trend assessments should determine the following within each state boundary: 1) Mean town (colony) size, 2) Number of towns, 3) Proportion of larger sized towns contributing to complex dynamics, 4) Total number of occupied acres, and; 5) Population fragmentation index (distance to nearest town). Protocols will also include an element to monitor plague that details sampling techniques, precautions, schedules, and identified laboratories capable of conducting plague testing. Plans should include provisions if disease is found to be limiting or reducing local prairie dog populations.

E. Each work group will develop at least three population level objectives for areas within their state and **include them in the state management plan**. This will allow for the greatest flexibility and an adaptive management approach. Population and habitat objectives identified within the plans will be reassessed, as new information becomes available.

(1) For planning purposes, state boundaries will be used. Although several BLM and USFS districts may occur within a state, each may or may not involve individual management plans. A statewide plan should summarize population information and be used from the population objective standpoint. Work groups will identify prairie dog management areas and develop population level objectives for these areas and **include them in their state management plan**. For example, it may be desired in a state plan to maintain USFS lands at maximum levels but state lands may be maintained at near optimum levels identified for that management area. The three levels and a discussion of each level are as follows:

a. <u>Maximum level-</u>When acres of prairie dogs are above this level, and reductions are desirable, actions may be taken to reduce prairie dog populations. For example, actions might include: relaxation of hunting regulations, promoting areas of shooting, translocation, or subsidizing or directing specific control efforts.

b. Optimum level-The ideal or sustainable level of prairie dogs. Actions would likely include some form of managed sport shooting. Towns that are expanding may involve control while towns that are stable would likely be left alone. Towns that are declining would involve local protection efforts such as a shooting closure. Incentives to private landowners or grazing management practices would be used to maintain prairie dog population levels.

c. Protective level-If an area level falls below a certain level, protection measures should be taken. Efforts could include sport shooting restrictions, stricter criteria for control efforts, increased landowner incentives to encourage colonies to expand into unoccupied habitat, and establishment of disease control protocols. At this point, reintroduction or translocation efforts might be considered.

(2) Population levels will be coordinated with the BTPDCT, based on objective science, and involve local discussions and consensus agreements between wildlife, agricultural, and development interests.

(3) Work groups should first look at maintaining and expanding populations on federal lands, and consider these areas as the core area for conservation. After identifying manageable level for these lands, work groups should work with Native American tribes on black-tailed prairie dog conservation on tribal lands. Because the largest amount of occupied prairie dog habitat presently occurs on these lands, maintaining and enhancing populations in these areas will contribute the greatest in the shortest amount of time toward the conservation of the species.

(4) Regardless of landownership patterns, when viewed across the prairie dog range, the prairie dog population numbers contained in each state plan must add up to a total that has been determined to be within a biologically defensible range. The total must be capable of sustaining itself and be stable enough to preclude the need for federal or state listing as a threatened or endangered species.

F. Each work group will identify corrective measures that will be taken when the number of occupied acres falls below target levels and **include them in their state management plans**. Examples of corrective measures, depending on circumstances, could include: regulations or limits on shooting, restriction of control efforts, implementation of mechanisms to control the spread of disease, reestablishment of exterminated colonies and/or establishment of new colonies, and use of habitat improvement techniques.

G. Work groups will review state, federal, or tribal subsidies to control prairie dogs. Control subsidies should be used only when prairie dog populations are above the optimum management level and control is a desired and legal action. State or federal funding for prairie dog control should only be used as a management tool in conjunction with population levels in the state management plan.

H. Work groups will establish mechanisms to work with governmental, tribal and private land managers to assure the state's overall objectives for the optimum level of occupied acres are met.

4. Cooperation with Mexico, Canada, and Native American tribes.

A. The BTPDCT will ensure that coordination with Mexico, Canada, and Native American tribes occurs within the framework of the annual meetings of the Trilateral Commission, which is comprised of the United States, Mexico, and Canada, Native American Wildlife Society meetings, and any other meetings.

B. Through the BTPDCT, a relationship will be fostered with Mexico, Canada, and Native American tribes that will hopefully encourage them to determine the present distribution and status of black-tailed prairie dogs and their habitats within their boundaries, and to identify possible refugia or conservation plans for them. As relevant information becomes available from Mexico, Canada, Native American tribes, and the BTPDCT it will be disseminated to all state work groups. When information is available from Mexico and Canada, the BTPDCT will generate a distribution map to assess the current, rangewide distribution for black-tailed prairie dogs.

5. Identify, maintain, and promote existing and other suitable prairie dog habitats.

A. **By October 31, 2000** each state wildlife agency will coordinate with federal land management agencies, state land departments, participating tribes, and private landowners to conduct black-tailed prairie dog habitat inventories. This will include both unoccupied and occupied habitat. Work groups need to identify specific individuals responsible for inventory coordination within their particular land area. At a minimum, these inventories will identify areas that contain characteristics conducive to prairie dogs. GIS technology should be used while surveying and producing maps. More specific mapping resources are likely available for certain federal, state, and tribal properties.

On-the-ground habitat inventories, ground-truthing, or other on-the-ground studies conducted on private or tribal lands pursuant to this Conservation Agreement, shall not occur without prior permission from the landowner or tribe.

B. By **March 31, 2001**, each work group will produce state-specific maps delineating land ownership patterns overlaid with suitable occupied and unoccupied black-tailed prairie dog habitat, insofar as such habitat can be delineated at that time. Private lands on such maps will not be identified as to individual owners, except upon written consent of the landowner. These maps will be a primary basis for evaluating constraints to, and opportunities for, prairie dog habitat management within each state. The BTPDCT will identify a central repository for national inventory information.

C. Through the BTPDCT and state work groups, federal, state, tribal, and private land managers will be encouraged to conserve or enhance suitable or potentially suitable habitat, including corridors connecting these habitat blocks, to ensure that the black-tailed prairie dog's current and future habitat needs (including natural dispersal and habitat expansion) are appropriately addressed in the United States. In doing so, the cooperators will consider state, federal, tribal, and private cooperation, funding sources, and availability of suitable habitat.

D. State agencies will pursue conservation and enhancement agreements for suitable prairie dog habitat with federal and state land managers and willing private landowners, where such protection will address conservation objectives for the species. Conservation agreements might include supporting federal and tribal agencies in reducing control efforts in important core areas or voluntary measures by private landowners. Condemnation shall not be used as a land protection mechanism. Examples of voluntary habitat agreements that may be developed are: State Stewardship Agreements; USFWS Partners for Wildlife Agreements; and conservation easements among private organizations and government agencies.

Efforts to design or implement habitat protection or other conservation measures for private lands under this Agreement or state management plan shall only occur in cooperation with willing landowner(s). Prioritization will be given to those landowners that have prairie dog colonies or complexes that are highly rated under the criteria discussed under Section 3B. Private property owners shall not be involuntarily subject to any such protection or enhancement agreement under this Agreement or state management plan.

E. State work groups, in cooperation with the BTPDCT and the scientific advisory group, will monitor and identify new, continued, or diminishing threats to prairie dog habitat and population viability.

F. Incentives for prairie dog conservation need to be identified and implemented whenever possible to promote private landowner participation. Work groups will investigate the following mechanisms for incentives:

(1) Establish a mechanism or process for landowners that desire to remove

prairie dogs emigrating from adjoining federal, state, private or tribal lands.

(2) Direct payments from private funds (i.e. nongovernmental organizations, energy, natural gas, and railroad industries, and developers) that would maintain, enhance, and expand occupied prairie dog acres.

(3) Reduced grazing fees for leases on state or tribal grazing lands that are occupied by prairie dogs.

(4) Federal or state incentive programs, such as 2002 Farm Bill or the TPWD's Landowner Incentive Program, to provide incentives for maintaining viable prairie dog populations and habitat on private lands. Investigate other existing mechanisms to provide financial incentives when properties are evaluated for acceptance into government programs.

(5) Use tools provided for in the Endangered Species Act or in policies of the Service to promote black-tailed prairie dog conservation. Examples are the Safe Harbor and Candidate Conservation Agreements (if this species becomes a candidate for federal listing).

(6) Develop cooperative agreement strategies to promote black-tailed prairie dog conservation, such as MOUs and MOAs. Encourage participation in land use planning by tribal, state, county, municipalities, and federal entities for the purpose of promoting black-tailed prairie dog conservation.

An incentive is not necessarily a monetary incentive. For example, an assurance that a prairie dog complex will not be allowed to expand beyond certain boundaries or onto adjoining private land is important for securing landowner tolerance. In such cases, cooperating entities will establish programs and policies to avoid conflicts with adjoining landowners that do not wish to furnish habitat for black-tailed prairie dogs.

6. Public education.

A. The BTPDCT will provide information, education, and technical assistance on black-tailed prairie dog conservation and management to Conservation Agreement partners in a timely fashion to include in their educational materials.

B. Work groups will develop and distribute educational materials and implement projects that will help improve prairie dog conservation and management on public, private, and tribal lands. An educational component will be **included in the state management plans**. Materials and projects may include:

(1) Informational brochures targeting the general public and land managers.

These brochures will emphasize the need for prairie dog conservation and contain a description of the natural history of prairie dogs and a list of beneficial and detrimental management practices. Management discussions should mention practices that allow for livestock and prairie dogs to be managed incorporating nonlethal control of prairie dogs and the concepts of integrated pest management. Brochures will also recognize the potential detrimental impacts and benefits of black-tailed prairie dogs to private landowners and explain management needs and challenges within the state.

(2) Fact sheets that explain the effects of plague on prairie dog colonies and possible transmission to humans.

(3) State updates, or newsletters, to be distributed to public and private land managers within the state's prairie dog range. This update would keep land managers informed of conservation issues and new technology being developed for prairie dog conservation. It would also serve as an avenue for members of the work group to receive valuable input from all stakeholder groups.

(4) Demonstration areas that would educate land managers on components of prairie dog habitat, how to manage for prairie dog habitat, and what other uses, such as livestock grazing, which can be integrated with prairie dog conservation.

(5) Local newspaper, radio, and television stories, segments, or series that inform the public about the prairie dog conservation effort.

Educational materials emphasizing prairie dog conservation that could be incorporated into existing school curricula, including a teacher packet for use during visits to prairie dog towns and a video describing black-tailed prairie dog ecology, controversy, and activities.

(6) A database that contains an annotated bibliography of historical and current information on prairie dogs.

(7) An Internet website that provides prairie dog information. Members of the state work group will provide information to update the database and web page, and the pages should be linked to other state websites.

(8) Watchable wildlife maps and associated materials directing the public to prairie dog viewing sites or areas closed to shooting.

(9) Conducting landowner meetings to identify issues and concerns and seek constructive solutions to meet conservation objectives.

C. Work groups will identify the recreational, educational, scientific, and economic benefits and concerns associated with prairie dogs. They will use this information when developing conservation guidelines and educational materials. Methods to collect this information may include:

(1) A formal scientific survey of the public to identify their concerns/issues/needs, which can be addressed by conservation and management strategies.

(2) Literature and Internet searches.

Work groups will implement and promote projects that provide balanced information on the benefits and determents of prairie dogs.

7. Research Needs

Some of the research and information needs identified below may already be known, and completion of a thorough literature review will provide answers to some questions. In some cases, the information presented may only be speculation or altogether unknown, thus further research is necessary.

A. With the assistance of scientific expert committee, the BTPDCT will ascertain how much is already known and prioritize information needs. This could **occur by October 31, 2000** in the form of a workshop or symposium.

B. State work groups will prioritize research needs for their state and will **include them in their management plans**. Works groups need to consider both regional and rangewide needs. In developing state management plans, identified research projects might support the following needs:

(1) Plague

Plague typically destroys all prairie dog colonies within a complex within a few years of its introduction into the complex (Knowles 1992). The more dense the complex, the more complete the mortality (Knowles 1995). Plague infected fleas can remain alive in prairie dog burrows for up to one year following the death of prairie dogs (Lechleitner et al. 1968). Thus prairie dog recolonization following an epizootic is slow, and at times, does not reach the same densities as before the plague event. Once established in an area, plague becomes persistent and periodically erupts, with the potential to extirpate local black-tailed prairie dog populations (Mulhern and Knowles 1995). Prairie dog colonies virtually eradicated by plague require approximately 4-5 years to regenerate and then again become susceptible to a plague epizootic (Cully 1989). Recovery from an epizootic may take as long as 10 years

(Knowles 1995).

Plague was first observed in Gunnison's prairie dogs in northwestern Arizona in 1932 (Eskey and Haas 1940). In 1946, plague was first observed in black-tailed prairie dogs in Texas (Cully 1989). The first plague epizootic in black-tailed prairie dogs in Kansas was verified on the Cimarron National Grassland in 1996 (USFWS 1999). Plague is believed to be the primary limiting factor in four of Montana's larger prairie dog complexes, and will likely spread to other complexes (Knowles 1992). Plague has not been documented in South Dakota black-tailed prairie dog populations. Plague work is underway regarding black-footed ferret reintroductions and BTPDCT needs to coordinate with this effort. Further research and information are needed on:

a. The extent and cycle of plague throughout the black-tailed prairie dog range.

b. The amount of time needed for a prairie dog complex to fully recover from plague and whether smaller complexes are more vulnerable.

c. The mechanisms that allow some prairie dogs to survive an epizootic within a colony; whether some individuals have a level of resistance to the disease.

d. The effect of colony size and spacing has on the severity of the spread of plague.

e. Whether plague is more virulent in the southern or western portion of the black-tailed prairie dog range.

f. The factors that have limited the spread of plague to areas and prairie dog colonies unaffected by the disease.

g. The factors that allow plague to enter a prairie dog town, how plague affects the town and repopulation of the town.

h. Whether periodic dusting of burrows with an insecticide is an effective means of plague control; and other potential methods of plague control.

i. Methods to monitor and control plague efficiently and economically.

(2) Land Conversion/Loss of Habitat

Much of the Great Plains grassland habitat today exists as isolated blocks of short and mixed grass prairie surrounded by cropland. The remaining areas of prairie have often been considerably altered for livestock production. Prairie dog colonies create patches of distinct habitat within the native grassland. Further research and information are needed on:

a. The importance of prairie dog occupied habitat patches in maintaining local populations of associated species.

b. Whether prairie dogs can be sustained in areas of repeated summer fallow or dry land cultivation.

c. The degree to which black-tailed prairie dog populations are influenced by cattle and native grazing species.
d. Whether habitat conditions can be altered to enhance reintroduction/translocation efforts once burrow systems have deteriorated.

(3) Grazing Competition

Prairie dogs can markedly modify the landscape. Their burrowing and foraging activities affect vegetation, soil, and water transport. Direct dietary overlap between prairie dogs and cattle may not necessarily limit forage availability for either group. Prairie dogs can indirectly compete with cattle by clipping vegetation without consuming it, resulting in a smaller quantity of forage available for livestock consumption. The remaining vegetation, however, often has a seasonally higher nutritional value than that on other areas. Drought and overgrazing may heighten competition for forage between the prairie dogs and livestock. These factors, however, also encourage expansion of prairie dog colonies into new areas. During wet years, competition between the cattle and prairie dogs may be reduced, and colony enlargement inhibited where dense vegetation acts as a barrier. Further research and information are needed on:

a. Whether cattle and wild ungulates preferentially graze on prairie dog towns.

b. Whether cattle grazing in pastures occupied by black-tailed prairie dogs gain as much weight as cattle grazing in similar pastures without prairie dogs.

c. Whether black-tailed prairie dog foraging and burrowing activities reduce grass and increase forb and shrub abundance and if range conditions improve with prairie dogs present.

d. Whether soil churning by prairie dogs increases plant diversity and nutrition, thereby benefiting cattle and other wildlife.

e. Whether the more closely cropped vegetation within a prairie dog town is substantially more nutritious than adjacent rangeland.

f. Determine the occurrence of livestock injuring themselves in prairie dog burrows.

g. Determine if the potential benefits of increased nutritional value of the vegetation when prairie dogs are present offsets the potential losses to forage quantity and availability for livestock when prairie dogs are absent.

(4) Prairie Dog Control

The use of strychnine for prairie dog control during the 1920s and 1930s likely reduced prairie dog numbers 90% rangewide, but probably did not eradicate prairie dogs from extensive areas (Knowles 1992). Prairie dogs saw a period of recovery in the 1940s. But this recovery was soon reversed in the 1950s and 1960s when Compound 1080 provided land managers the means to eliminate prairie dogs from widespread areas (Knowles 1992). Presently, zinc phosphide, the only current EPA registered bait for prairie dog control, is only about 90% effective in controlling prairie dogs (Knowles 1992). Gas cartridges and aluminum phosphide are also registered for prairie dog control. Further information is needed on:

a. Whether prairie dogs are capable of population recovery following extensive control efforts.

b. Determine the effect of prairie dog poisoning on non-target species.

c. Determine the effective level of control for reducing potential competition with livestock.

d. Whether nonlethal control measures are as effective as lethal methods.

e. Determine the amount of time or minimal colony size needed for a prairie dog complex to recover following control efforts.

(5) Recreational Shooting

Recreational shooting has become quite popular in recent years. The exact effect of recreational shooting on the various components of a prairie dog town, in both small and large complexes, has yet to be determined. In large, healthy black-tailed prairie dog populations, recreational shooting impacts may be compensatory to natural mortality, and therefore not a predominant limiting factor (USFWS 1999). Mortality from recreational shooting in small local populations, however, may be additive (USFWS 1999). Recreational shooting may also contribute to population fragmentation and slow or deter recovery of colonies reduced by other factors such as plague. Further research and information are needed to:

a. Determine the degree of shooting pressure on prairie dogs that will force them to spend a greater proportion of time in alert postures and less time foraging.

b. Determine the effect of colony population dynamics and colony maintenance by having prairie dogs spending more time in alert positions.

c. Whether there is a minimum threshold of prairie dogs required to keep vegetation clipped and to watch for predators, and if shooting reduces the prairie dog colony population below that threshold.

d. Whether intensive shooting has a statistically significant impact on the density and composition of local prairie dog colonies and social structure and interactions.

e. Determine the effects of shooting on other non-target wildlife.

f. Whether extensive shooting, especially of pregnant or nursing females, significantly reduces annual recruitment and the ultimate population dynamics of a colony.

(6) Population Viability Analysis

Larger prairie dog colonies are likely more resistant to various population limiting factors. Smaller colonies, however, may be more susceptible to factors affecting isolated populations (e.g. stochastic events and inbreeding), in addition to the major factors that continue to suppress all prairie dog colonies (e.g. plague, poisoning, habitat loss). More fragmented, isolated and less connected populations usually have higher extinction rates. Further research and information are needed to determine:

a. Whether smaller isolated prairie dog towns have higher extinction rates than larger towns within complexes.

b. Whether isolated prairie dog colonies result in the loss of additional genotypes.

c. The minimum viable population.

d. The degree of colony interconnectivity and maximum dispersal capabilities.

e. The genetic integrity of the species.

f. Relationship between colony size, isolation and spread of plague.

(7) Prairie Dog Associated Species/Shortgrass Prairie Keystone Species

The black-tailed prairie dog has been described as a keystone species of the shortgrass prairie, suggesting the species influences ecosystem functions through their activities in unique and significant ways (USFWS 1999). If true, then the estimated 99% decline of occupied black-tailed prairie dog habitat in the Great Plains should have initiated changes in ecosystem structure resulting in a decline of overall species diversity.

Black-tailed prairie dog-associated species can be categorized as prey dependent or habitat dependent, and obligatory or facultative. Although the vast majority of associated species are not dependent upon prairie dogs for their survival (facultative), it has been implied that many species of birds and small mammals occur at higher densities on prairie dog colonies than adjacent areas without colonies (Miller et al. 1994). For prey dependent species, prairie dog colonies represent patches of dense prey availability. For habitat dependent species, colonies represent patches of low growing vegetation that are high in nitrogen and low in stem content. Prairie dog colonies increase areas of bare ground and provide burrows for shelter.

The black-footed ferret is probably the only truly obligatory predator of prairie dogs (Knowles 1992). The swift fox and ferruginous hawk are considered to be generalized prairie dog predators. The mountain plover and burrowing owl are believed to be prairie dog habitat dependent species. In Montana, the mountain plover has been suggested as on the verge of being an obligatory habitat species with black-tailed prairie dogs (Knowles 1992). Also in Montana, the decline of the ferruginous hawk has been associated with the decline of prairie dogs (Knowles 1992). Current information suggests, however that the swift fox's status is unrelated to prairie dogs. The burrowing owl is closely associated with prairie dogs, primarily because of the availability of nest burrows. Burrowing owls, however, do not normally feed on prairie dog towns, and the geographic range of this species is much greater than that of all prairie dog species combined. Further research and information are needed to determine:

a. Whether the estimated decline of occupied black-tailed prairie dog habitat in the Great Plains has initiated changes in ecosystem structure resulting in a decline of overall species diversity.

b. Other prairie dog obligate species besides the black-footed ferret.

c. Whether habitat associated species occur in higher densities on towns as opposed to on suitable habitat without prairie dog towns.

d. Whether suspected prey- and habitat-associated species abundance are linked to prairie dog towns throughout the entire prairie dog range or only in localized areas and situations.
e. Ideal prairie dog complex size including town size and proximity for obligate species.

(8) Commercial use of prairie dogs

A more recent impact on prairie dogs is the commercial exploitation in the pet trade. Animals are sold in foreign markets for as high as $700 a pair. Further research and information are needed to determine:

a. The amount of commercial trade that is occurring within each state.

b. The effects of commercial take methods on non-target species.

8. State regulatory review.

In some states, prairie dog management authority rests with both the state/tribal wildlife and agricultural agency. Local governments, state, federal, and tribal agencies need to consult with each other regarding actions that result in take. The state wildlife agencies will take the lead in establishing a process of communication with entities regarding management to ensure black-tailed prairie dog population viability. By **August 15, 2001**, state work groups will investigate, evaluate, determine the feasibility, and if necessary, change state regulations to clarify regulatory authority and mandates for prairie dog management. Statutes that mandate control will either be eliminated or modified such that they do not restrict protection efforts should they become necessary.

A. Recreational Shooting-Prairie dog management should include biologically based shooting seasons and methods to estimate hunter effort and harvest. By **August 15, 2000**, state wildlife agencies need to investigate, evaluate, and if necessary and possible, change state hunting regulations to conserve or enhance prairie dog populations. As with other harvested species, states should develop mechanisms to direct effort away from areas where prairie dogs are depleted or where other grassland species could be impacted.

B. Control-Work groups will review federal, state, and tribal policies directed at control and develop a management scheme to guide control activities. Guidelines **will be included in state management plans**. Mandatory control and eradication will be investigated, evaluated, and if necessary and possible, state regulations will be modified to ensure the species viability within an area. Control activities will include lethal and nonlethal methods.

C. Commercial use-Work groups will review both federal and state policies directed at commercialization of prairie dogs and develop a management scheme to guide commercial activities. Guidelines **will be included in state management plans**.

9. Evaluation of progress and accomplishments.

A. By the end of January of each year, following execution of the Conservation Agreement, the BTPDCT will issue a written report on activities implemented to date to conserve the black-tailed prairie dog. The report will be submitted to the Service, and made available to all interested parties. Within 60 calendar-days of receipt of each report, the Service will inform the states in writing of any areas in which progress is not sufficient to warrant continuation of this Agreement. If such deficiencies are identified, within 90 calendar-days of notification the states will jointly determine whether to implement mutually acceptable, and agreed to by all parties to the Agreement, curative measures.

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this approach can be applied to systems that have a time series of population-size measurements. Another approach to incorporating uncertainty in parameters is using Bayesian methods to construct the PVA model. Bayesian techniques are an alternative to the frequentist methods that characterize parametric and nonparametric approaches that most students are taught in statistics classes. Paul Wade presents an overview to Bayesian thinking and shows how it can be used in PVA. Barbara Taylor and colleagues apply a Bayesian approach to classifying the category of threat that a species faces. They compare Bayesian models to standard PVA approaches and other methods for predicting extinction rates.

8

Definition and Estimation of Effective Population Size in the Conservation of Endangered Species

Robin S. Waples

ABSTRACT

Effective population size (N_e) is one of the most fundamental evolutionary parameters of biological systems, and it affects many processes that are relevant to biological conservation. N_e is difficult to estimate in natural populations, however, and a variety of factors complicate its application to the conservation of endangered species in general and population viability analyses in particular. Complexities include (1) ambiguity arising from multiple ways of defining N_e, (2) difficulty in adequately accounting for spatial and metapopulation structure and their effects on N_e, (3) sampling biases and other difficulties involved in evaluating N_e in species with overlapping generations, (4) confusion regarding the magnitude (and meaning) of the ratio N_e/N, and (5) concerns regarding precision and bias of indirect genetic methods for estimating N_e. Greater attention to these issues will allow effective-size considerations to be more fully integrated into endangered-species management.

INTRODUCTION

Allendorf and Ryman (chap. 4 in this volume), Hedrick (chap. 17 in this volume), and Haig and Ballou (chap. 18 in this volume) have stressed the importance of genetic considerations in risk analysis and recovery planning for endangered species. In this chapter, I focus more narrowly on what is arguably the most important genetic parameter in evolutionary biology—effective population size (N_e). N_e is the primary factor responsible for the rate of genetic drift, the rate of loss of diversity of neutral alleles, and the rate of increase in inbreeding experienced by a population. Effective size also determines the relative evolutionary importance of directional (migration and selection) and stochastic (random genetic drift) factors. Migration and selection are deterministic in large populations but can be overwhelmed by random processes in small

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ones, in which favorable alleles can be lost and deleterious alleles can become fixed by chance alone—with profound effects on fitness and population viability.

N_e is difficult to estimate in natural populations, and a variety of factors related to its definition and interpretation complicate its application to the conservation of endangered species in general, and population viability analyses (PVAs) in particular. Complexities include (1) ambiguity arising from multiple ways of defining N_e, (2) difficulty in adequately accounting for spatial and metapopulation structure and their effects on N_e, (3) sampling biases and other difficulties involved in evaluating N_e in species with overlapping generations, (4) confusion regarding the magnitude (and meaning) of the ratio N_e/N, and (5) concerns regarding precision and bias of indirect genetic methods for estimating N_e. Discussion of these issues below is intended to allow considerations of effective size to be more fully integrated into endangered-species management. We shall see that, although the basic concept is elegantly simple, almost everything else involving effective population size is much more complicated.

DEFINITIONS OF N_e

In finite populations (i.e., in all biological populations), random genetic drift leads to changes in allele frequency and loss of genetic variability. In "ideal" populations (Fisher 1930; Wright 1931)—those with random mating, an equal sex ratio, discrete (nonoverlapping) generations, and random variation in reproductive success—genetic drift occurs at a rate described by an inverse function of population size (N). Because real populations almost never satisfy the conditions of an "ideal" population, Wright (1931, 1938) developed the concept of "effective population size" (N_e), which describes the size of an ideal population that would have the same rate of genetic change as the population under consideration. Departures from the "ideal" conditions generally cause N_e to be less than N, and often a good deal less.

Several different effective sizes have been identified in the literature (Ewens 1979; Crow and Denniston 1988; Caballero 1994), the two most common being variance effective size (N_{eV}), which is related to the rate of allele-frequency change, and inbreeding effective size (N_{eI}), which is related to the rate of increase in inbreeding. Typically, inbreeding is measured as the probability that the two alleles in an individual can be traced back to the same gene in a common ancestor, in which case the alleles are considered to be *identical by descent*. Formulas for N_{eI} and N_{eV} are

(1)
$$N_{eI} = \frac{N\bar{k} - 2}{(\bar{k} - 1) + V_k/\bar{k}}$$

and

(2)
$$N_{eV} = \frac{N\bar{k} - \bar{k}}{1 + V_k/\bar{k}}$$

(Crow and Kimura 1970, eq. 7.6.2.17, p. 359, respectively), where N is the population size in the parental generation, $\bar{k}$ is the mean number of offspring produced per individual, and V_k is the variance of k across individuals. If reproductive success is random and population size is constant, then $V_k = \bar{k} = 2$ and the population is "ideal" ($N_e \approx N$ except for small adjustments due to the mating scheme; see Crow and Denniston 1988 for details). In natural populations, however, V_k is usually greater than $\bar{k}$, leading to $N_e < N$. High V_k values can be caused by reproductive differences among individuals within sexes or by an unequal sex ratio, which leads to differences between the sexes in mean reproductive output per individual.

In stable populations the two effective sizes are similar, and it is not important to distinguish between them for conservation purposes. Populations of conservation interest often are changing rapidly in size, however, and in this situation N_{eV} and N_{eI} can be very different. Table 8.1A shows how N_{eI} and N_{eV} vary over a number of generations in an otherwise ideal population with cyclical variations in N. When population size drops sharply (from 100 to 10 between generations 2 and 3), N_{eV} reflects the drop immediately, while the change in N_{eI} lags by a generation (see Ryman et al. 1995). The bottleneck has an immediate effect on allele frequencies (and hence N_{eV}) because the amount of allele-frequency drift depends entirely on the number of individuals in the progeny generation. Thus, the magnitude of drift will, on average, be much higher if only 10 progeny are produced than if the population had remained constant at 100. In contrast, the bottleneck will have no immediate effect on inbreeding because the probability of identity by descent in the progeny generation is determined by the number of parents; a sample of 10 individuals produced by 100 parents will on average be no more inbred than if 100 or 1,000 progeny were produced. The effects of the bottleneck on N_{eI} do not appear until the following generation when progeny of the 10 parents, which have a high probability of having two alleles that are identical by descent, mate with each other.

Note that over a full cycle (five generations), the harmonic mean

Table 8.1 Changes over Time in Inbreeding (N_{eI}) and Variance (N_{eV}) Effective Population Sizes

Generation	N	$\bar{k}$	N_{eI}	N_{eV}
A. Cyclical fluctuations				
1	100	2	99	99
2	100	0.2	90	10
3	10	200	10	900
4	1000	0.2	990	100
5	100	2	99	99
6	100			
Harmonic mean			38	38
B. Declining population				
1	1000	1	998	500
2	500	0.8	498	200
3	200	1	198	100
4	100	1	98	50
5	50	0.4	45	10
6	10			
Harmonic mean			123	36

Notes: Changes are for a hypothetical population with variable N that is "ideal" in other respects (discrete generations, random mating, equal sex ratio, random variation in reproductive success). N_{eI} and N_{eV} were computed using equations 1 and 2, respectively. $\bar{k}$ is the mean number of progeny per parent, V_k is the variance of k, and V_k is assumed to equal $\bar{k}$.

effective size is the same for the two measures ($N_e \approx 38$). This suggests that even with variable population size it may not always be important to distinguish inbreeding and variance effective sizes for conservation purposes. However, there are several situations in which the distinction can be important. First, if there is concern that low short-term N_{eI} may cause significant inbreeding depression, then conservation measures to avoid this situation must be applied at the appropriate time. Frankham (1995a) and Hedrick and Kalinowski (2000) reviewed evidence for inbreeding depression in natural and captive populations and provided several examples demonstrating that this is a real conservation concern. Second, most natural or captive populations do not exhibit such tidy cycles in abundance as shown in table 8.1A. Many populations of conservation concern are declining, and in this case N_{eI} can be substantially higher than N_{eV} for a considerable period of time (as illustrated in table 8.1B). Conversely, in recovering populations N_{eV} will recover faster than N_{eI} to prebottleneck levels.

Finally, Ryman et al. (1995) showed that variance and inbreeding effective sizes behave differently under supportive breeding, in which part of the gene pool is taken into captivity and enhanced relative to the wild component. See Nomura (1999) and Ryman et al. (1999) for

more debate on this complex issue. As captive breeding is used in recovery programs for many threatened and endangered species, it is important to clarify and resolve this issue. Hedrick et al. (1995) and Hedrick (chap. 17 in this volume) provided an example in which both N_{eV} and N_{eI} were estimated for an endangered species subject to a captive-breeding program. In their example, it does not appear that the captive-breeding program had a significant impact on the effective size of the larger population, a result that can be attributed to relatively high N_e in the captive phase and relatively low contribution of captive fish to natural spawning. Waples and Do (1994) considered the genetic effects of supportive breeding in some detail and showed that whether increased population size due to captive breeding persists after the program is terminated has a profound effect on N_e and levels of inbreeding in the postsupplementation population.

N_e IN SPATIALLY STRUCTURED POPULATIONS

Spatial structure of a population is important to consider in evaluating N_e because in general the effective size of the overall population (N_{eT}) is not equal to the sum of the N_e's of the subpopulations (Nunney 1999). This is because population structure affects the variance in reproductive success of individuals within and among subpopulations. The nature of these effects depends heavily on the details of the model under consideration.

Wright (1943) was the first to consider the effective size of structured populations. In his finite island model, each of n subpopulations has the same fixed number of individuals (N). Each subpopulation is "ideal" as described above, so subpopulation $N_e = N$. The subpopulations ("islands") are connected by migration; each subpopulation contributes a fraction m of its individuals to a global migrant pool every generation, and each subpopulation receives the same fraction of migrants drawn randomly from the migrant pool. Under these conditions,

$$N_{eT} \approx \frac{N_T}{1 - F_{ST}}, \tag{3}$$

where $N_T = nN$ is the total number of individuals in the metapopulation and F_{ST} is Wright's measure of genetic differentiation among subpopulations. Inspection of equation 3 indicates that, if there is any population subdivision ($F_{ST} > 0$), N_{eT} will always be larger than N_T. Since $N_e = N$ within each subpopulation, equation 3 also implies that metapopulation N_{eT} is greater than the sum of the subpopulation N_e's. I will consider this result in some detail because understanding why population subdivision increases N_{eT} in Wright's model is critical to understanding the complex way in which many factors can affect the relationship between subpopulation and metapopulation effective size.

The result in equation 3 is due to two factors, both of which are a direct consequence of the island model's assumptions that each subpopulation is of constant and equal size and that each contributes exactly the same number of propagules to the migrant pool in the next generation. To see the effect of these assumptions on N_{eT}, consider as a point of reference an ideal population of size N_T. Within this population one could imagine hypothetical groupings of individuals into arbitrary subunits, and at any given point in time the collective reproductive success of the different groups would vary randomly—some groups contributing more to the next generation and some less, just by chance, driven by random variation among individuals in reproductive success. Now consider that these subunits are not imaginary but real and reflect permanent partitioning of the global population. Because each subunit is of fixed size N, the subunits can no longer vary among themselves in reproductive success. This constrains the degree to which individuals within and among subpopulations can differ in reproductive success, and the effect is greater the smaller N becomes. In the extreme case where each of the n subpopulations has exactly two individuals, every individual in the global population will have equal reproductive success, so $V_k = 0$ and $N_{eT} \gg N_T$ (in agreement with equations 1 and 2). The first factor operating in the island model is thus an increasing constraint on variance in reproductive success as the number of subpopulations increases and the size of each decreases.

The second, and related, factor that leads to the result in equation 3 is that the island model does not allow extinction of subpopulations, since all are constant in size. As subpopulations become more isolated, F_{ST} increases as they tend to become fixed for different alleles. Although genetic diversity within subpopulations declines as they become more isolated and cannot receive new genes through migration, genetic variation within the global metapopulation is frozen in place because different alleles, by chance, become fixed in different subpopulations. Again, this effect is enhanced as the number of subpopulations increases and the size of each decreases.

The interplay of these two factors in causing the effect Wright detected can be illustrated by substituting in equation 3 the equilibrium value of F_{ST} in the island model ($F_{ST} \approx 1/(1 + 4mN_e)$) and rearranging to yield a convenient way of expressing the effects of subdivision on the ratio N_{eT}/N_T (after Nunney 2000):

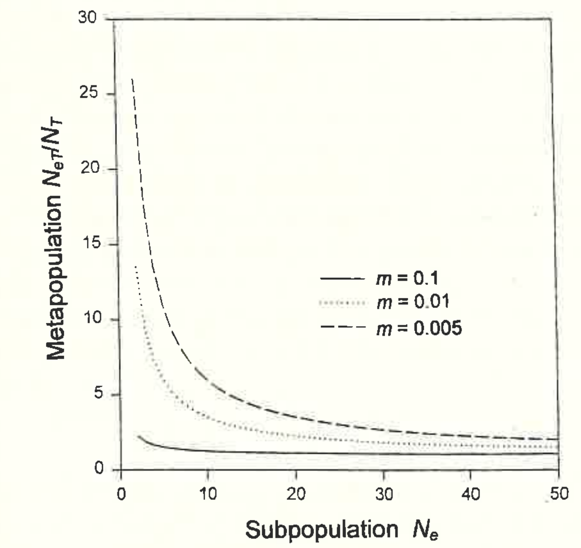

Fig. 8.1 The ratio of metapopulation effective to total size (N_{eT}/N_T) in Wright's island model as a function of subpopulation effective size (N_e) and migration rate (m; see equation 4). This figure assumes that N_T is fixed, so subpopulation N and N_e decrease as the number of subpopulations increases.

$$\frac{N_{eT}}{N_T} \approx 1 + \frac{1}{4mN_e}. \qquad \textbf{(4)}$$

Figure 8.1 illustrates this result. With N_T held constant, for any given migration rate, metapopulation N_{eT} (and hence the ratio N_{eT}/N_T) increases with increasing fragmentation of the global population (higher n and lower N_e in each subpopulation). For any given subpopulation size, metapopulation N_{eT} increases as migration rate declines and more and more of the genetic variation is "frozen" into different states in different subpopulations.

Since the validity of equations 3 and 4 depends on the extent to which forces exist that cause N to be equal and constant across subpopulations, it is important to consider whether such forces are in fact likely to occur. Ray (2001) suggested one possible scenario: if suitable habitat patches are well isolated, if the patches are similar in local carrying capacity, and if local population regulation is effective in stabilizing population size, subdivision can constrain the variance in reproductive success, leading to higher N_{eT}. The design of nature reserves and captive-breeding programs for endangered species may also provide opportunities for equalizing reproductive success among subpopulations. However, there does not appear to be a general force that constrains natural subpopulations to be equal and constant in size, so there is no reason to expect N_{eT} to be larger than N_T merely as a consequence of population subdivision. As discussed below, other models describe conditions under which population subdivision can be expected to reduce N_{eT}.

Whitlock and Barton (1997) examined the effective size of subdivided populations in some detail. One of the models they considered differed from the island model above only in that the subpopulations were allowed to vary in their contribution to the next generation through different migration rates, with the contribution to the overall migrant pool determined by subpopulation productivity. Under these conditions,

$$N_{eT} \approx \frac{N_T}{(1 + P)(1 - F_{ST}) + NPF_{ST}n/(n - 1)}, \tag{5}$$

where P is the variance in productivity among subpopulations. Setting $P = 0$ leads to Wright's result in equation 3. It can be shown that, if P is larger than would be expected from random variation among individuals, population subdivision will reduce N_{eT} relative to N_T (Whitlock and Barton 1997). If $F_{ST} = 0$, then equation 5 simplifies to $N_{eT} \approx N_T/(1 + P)$. That is, even if there is no permanent subdivision, but instead individuals assort randomly into temporary "subpopulations" each generation for breeding, N_{eT} will still be less than N_T if productivity differs among sites ($P > 0$). In this case, directional differences in subpopulation productivity are overlaid on random differences among individuals in reproductive success, with the overall effect of increasing variance of reproductive success within the total population.

Nunney (1999) considered a similar model that also relaxes the assumption of the island model about equal contribution of migrants. In Nunney's "interdemic genetic drift" model, variations in subpopulation productivity (and hence contribution to the migrant pool) are generated by accumulation of random differences among individuals in reproductive success. He also allowed for the possibility of inbreeding within subpopulations, measured by Wright's inbreeding statistic F_{IS}, and obtained the following relationship:

$$N_{eT} \approx \frac{N_T}{(1 + F_{IS})(1 + F_{ST}) - 2F_{IS}F_{ST}},$$

If mating is random within subpopulations, then the expectation of $F_{IS} = 0$ and this reduces to

$$N_{eT} \approx \frac{N_T}{1 + F_{ST}}, \tag{6}$$

which is exactly the opposite of Wright's result: with population subdivision ($F_{ST} > 0$), N_{eT} of the overall population is less, not greater, than total population size, provided that the subpopulations are not constrained to contribute equally to the migrant pool.

In the classical metapopulation (Levins 1970), extinction and recolonization of subpopulations (or patches) is common. Maruyama and Kimura (1980) and Gilpin (1991) showed that the extinction/recolonization process can dramatically reduce N_{eT}, particularly if the number of occupied patches is so low that the overall metapopulation is in danger of extinction. Whitlock and Barton (1997) showed that, if variance in island productivity in their model was due to subpopulation extinction and recolonization, then the following relationship approximately holds (see Nunney 2000):

$$N_{eT} \approx \frac{n}{4(m + e)F_{ST}}, \tag{7}$$

where e is the rate of subpopulation extinction. Notably, in this situation, N_{eT} of the metapopulation is proportional to the number of subpopulations rather than to N or N_T.

To examine some of the many factors that can influence the effective size of a metapopulation that is not at significant short-term extinction risk, Hedrick and Gilpin (1997) used computer simulations to monitor changes in heterozygosity (H) as an index of N_{eT}. In their model, individual patches could be vacant for one or more time periods, after which the probability of recolonization depended on the number of extant source patches and their colonization ability. Hedrick and Gilpin found that, under these conditions, N_{eT} of the metapopulation depends more on metapopulation dynamics than on the carrying capacity of the patches. The rate of patch extinction and the characteristics of the founders that recolonized vacant patches were found to be particularly important. If patch extinction probability was high, entire lineages were regularly lost, thus reducing H and N_{eT}, often by one or two orders of magnitude or more. Similarly, if new patches were colonized by just a few founders, or if the founders came from the same subpopulation rather than from the metapopulation at large, H and N_{eT} were also greatly reduced.

Hedrick and Gilpin (1997) concluded that the relatively high levels of allozyme and DNA heterozygosity found in most species suggest that they have not spent their evolutionary history functioning as classical Levins-type metapopulations. This conclusion, however, should be tempered by consideration of factors not included in their model. For example, although spatial subdivision often increases the probability of subpopulation extinction, it also may increase the independence of local extinctions. Ray (2001) showed that, if the probability of local extinction scales logarithmically with population size, then even large subpopulations are subject to extinction, and under these conditions, strong population subdivision can promote retention of more genetic diversity and increase N_{eT}.

In summary, N_{eT} of a metapopulation can be either greater or less than the sum of the N_e's for the component subpopulations. Results discussed above demonstrate that whether N_{eT} is increased or decreased by population subdivision depends heavily on parameters such as variance in size and productivity of subpopulations, the patterns of migration, and extinction and recolonization rates. Conservation biologists should consider these factors carefully in evaluating conservation programs for endangered species. They should also be careful to distinguish between the effective size of a subpopulation and the metapopulation as a whole, since results described above indicate that the two parameters can respond very differently to the same conditions. As migration rate increases, the concept of a subpopulation N_e has less and less meaning, since the subpopulation is not acting as an independent unit. We should also not lose sight of the fact that most population genetics theory (and many models) provide results expected at equilibrium. This will not often be a reasonable assumption, particularly for species of conservation concern. For example, Hedrick and Gilpin (1997) pointed out that anthropogenic fragmentation of the natural landscape may have formed (and may continue to be forming) unnatural, nonequilibrium metapopulations with dynamics that have dramatically reduced recent N_{eT} in many species.

Finally, it is also worth noting here that the assumptions in Wright's island model (equal and constant subpopulation size) that are responsible for his conclusions regarding population subdivision and N_{eT} are common to many other models used in conservation biology. In particular, any model that divides a global population into subsets while placing constraints on the mean or variance of subpopulation parameters can have the same effect as Wright's model—artificially reducing V_k and upwardly biasing N_e.

N_e AND OVERLAPPING GENERATIONS

Most population genetics theory deals with generations that are discrete. Although convenient as a theoretical construct, this scheme does not conform to the life history of many biological species. Discrete-generation models for N_e are fairly robust for organisms with overlapping

generations, provided that the populations are demographically stable (Felsenstein 1971; Hill 1972). These models, however, have generally dealt with population parameters and have ignored sampling considerations. Since conservation biologists rarely know population parameters (and generally consider themselves fortunate to have at least some demographic or genetic data for their organism of interest), and because opportunities for sampling bias are considerably greater in organisms with overlapping generations, this topic deserves mention here.

One fundamental problem is that almost all sampling theory assumes a random sample from the population, and for effective population size this means sampling from an entire generation. This can be easy to achieve in organisms with discrete generations, because all the individuals in a generation may co-occur in time and space, but it is rarely simple for organisms with overlapping generations. In such species, at a given time individuals in any particular life stage (e.g., juveniles or mature adults) may constitute only a fraction of a generation. To sample an entire generation, therefore, it is often necessary to obtain an array of temporally spaced samples. Apart from the logistic challenges this presents, it may be difficult to determine the appropriate weightings to place on the individual samples, which ideally should reflect the (generally unknown) relative contribution of the component sampled to the generation as a whole.

Another complication is that V_k, which has a profound effect on N_e (see equations 1 and 2), represents the *lifetime* variance in reproductive success among individuals. Unfortunately, even when data on reproductive success are available, they typically apply to offspring produced in one season rather than in an entire lifetime, making it difficult to evaluate cumulative reproductive success of individuals.

What can be done to alleviate these difficulties, which can result in substantial bias in estimating effective population size and other genetic parameters in species with anything but the simplest life histories? One option is to ignore the sampling effects under the assumption that they will be minor. This may be reasonable if the number of intervening generations is large enough, in which case the bias from sampling error may be small relative to the signal from genetic drift. Miller and Kapuscinski (1997) made this assumption in using a discrete-generation model to estimate effective size over a period of more than 30 years in a northern pike (*Esox lucius*) population. Alternatively, a series of stratified random samples can be combined to represent the generation as a whole. Although determining the optimum sampling and weighting scheme to accomplish this will be difficult without extensive life-history and demographic data for the species of interest, simply combining multiple samples temporally spaced across a generation could substantially reduce potential biases. Nunney and Elam (1994) showed that, under some circumstances, reasonably accurate estimates of N_e for species with overlapping generations can be made using demographic data for just one or a few seasons.

Genetic methods may be able to help determine whether a sample collected from the wild can be considered quasi-random and, if not, the magnitude of potential biases. Hansen et al. (1997) used genetic data to evaluate this issue in brown trout (*Salmo trutta*) populations and found significant allele-frequency differences among age classes. Furthermore, examination of family relationships within the youngest cohort suggested that most of that sample was derived from just three full-sib families. These data clearly illustrate potential biases that can arise from assuming that samples taken from species with overlapping generations adequately represent an entire generation. Herbinger et al. (1997) used a similar approach to evaluate a natural cohort of cod larvae sampled intensively over a 21-day period. They found no evidence of any temporal or spatial family structure and concluded that the larvae came from a relatively large, homogeneous gene pool produced by a large effective number of spawners (≥2,800).

If age data are available, it may be possible to partition the samples into cohorts and make explicit adjustments for sampling (Waples 1991; Jorde and Ryman 1995, 1996). Unless there is a way to link offspring from different cohorts to the same parents, however, it will be difficult to evaluate lifetime reproductive success and, therefore, generational N_e. The unusual life history of Pacific salmon, which have variable age structure but which all die after spawning, has features of both discrete and overlapping generation models. Waples (1990a,b) showed that, because yearly reproductive output is equal to lifetime reproductive output in these species, fairly straightforward adjustments to standard discrete-generation models can be used to obtain generational estimates of N_e in Pacific salmon.

THE RATIO OF EFFECTIVE TO TOTAL POPULATION SIZE

Much has been written in the recent literature about the N_e/N ratio in natural populations. The relevance of this debate to conservation of endangered species is readily apparent: because N is generally much easier to estimate than N_e, establishing an empirical relationship between the two parameters would allow at least crude estimates of N_e for many more species. Unfortunately, there is no consensus regarding even the approximate range for N_e/N in natural populations. At one extreme Nunney (1993) argued that N_e/N would be 0.5 or higher except under special circumstances; at the other extreme, Hedgecock (1994) argued that, in marine organisms with high fecundities and high mortality in early life stages, "sweepstakes" survival and recruitment of related individuals can lead to very nonrandom mortality across families, with the result that N_e can be several orders of magnitude less than N.

Table 8.2 Contribution of Various Factors to the Mean Ratio N_e/N

Factor	Mean N_e/N
Sex ratio, S	0.64
Family-size variance, V	0.46
$S + V$	0.35
$S + VB$ + variable N	0.11

Notes: Estimated for 102 vertebrate, invertebrate, and plant species using demographic and genetic data (Frankham 1995b).

I will not attempt to resolve this debate here, but I would like to point out that at least part of the confusion regarding N_e/N ratios can be attributed to a lack of clarity regarding (1) the treatment of variable population size and its effects on N_e/N, and (2) the relationship between generational and long-term N_e/N. Frankham (1995b) reviewed empirical estimates of N_e/N for over 100 species of vertebrates, invertebrates, and plants (table 8.2) and found that the mean N_e/N ratio varied from 0.64 (using only an adjustment for uneven sex ratio) to 0.11 for a "composite" estimate (which included adjustments for sex ratio, variance in reproductive success, and temporal changes in N). From these results Frankham concluded that variable population size is the most important factor influencing the ratio N_e/N, and that N_e/N is generally lower for natural populations than many have realized. Vucetich et al. (1997) and Vucetich and Waite (1998) examined this issue analytically and also concluded that variable N has a profound effect on N_e/N ratios.

Unfortunately, the conclusions of Frankham, Vucetich, and others regarding the importance of variable population size to the ratio N_e/N are difficult to evaluate because they are confounded by a statistical artifact in computation of the N_e/N ratio for a time series. Specifically, in these papers long-term N_e/N was computed as the harmonic mean N_e ($\tilde{N}_e$) divided by the arithmetic mean N ($\bar{N}$). The effects of mixing arithmetic and harmonic means in a ratio are illustrated in table 8.3, which shows a hypothetical series of N_e and N values for five generations. In each generation, N_e/N is 0.4, similar to the mean ratios Frankham found using adjustments for variance in reproductive success (0.46) or sex ratio and reproductive variance (0.35). The ratio over the whole time series in this example is also 0.4, provided it is computed as $\tilde{N}_e/\tilde{N}$,

Table 8.3 Computation of Long-Term N_e/N in a Hypothetical Population with Variable N but Constant N_e/N per Generation

Generation	N	N_e	N_e/N
1	1000	400	0.4
2	500	200	0.4
3	150	60	0.4
4	2000	800	0.4
5	5000	2000	0.4
Arithmetic mean ($\bar{N}$, $\bar{N}_e$, $\overline{N_e/N}$)	1730	692	0.4
Harmonic mean ($\tilde{N}$, $\tilde{N}_e$, $\tilde{N}_e/\tilde{N}$)	482	193	0.4
Harmonic mean N_e/arithmetic mean N ($\tilde{N}_e/\bar{N}$)			0.11

$\bar{N}_e/\bar{N}$, or any function of the individual generation N_e/N ratios. It can also be shown that 0.4 is the expected value of the harmonic mean N_e divided by the N values each generation (Kalinowski and Waples in press). When long-term N_e/N in table 8.3 is computed as $\tilde{N}_e/\bar{N}$, however, the result is 0.11, the same mean value Frankham (1995b) found for comprehensive estimates of N_e/N. This simple example shows that a reduction in N_e/N of the magnitude attributed to variable N can also be generated entirely by the statistical artifact of mixing arithmetic and harmonic means in a ratio.

This does not mean that variations in N are not important as a factor influencing N_e. If there is a strong relationship between N and N_e within generations, variable population size can have a profound influence on long-term N_e, because effective size for a series of generations is approximately the harmonic mean (rather than the arithmetic mean) of the single-generation N_e's (Wright 1938). However, I would argue that variations in N contain no additional information about the long-term ratio N_e/N beyond that contained in the individual generation values N_e/N. Variations in N by themselves do not affect the long-term ratio N_e/N, unless that ratio is calculated using a mixture of harmonic and arithmetic means. The example in table 8.3 raises the question, "What biological information is conveyed by a long-term N_e/N ratio when it is computed as $\tilde{N}_e/\bar{N}$?" This formulation ignores the information contained in the N_e/N ratios for individual generations and produces a quantity that is difficult to interpret biologically. Kalinowski and Waples (in press) provide biological interpretations for $\tilde{N}_e/\bar{N}$ and another method ($\tilde{N}_e/\tilde{N}$) for computing the long-term N_e/N, show how the two indices are related mathematically, and evaluate their properties.

INDIRECT METHODS FOR ESTIMATING N_e

Because N_e directly controls the rate of change in numerous genetic parameters in natural populations, various researchers have reasoned

that by measuring these genetic parameters one can obtain an estimate of N_e. Although these indirect genetic methods for estimating N_e typically have a large stochastic variance, they have achieved some popularity because direct demographic estimates of N_e (based on sex ratio and reproductive success) are so difficult to obtain for many species that indirect genetic estimates may be of considerable use even if they are imprecise.

Waples (1991) identified three types of genetic methods for estimating N_e: those that estimate current N_e, those that estimate long-term or historical N_e, and those that provide information about population bottlenecks (see Schwartz et al. 1998 for further discussion). Estimates of historical N_e, which represents the long-term effective size that would be expected to produce currently observed levels of neutral genetic diversity, are of limited use in conservation of endangered species because of several factors: (1) they are sensitive to errors in estimating mutation rate, (2) they can be very sensitive to violations of assumptions of selective neutrality and no immigration, and (3) they assume equilibrium conditions that may take thousands or millions of generations to achieve (Avise et al. 1988; Waples 1991). Methods for estimating current N_e and evaluating bottlenecks are more promising for practical application and are discussed below.

Methods to Estimate Current N_e

Two methods (temporal changes in allele frequency and magnitude of gametic disequilibrium) have been used to estimate current or recent N_e in natural populations (Hill 1981; Nei and Tajima 1981; Waples 1989). A third method, based on heterozygote excess, has been proposed (Pudovkin et al. 1996), but it probably has too little power for application to most realistic problems involving endangered species. Both bias and precision can be a concern for indirect estimates of N_e. Biases arise from violation of the basic assumptions (random mating, random sampling, selective neutrality, no migration or immigration). Violations of strict selective neutrality are common but may introduce little bias unless the selection is strong; see Waples (1991) for discussion. As discussed above, sampling considerations are particularly important for organisms with overlapping generations. Estimates of N_e can also be seriously biased if they are applied to a subpopulation that has significant genetic linkages to other subpopulations within a larger metapopulation.

Precision is a concern for indirect estimates of N_e because they depend on evolutionary processes that are inherently stochastic and can only be predicted in a statistical sense. Only by averaging over a large number of replicate trajectories can a reliable signal be detected.

Fortunately, two factors mitigate the inherent lack of precision of methods based on random genetic processes. First, concerns for endangered species usually center not on how large N_e is but whether it is too small. Because the genetic signal detected by indirect estimates of N_e is proportional to $1/N_e$, the strength of the signal relative to stochastic noise is larger in small populations. As a consequence, although it may be difficult using indirect genetic methods alone to distinguish between $N_e = 500$ and $N_e = 5{,}000$ (both appearing to be "large" because the drift signal is weak), the power to detect situations in which N_e is low is generally much higher. For example, assume that one has two juvenile samples of 100 individuals each taken five generations apart from a single population, and that analysis of these samples provides genetic data for 20 diallelic loci. If the population's true N_e is 500, the temporal method will be expected to yield a wide confidence interval for its estimate of effective size (95% confidence interval [CI] = 117 to ∞, using formulas presented in Waples 1989). In contrast, if true N_e is only 50, then the expected confidence interval is much smaller (95% CI = 22 to 100) and provides evidence that the population's effective size is small enough to warrant conservation attention. Indirect genetic methods thus have some utility in monitoring species of conservation interest and may have reasonable power to detect low N_e before serious problems result.

Second, recent advances in molecular genetics permit large numbers of genetic markers to be brought to bear on problems of conservation interest. Each independent marker increases precision of indirect estimates of N_e. Although highly polymorphic microsatellites present some thorny statistical problems regarding sample sizes and the appropriate mutational model (Chakraborty 1992; O'Connell and Wright 1997), they potentially can be very useful in the temporal method for estimating N_e, since that method is less sensitive than the disequilibrium method to biases caused by low-frequency alleles. As demonstrated by Miller and Kapuscinski (1997), microsatellites can also be used to obtain historical estimates of N_e from archived samples.

Another way to deal with the limitations posed by lack of precision in indirect estimates of N_e is to integrate information across one or more dimensions. This can be done, for example, by combining the temporal and disequilibrium methods to obtain an overall estimate of N_e (as suggested by Waples 1991), or by combining data across years, populations, or species to reveal general patterns. Figure 8.2 illustrates results of applying both of these strategies to estimation of effective population size in Snake River spring/summer chinook salmon (*Oncorhynchus tshawytscha*), which have been listed as a threatened species under the U.S. Endangered Species Act since 1992 (Waples 1995). Fifteen natural

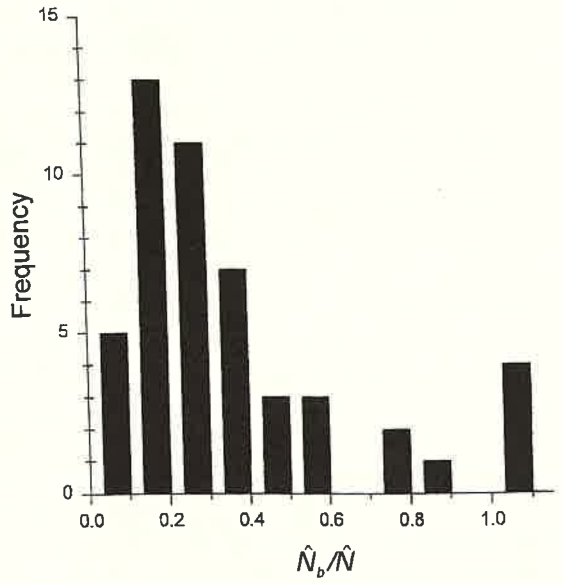

Fig. 8.2 Preliminary estimates of $N_e\!:\!N$ (ratio of effective to total population size) for yearly samples of Snake River chinook salmon. A combination of two indirect genetic methods (temporal changes in allele frequency and gametic disequilibrium) were used to estimate the effective number of breeders each year ($\hat{N}_b$), and this was compared to an estimate of the total number of spawners ($\hat{N}$). Allozyme data (Waples et al. 1993, and unpublished data) were taken for 33 polymorphic gene loci analyzed in collections from 15 natural populations sampled in three to six years over the period 1989–1994; harmonic mean sample size was 76 individuals. Each unit in the histogram represents an estimate for one year in one population.

populations were sampled three to six times over a six-year period and analyzed for 33 polymorphic allozyme loci (Waples et al. 1993). Preliminary estimates using the temporal and disequilibrium approaches were derived using methods of Hill (1981) and Waples (1990b) and combined (unweighted harmonic mean of the two estimates) to obtain a single estimate of the effective number of breeders ($\hat{N}_b$) each year. Counts of adult fish or expansion from counts of redds (nests) allowed an estimate of the ratio $\hat{N}_b/\hat{N}$ in each year.

Two general observations can be made from the results plotted in figure 8.2. First, although they use information for a large number of individuals and gene loci and two independent methods for estimating effective size, the yearly $\hat{N}_b/\hat{N}$ ratios still show a relatively high variance. For example, $\hat{N}_b/\hat{N}$ was >1 for four samples, which is unlikely to be true for natural populations. This means that individual $\hat{N}_e$ or $\hat{N}_e/\hat{N}$

7. SELECTION AND DRIFT IN METAPOPULATIONS

Hanski and Gaggiotti, by Michael C. Whitlock

7.1 INTRODUCTION

The distribution of a species over space has many interesting and important evolutionary consequences. All of the basic population genetic forces — drift, selection, migration, mutation, and recombination — act differently in a spatially structured population. Genetic drift can be enhanced or diminished relative to a panmictic population of the same total size. Selection can be more or less effective. Migration is impossible without a spatial context; the consequences of mutations tend to be lowered, and the effective recombination rate is reduced. This chapter reviews some of the effects of population structure, in particular focusing on how selection and drift are changed by the fact that species exist in space. This chapter takes a heuristic and largely nonmathematical look at these issues, trying to express intuitively some recent results in spatial population genetics. This chapter focuses on the dynamics of a single locus, whereas the topics of multilocus selection and quantitative genetics are discussed in Chapters 9, 11, and 12.

One very important summary statistic about the effects of population structure turns out to be one of the oldest: Wright's F_{ST}. There are several ways to define F_{ST}, but they all are standardized measures of the genetic differentiation among populations. Here let us define F_{ST} as the variance in allele frequencies across populations (V_{among}), standardized by the mean allele frequency ($\bar{p}$): $F_{ST} = V_{\text{among}}/\bar{p}(1 - \bar{p})$. F_{ST} has several key features that make

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it useful and interesting for the study of evolution in structured populations. First, F_{ST} has the same expectation for all neutral autosomal loci, although even neutral loci can vary substantially around this expectation. Moreover, this expectation is determined by the demographic properties of the species, such as migration rates, local population sizes, and geography F_{ST} can therefore encapsulate a lot of useful information about the demographic history of a species. F_{ST} tends to be larger if local populations are not connected by high rates of migration and/or if local population sizes are small. Finally, F_{ST} is readily measurable from easily obtained data on real populations, and there is already a lot of information about F_{ST} in nature.

There are other useful ways to view the information conveyed by F_{ST} beyond its use as a measure of genetic variance among populations. F_{ST} is also an indication of the amount of relatedness among individuals in the same demes. If F_{ST} is high, then individuals in the same demes are highly related to one another; in other words, they share many alleles. All else being equal, this also pertains to alleles within a diploid individual: if F_{ST} is high, individuals are more likely to be homozygous than would be predicted by Hardy–Weinberg frequencies. These various interpretations and implications of F_{ST} are useful in interpreting the results that follow. It turns out that because F_{ST} represents both the relatedness of individuals within a deme and the excess homozygosity, it is often the only extra parameter needed to describe how population structure changes the pace of evolution.

This chapter reviews the effects of spatial population structure on the amount of genetic drift and the response to selection. The greater part of the chapter then uses these results to discuss basic evolutionary genetic quantities in structured populations, such as the balance point between mutation and selection, mutation load, inbreeding depression, the probability of fixation of new alleles, and other basic quantities. It turns out that these fundamental evolutionary processes are sometimes strongly affected by even a weak population structure.

7.2 GENE FREQUENCY CHANGE IN METAPOPULATIONS

Gene frequency can change in a species by four mechanisms: selection, drift, introgression from other species, and mutation. This section reviews mathematical models that show the effect of population structure in the two more important of these forces, selection and drift.

Genetic Drift

Genetic drift is the change in allele frequency from one generation to the next caused by random sampling of alleles. Genetic drift is nondirectional, meaning that the average change due to drift is zero, but as the population size gets small, the actual change in allele frequency in any given generation can be relatively large.

Effective Population Size

The smaller the effective population size, the more random effects can become important. A key term here is "effective" — the actual amount of genetic drift in a population is determined not only by the actual number of individuals in the population, but also by other factors, such as the distribution of reproductive success in the species. The *effective size*, N_e, of a population is defined as the size of an ideal population, which would be expected to have the same amount of genetic drift as the population in question. An *ideal population* is one in which each of the alleles in the offspring generation have an equal and independent chance of having come from each of the parental alleles. An ideal population would function as though each parent allele contributes an equal and large number of copies to a gamete pool, and then offspring would be formed by random draws from this gamete pool.

Real populations are not ideal though for several reasons. First, and most importantly, in real populations, each individual is not expected to contribute equally to the next generation: some are very fit and have a high reproductive success, whereas others die before even reproducing. This variance in reproductive success tends to reduce the effective population size and therefore increase the rate of genetic drift. Second, in real populations, new individuals are not necessarily formed at random from the available alleles. For example, with inbreeding, individuals are formed with a higher than random chance of having similar alleles at homologous sites. Such inbreeding tends to decrease N_e because each individual effectively carries fewer copies of alleles. Finally, both variation in reproductive success and nonrandom mating can be inherited across generations, and the correlations in reproductive success which result can also affect N_e.

In structured populations, these three factors are even more important. When organisms live in different places, they are likely to experience different conditions, and therefore there is likely to be greater variance in reproductive success than in a single well-mixed population. Population structure causes a kind of inbreeding because locally mating individuals are likely to be related. Finally, if local conditions are correlated positively from one generation to the next, variance in reproductive success will also be correlated among parents and offspring, assuming limited migration.

The effective size of structured populations has been well reviewed by Wang and Caballero (1999).

The Island Model

Describing the effective size of subdivided populations has a long history, beginning with Sewall Wright in 1939. In this paper, Wright derives the effective population size of a species subdivided by an island model, finding it to be

$$N_{e,Island\ Model} = \frac{Nd}{1-F_{ST}}, \tag{7.1}$$

where N is the number of individuals in a deme, d is the number of demes, and F_{ST} is given, for large d at equilibrium, by

$$F_{ST,Island\ Model} \cong \frac{1}{4Nm+1}. \tag{7.2}$$

Here, m is the migration rate among demes. In the island model, each deme contributes a proportion m of its individuals to a migrant pool and then receives the same number of migrants chosen randomly from that migrant pool. It is important to note that these are not random proportions, but that each deme gives and receives exactly *Nm* individuals to and from the migrant pool each generation, and each deme consists of exactly *N* individuals. As a result, each deme contributes exactly equally to the next generation. This seemingly innocuous assumption turns out to have fairly important effects on interpreting results obtained from the island model.

If each deme contributes exactly equally to the next generation, then there is no variance in reproductive success among demes. We know from classical population genetics that a lower variance in reproductive success means higher N_e, and in fact this is the case with structured populations as well. Look again at Eq. (7.1). Give that F_{ST} is a quantity that ranges between 0 and 1, the N_e for an island model is always something greater than Nd, in other words greater than the total number of individuals in the metapopulation as a whole. This is because of the assumption that there is no variance among demes in reproductive success.

Relaxing Island Model Assumptions

A more general model of the effective size of structured populations has been derived (Whitlock and Barton, 1997). The general form of the equation for N_e in a species that has reached demographic equilibrium is given by

$$N_e = \frac{\overline{N}d}{\sum_i \frac{N_i w_i^2 (1-F_{ST,i})}{\overline{N}d} + 2\sum_i \sum_j \frac{w_i w_j N_i N_j \rho_{ij}}{\overline{N}d}} \qquad (7.3)$$

where N_e is shown to be a function of the local population sizes (N_i), the relative contributions of each deme (w_i), the F_{ST} predicted over a set of demes with demographic properties such as deme *i* ($F_{ST,i}$), and the correlation among demes of allelic identity (ρ_{ij}, which is defined similar to F_{ST}, but instead using covariance of pairs of demes). This equation makes few assumptions about the nature of the spatial subdivision among populations, allowing for variable migration rates over different population pairs, including isolation by distance, local changes in population size, including local extinction, and new population formation via colonization or fission.

While general, Eq. (7.3) is a bit unwieldy for intuitive use. To aid in explaining a few key features of this result, let us use a simplified version of this equation that makes a few more assumptions. If all demes have the same size as each other, but contribute unequally to the next generation via differential migration, then we can write *V* as the variance among demes in the expected reproductive success of individuals from that deme (i.e., $V = \mathrm{Var}[w_i]$). The effective population size is then

$$N_e = \frac{Nd}{(1+V)(1-F_{ST}) + 2NF_{ST}Vd/(d-1)} \qquad (7.4)$$

(Whitlock and Barton, 1997).

Let us examine two extremes using Eq. (7.4). If, as in the traditional island model, the variance among demes in reproductive success is zero, then Eq. (7.4) reduces to Eq. (7.1) [This is true not only for the island model, but for any model for which each deme is equal in size and contributes exactly equally to all other demes, provided that all demes are ultimately reachable by each deme via migration (Nagylaki, 1982). This includes classic stepping stone models.]

At the other extreme though, let us imagine that one deme is extremely successful and produces all of the offspring that fill all *d* of the demes. In this case, we would intuitively predict that the effective population size of the whole system should be the same as the size of the single successful deme, and Eq. (7.4), with appropriate modification, shows us that this is in fact the case. (In this extreme, the F_{ST} would be zero and the variance among demes of allelic reproductive success would be $d - 1$.) This extreme example tells us that N_e can be much smaller than the census size with population structure.

The truth obviously lies somewhere in the middle. It turns out that the boundary between whether population structure increases or decreases N_e is approximately whether or not demes have greater or less variance in reproductive success than would be expected by a Poisson distribution. In other words, if demic structure acts to increase variance in reproductive success relative to that expected by chance, N_e would be reduced. Only if the effects of population structure are to reduce the variance among demes in reproductive success to less than random would N_e be increased. This is perhaps biologically unlikely, yet this is the requirement for the results from the simple island model to hold qualitatively. In real species, the opposite is likely to be true: different demes are likely to have different amounts of resources, and different demes are likely to experience different levels of other ecological factors that might affect success, such as levels of parasitism, disease, predation, weather fluctuations, and other catastrophes. Realistic ecology implies higher than random variance among demes in reproductive success, and therefore the effective size of a subdivided species is likely to be reduced, perhaps substantially. The island model is not a good descriptor of typical population structure, for this and many other reasons (see Whitlock and McCauley, 1999).

Extinction and Colonization

It will be useful to consider a couple of specific cases that go beyond the simple island model. One aspect of population structure that has attracted some attention is the possibility of local extinction and recolonization (Slatkin, 1977; Maruyama and Kimura, 1980; Whitlock and Barton, 1997). The models considered in these papers are similar: the basic structure is like an island model, except that each deme has some chance per generation of going extinct independently of its genotype frequencies. An equal number of new demes are colonized, either in the same places recently vacated by the extinction events or in other vacant sites, by a small number of individuals. As a major, unrealistic simplification, each new deme then immediately grows back to *N* individuals, like all other demes.

With local extinction and recolonization, population structure contributes in an obvious way to the variance in reproductive success among demes. Even though this model is based on the island model, even a small rate of extinction is enough to cause the effective population size of the species to be reduced rather than increased. The main reason is perhaps obvious: with extinction and recolonization, some demes have zero reproductive success,

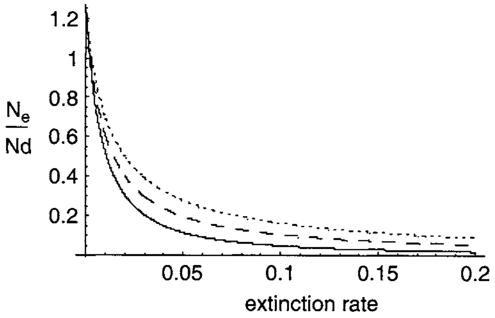

Fig. 7.1 The effective size (displayed as a proportion of the census size) of a metapopulation with local extinction and colonization. Here each deme has 100 individuals, and each new population is founded by four individuals. These colonists have a probability ϕ that they come from the same source population, with $\phi = 0$ in the dotted line, $\phi = 1/2$ in the dashed line, and $\phi = 1$ in the solid line. The migration rate was 0.01 in all examples. As the local extinction rate increases, the effective population size is reduced greatly.

whereas others — those that manage to survive and send colonists to start new demes — have a reproductive jackpot. Thus there is a great deal of variance among demes in reproductive success, which causes the effective size to be reduced. This reduction can be extreme (Fig. 7.1).

Sources and Sinks

In some species, some populations have large amounts of resources, whereas others have so few that they cannot replace themselves without migration (Pulliam, 1988; Dias, 1996; Holt and Gaines, 1992). These so-called "sources" and "sinks," respectively, cause the population dynamics to be different from the island model: demes do not contribute equally to the migrant pool, and therefore there is variance in reproductive success. If the quality of patches of resource is correlated positively over time, then the effect on N_e is even more extreme.

The effects of source–sink structure and correlation over time in patch suitability can be best seen by another extreme example. Imagine that a fraction of demes, say 20%, reside in productive source patches, and the other 80% of demes are what Bob Holt has called "black-hole" sinks — that is, these demes never contribute migrants to other demes and only persist because of migration from source populations. In this case, it is clear that only alleles in individuals in source populations can contribute to future generations and so the only individuals that matter to the evolution of the species are in the source populations. Therefore the N_e of the species should reflect only the effective size of the source populations alone. Thus the N_e of this species should be only 20% of what it would have been with equal migration.

To be more general, we can apply useful results from Nagylaki (1982), who showed that the N_e of a system of populations with a constant migration matrix could be described with the left eigenvector of that matrix. (This assumes a few technical details, such that all demes are ultimately reachable by migration from all other demes, even if it takes multiple steps.) Consider a case where migration is via a migrant pool so all emigrants from all demes are

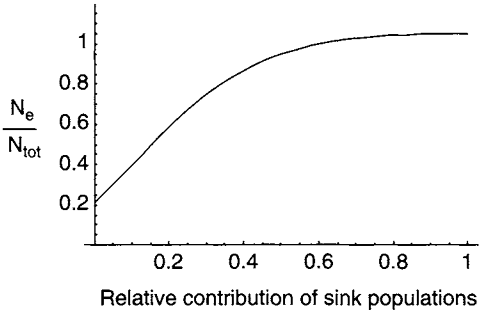

Fig. 7.2 The effective size of a species in which 20% of the demes are sources and the rest are sinks. The *x* axis varies the contribution of the sink populations, expressed as a fraction of the contribution of the sources. Here each 100 demes have 100 individuals, and each receives five immigrants per generation sampled from the migrant pool. As the contribution of sinks reaches zero, the effective size of the system is the same as an island model with only the 20 source populations.

mixed together and then moved on to recipient demes at random with respect to where they originate. Source demes contribute a large number to the migrant pool, whereas "sink" demes contribute a fraction of that number. For simplicity, each deme receives a constant number of immigrants from the migrant pool. This ensures that the F_{ST} among sources and among sinks are approximately equal. Figure 7.2 shows the effective size of these systems as a function of the relative contribution to the migrant pool by sinks. [To make the calculations in Fig. 7.2, Nagylaki's (1982) results were used, accounting for the fact that Nagylaki's definition of N_e differs from the usage here. Nagylaki calculates the N_e that would give the same amount of variance *within* a deme at mutation–migration–drift balance; in other work including in this chapter N_e predicts the amount of variance predicted by the average allele frequency of the species as a whole. The second of these two quantities can be found from the first by dividing by 1-F_{ST}. Details are given in Whitlock (2003).]

Note that with this form of source–sink structure, the effective size of the species is just the effective size of just the source populations when the sinks do not contribute to the future, and it reduces to the island model results when "sinks" contribute equally to sources.

Selection

With good reason, the study of selection in subdivided populations has, in the past, focused on the effects of spatially heterogeneous selection (e.g., Felsenstein, 1976). A great deal of important and interesting evolutionary biology results from variation in selection over space, but population structure, perhaps surprisingly, has a lot of interesting effects even on uniform selection. Arguably, most loci have approximately similar selection in different demes, even though the more obvious and more polymorphic cases may reflect spatially divergent selection. This chapter focuses on this special case in which genotypes have the same relative fitness in each population of the species.

When selection is uniform across populations, it becomes possible to follow the state of the metapopulation by following the mean allele frequency across all local populations, $\bar{q}$. Consider simple selection between two alleles at the same locus, with the fitnesses of the three genotypes given by $1 : 1 + h\,s : 1 + s$. In this case, the change in allele frequency due to selection within each population is a third-order function of q; therefore, to understand how the mean allele frequency would change by selection requires knowing the expected values of q, q^2, and q^3. Fortunately, under most circumstances the dynamics of the expected value of q^3 can be well enough predicted by an understanding of changes in the first two, which reduces the problem to understanding $\bar{q}$ and $E[q^2]$. The expected value of q^2 may seem like an exotic quantity to keep track of, but remember that the variance among demes is derived easily from $\bar{q}$ and $E[q^2]$, and F_{ST} is derived easily from the variance in allele frequency and $\bar{q}$. Thus, a very good understanding of the change in allele frequency across a metapopulation can be obtained by knowing $\bar{q}$ and F_{ST}. Moreover, as long as the selection coefficient is not much greater than the rate of migration into a deme, the F_{ST} predicted from neutral theory works extremely well to predict allele frequency change in structured populations. These conclusions are derived and discussed in greater detail in Whitlock (2002).

[One technical note is necessary: when calculating these quantities, it is essential to weight each individual equally. The usual calculations of F_{ST} weight each local population equally, independent of size. Most models of population structure have assumed equal deme sizes, and therefore they predict the right quantity. Most empirical measures do not measure the appropriate F_{ST} exactly. This may be an important issue in some cases; for example, if smaller demes have higher extinction rates, then the subset of the population with the highest F_{ST}'s would properly be weighted least.]

It will help to look at the equation for the change in mean allele frequency due to selection. From Whitlock (2002), we get

$$\Delta_s\bar{q} \cong \bar{p}\,\bar{q}\,s(1 - r)(F_{ST} + (1 - F_{ST})(h(1 - 2\bar{q}) + \bar{q})) \qquad (7.5)$$

where r is the relatedness of two random individuals competing for resources.

Let us consider the various parts of this equation in turn. First, we see that the response to selection is a function of the mean allele frequencies and the strength of selection $\bar{p}\,\bar{q}\,s$. These are the classic terms that would appear even without population structure: the response to selection is proportional to the allelic variance $\bar{p}\,\bar{q}$ and to the strength of selection.

Next, we find that the response to selection is proportional to one minus the relatedness of competing individuals. This last phrase deserves some explanation. Consider a classic dichotomy introduced by Dempster (1955; see also Christensen, 1975) between local and global competition for resources, i.e., soft versus hard selection. With soft selection, each deme contributes a number of individuals to the next generation (whether via resident individuals or migrants) *independent* of the genotypes of the deme. With hard selection, each deme contributes to the next generation in proportion to its mean fitness determined by its genotype distribution. Under soft selection, individuals are competing locally for resources, and therefore there is competition between relatives. The mean relatedness of individuals from the same deme (without inbreeding within demes) is given by $r \equiv 2F_{ST}/(1 + F_{ST})$. At the other extreme, under hard selection, there is no local competition for resources, and the relatedness of competing individuals is zero. Putting these equations into Eq. (7.5), we find that hard selection is always more effective than soft selection in changing allele frequency. With local competition for resources, if an individual does well because of having a good genotype, it will, through competition, reduce the resources available to other individuals in the same deme. With population structure, these other local individuals are likely to share alleles. Therefore the event that would have boosted the number of copies of this good allele in the next generation (the first individual doing well) is partially counterbalanced by competition against the same genotypes.

Note that for the relatedness term, increasing population structure tends to weaken the response to selection. With soft selection, increasing F_{ST} results in greater relatedness and therefore a lower response to selection, *all else being equal.*

Finally, we see in the last term $(F_{ST} + (1 - F_{ST})(h(1 - 2\bar{q}) + \bar{q}))$ a reflection of the effects of increasing homozygosity on the response to selection in structured populations. As F_{ST} increases, so does the proportion of individuals that are homozygous, even for the same mean allele frequency. Greater homozygosity, for the same q, increases the magnitude of the response to selection. This increase is particularly important if $\bar{q}$ is small and the allele is at least partially recessive ($h < 1/2$). In these cases, with panmixia, most alleles appear as heterozygotes and selection therefore cannot discriminate the recessive alleles. As F_{ST} increases, most of the selection is experienced by alleles in the homozygous state, where the alleles have relatively large effects. Thus, in opposition to the effect of relatedness given earlier through its effects on increasing homozygosity, population structure tends to *increase* the response to selection. For nearly recessive alleles, this boost can be extremely large.

This effect of excess homozygosity has been described much earlier with respect to inbreeding within populations (Ohta and Cockerham, 1974). In fact, with hard selection, there is no distinction between the effects of inbreeding due to population structure and that due to local inbreeding; they enter the response to selection equations in exactly the same way. With soft selection, however, the extra effects of competition among relatives change the relationship between F and response to selection.

The balance between these two effects (competition among relatives and homozygosity) depends on the details. With hard selection, there is no effect of relatedness, and population structure therefore always increases the rate of response to uniform selection. With soft selection, response to selection can be either increased or decreased depending on the dominance coefficient of the locus under selection and F_{ST}. The following section shows examples of both. The effects of population structure on even uniform selection are quite complicated.

With this selection equation available, a variety of results on basic selection become easy to derive. The next few sections of this chapter show some of these results.

7.3 MAINTENANCE OF GENETIC VARIATION IN SUBDIVIDED POPULATIONS

One of the oldest questions in population genetics is "what forces are most important in maintaining genetic variation ?" Population subdivision can affect the maintenance of genetic variation in a variety of ways. This section reviews a few of these briefly, focusing on the case of spatially uniform selection.

Mutation–Selection Balance

Estimates have shown that the genomic rate of mutation to deleterious alleles is reasonably high, ranging from a few per thousand individuals to much greater than one per each new individual (Lynch et al., 1999; Keightley and Eyre-Walker, 2000). Although natural selection operates to reduce the frequency of these deleterious alleles, they are not immediately eliminated completely. As a result, some deleterious alleles are always segregating in populations at a frequency determined by the balance between mutation and selection. Some have argued that levels of standing genetic variance observed in natural populations could be explained largely by this mutation–selection balance.

Mutation is likely not much affected by population structure, but the previous section showed that the efficacy of selection can be affected greatly by subdivision. At mutation–selection balance, the deleterious allele is likely to be rare, which simplifies Eq. (7.5) to

$$\Delta_s\bar{q} \cong \bar{q}s(1 - r)(F_{ST} + (1 - F_{ST})h) \tag{7.6}$$

The equilibrium allele frequency at mutation–selection balance is then given by

$$\hat{\bar{q}} \cong \frac{\mu}{-s(1 - r)(F_{ST} + (1 - F_{ST})h)} \tag{7.7}$$

(Remember that in the way we have defined fitness in this chapter, a deleterious allele has $s < 0$.) For recessive alleles in particular, the frequency of deleterious alleles at mutation–selection balance is much reduced with population structure due to the more effective selection against homozygotes. See Fig. 7.3, for some examples. As a result, the amount of variation maintained by mutation selection balance can be reduced greatly in large metapopulations, depending on the distribution of dominance coefficients. Most current estimates of the mean dominance coefficient of mildly deleterious alleles give answers around $h = 0.1$ (Houle et al., 1997; García-Dorado and Caballero, 2000; Peters et al., 2003), so the reduction in variance can be substantial even for relatively small F_{ST} values.

The predominant model of the genetic mechanism for inbreeding depression claims that inbreeding depression results from deleterious recessive alleles segregating in populations at mutation–selection balance. With population structure, the reduction in mean deleterious allele frequency

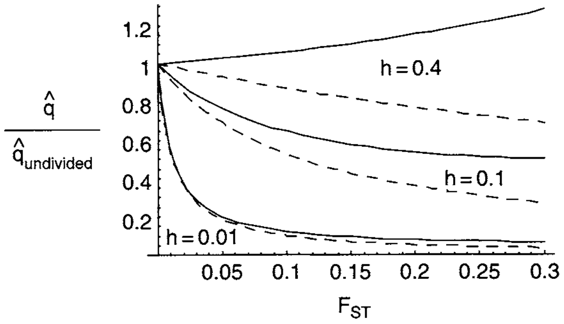

Fig. 7.3 The equilibrium value of the frequency of a deleterious allele can be changed substantially by population structure. Here solid lines indicate pure soft selection and dashed lines indicate pure hard selection. With very recessive alleles, the equilibrium allele frequency is reduced greatly relative to the case in an undivided population (where $\hat{q} \cong -\mu/hs$). Parameter values used for these calculations were $s = -0.1$, $\mu = 10^{-6}$, and the three lines correspond to $h = 0.4$, 0.1, and 0.01 from top to bottom. From Whitlock (2002).

results in a potentially large reduction in the amount of inbreeding depression predicted for a species, even at relatively low F_{ST} values (see Whitlock, 2002).

Balancing Selection

Balancing selection, by definition, occurs when selection acts to increase the frequencies of rare alleles. This can happen with overdominance, negative frequency-dependent selection (where rare alleles are favored because they are rare), or by spatially heterogeneous selection. Each of these are affected by the spatial population structure.

Overdominance

With overdominance, the heterozygote is the most fit genotype. For this section only, let us redefine the fitnesses of the three genotype **AA**, **Aa**, and **aa** as 1-s : 1 : 1-t, such that the fitness of the two homozygote genotypes is reduced by a factor s or t. With overdominance in a large randomly mating population, there is an intermediate equilibrium allele frequency that stably maintains variation in the population as a result of the heterozygote being selected for whenever one or the other of the two alleles becomes too rare.

In structured populations, the extra homozygosity caused by population structure can change the dynamics of the maintenance of variance. Nonrandom mating causes the marginal fitnesses of the two alleles to be determined more by their homozygous effects and less by their effects in heterozygotes. As a result, if the two homozygotes fitnesses are not equal ($s \neq t$), then the allele associated with the fitter homozygote will have a higher frequency than expected under random mating. Mathematically, that frequency is given by

$$\hat{q} \cong \frac{s - tF_{ST}}{(s + t)(1 - F_{ST})}, \tag{7.8}$$

so long as this value is between zero and one, which it need not be (Whitlock, 2002). If F_{ST} is large enough, the expected equilibrium leaves the population fixed for the allele with the most fit homozygote. Thus population structure tends to reduce the amount of variation maintained by overdominance.

Frequency Dependence

In some cases, the fitness function changes with the frequency of alleles in the population or species; this is called frequency-dependent selection. If selection displays negative frequency dependence, then alleles are more fit when rare than when the same allele is common. In this case, selection can act to maintain variation in a population because as alleles get rare (as they would on the path to being lost from the population), their fitness increases and therefore their frequency climbs again.

One of the most studied examples of negative frequency dependence is the self-incompatibility (SI) alleles common to many species of plants. With SI, pollen (or, in some cases, its parent plant) that shares alleles with the maternal plant are not allowed to fertilize ovules. These processes presumably evolved as a mechanism to prevent self-fertilization, but they also prevent unrelated individuals that share alleles from mating. As a result, rare alleles at the SI locus have higher fitness because they are able to mate with more other individuals in the population. All else being equal, the system always favors new alleles being introduced into the population, but real species have limited numbers of SI alleles because of loss due to genetic drift. The smaller the effective population size, the fewer SI alleles maintained at equilibrium.

With population structure, one might imagine that different alleles might be maintained in different populations, thereby increasing the total diversity in the species as a whole. It turns out that this is true for species with very low migration rates between demes, but with realistic, intermediate levels of migration the total number of SI alleles maintained is slightly lower than would be expected with panmixia (Schierup, 1998; Schierup et al., 2000; Muirhead, 2001).

Heterogeneous Selection

It has been known since at least the 1950s that spatially varying selection can maintain genetic variation, especially if there is soft selection (Levene, 1954; Dempster, 1955). The conditions for this are narrower than was commonly thought (Maynard Smith and Hoekstra, 1980), requiring strong, relatively symmetric selection. Felsenstein (1976) and Hedrick (1986; Hedrick et al., 1976) reviewed the theory and empirical evidence for and against the maintenance of genetic variance by heterogeneous selection.

A different form of heterogeneous selection can emerge in populations in which there is already a lot of genetic differentiation among populations. In these cases, epistatic interactions between loci can cause different alleles to be favored locally even when the underlying function describing the relationship between fitness and genotype is uniform across space (see Chapters 9 and 11). This sort of heterogeneous selection depends on there being selectively and epistatically different alleles in different local populations, which becomes important only under extremely restricted gene flow or extreme drift.

One special case of epistasis that may be quite common is that generated on approximately additively interacting alleles that form a phenotype under stabilizing selection. Stabilizing selection causes the fitness effects of alleles to vary depending on whether the sum of the effects of all other alleles in the individual add up to a value above or below the optimum for the trait; hence with stabilizing selection, a population near its optimum will have mainly epistatic variance for fitness associated with that trait (Whitlock et al., 1995). Barton and Whitlock (1997) have shown that with uniform stabilizing selection and low migration, the amount of genetic variance for a trait that can be maintained can be increased substantially as a result of this epistasis. However, this is only likely to be important in species with very high values of F_{ST}, in the range of $F_{ST} > \sim 0.2$.

7.4 ADAPTATION IN SUBDIVIDED POPULATIONS

Population structure can affect the pace of adaptive evolution. We have already discussed the conditions under which the response to selection is increased or decreased with population structure. The subdivision also allows novel patterns of adaptation, such as local adaptation (see Barton, 2001), shifting balance evolution [Wright (1931), but see Coyne et al. (1999) and Whitlock and Phillips (2000)], and more rapid evolution with epistatic interactions (Bryant et al., 1986; Goodnight, 1988; see Chapter 9). More fundamentally though, population structure strongly affects the pace of evolution even for those alleles that are uniformly selected without any complicating interactions with other loci. This section reviews the effects of population structure on the probability of fixation of new mutations.

Probability of Fixation

One of the most remarkable results in population genetics has to be Haldane's (1927) result that a new beneficial allele with heterozygous benefit of hs has only about $2hs$ chance of ultimate fixation. Haldane assumed that the species in question was ideal (i.e., its census size equaled its effective size) and undivided. Even in an infinite population, if a new allele is introduced as only a single copy, the fate of that allele is partially determined by stochastic changes in the numbers of copies of the allele left in each generation. It turns out that by introducing an allele as a single copy (as a rare mutation would likely do), even alleles with moderate selective advantage are more likely to be lost stochastically from the population than fix. Kimura (1964; see also Crow and Kimura, 1970) modified this result to allow for nonideal populations and allowed arbitrary dominance for deleterious alleles as well. He found that the probability of fixation of a beneficial allele is given approximately by $2hsN_e/N$, where N is the census size of the population.

In 1970, Maruyama achieved the first results on the probability of fixation in subdivided populations. He showed that in an island model, the probability of fixation for an additively acting allele was simply s. (For additive alleles, $h = 1/2$, so this result is equivalent to the $2hs$ of Haldane.) Maruyama (1974) and others (Slatkin, 1981; Nagylaki, 1982) extended this result to deal with any model such that each deme contributes exactly equally to the next generation; the probability of fixation with population structure with this restriction remained s. This was viewed by some as an invariant result of population structure; the claim was made that population structure therefore did not affect the probability of fixation of beneficial alleles. However, this conclusion was premature because other models of population structure are possible (and even more reasonable than the island model) and because the effects of dominance were not properly accounted for. The first demonstration that this was not true was a model of extinction and two specific types of recolonization by Barton (1993). In these cases, the probability of fixation was much reduced by population structure relative to the panmictic case.

The probability of fixation in a more general model of structured populations has been found (Whitlock, 2003). Based on Kimura's diffusion equations, this work shows that the probability of fixation can be derived from the equations for drift and response to selection presented earlier in this chapter. Moreover, as long as the strength of selection is lower than the typical immigration rate, the F_{ST} expected for neutral loci can be used in these equations, which expands their usefulness greatly. For dominance coefficients differing from 1/2, the equations cannot be solved directly, but the answers can be obtained with numerical integration. In the interests of space, this chapter will not review the mathematics of the general equations, but will focus on the additive case, as well as an approximation that works very well for beneficial alleles even with arbitrary dominance. More details can be found in Whitlock (2003).

For additive alleles, such that $h = 1/2$, the probability of fixation in structured populations is given by

$$u[q]=\frac{1-\exp[-2s(1-F_{ST})N_e q]}{1-\exp[-2s(1-F_{ST})N_e]} \tag{7.9}$$

for soft selection and

$$u[q]=\frac{1-\exp[-2s(1+F_{ST})N_e q]}{1-\exp[-2s(1+F_{ST})N_e]} \tag{7.10}$$

for hard selection, where q is the initial allele frequency of the allele in the metapopulation. If the population starts with a single copy of the new allele, then $q = 1/2N_{tot}$, where N_{tot} is the total size of the metapopulation. These equations look fearsome, but in fact they are quite similar to the equations for the panmictic case derived by Kimura (1964). There are two differences. First, the N_e here is the effective size of a subdivided population, given by Eq. (7.3). Second, the strength of selection s is now modified by a term involving F_{ST}, which reflects the change in the efficacy of selection from population structure.

For beneficial alleles, we can write a simple equation for the probability of fixation of a new mutant, even with arbitrary dominance:

$$u \cong 2s(1-r)(F_{ST}+(1-F_{ST})h)N_e/N_{tot}. \tag{7.11}$$

Here it is possible to see that this result builds directly on Kimura's. As F_{ST} goes to zero, this approaches the $2hsN_e/N$ given earlier.

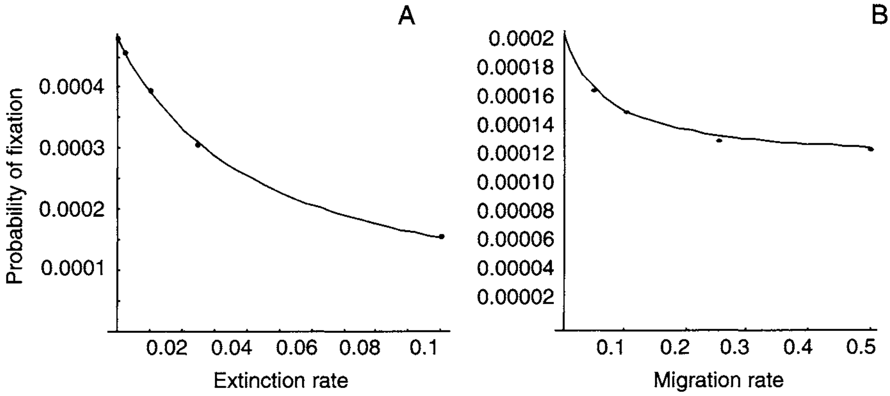

Fig. 7.4 Examples of the fixation probabilities of nearly recessive beneficial alleles ($h = 0.01$) with soft selection. (A) Extinction and recolonization. In this example, the migration rate between populations was 0.05, colonization occurred by four individuals with a probability of common origin of 1/2, $s = 0.002$, and there were 100 demes with 100 diploid individuals each. (Each point represents results from 10^7 simulations, so the standard error ranges from 6.9×10^{-6} on the left to 3.9×10^{-6} on the right.) As the extinction rate increases, the effective population size of the metapopulation decreases, and therefore so does the probability of fixation. (B) A one-dimensional stepping-stone model. With a stepping-stone model, F_{ST} (and therefore N_e) increases as the migration rate drops so the probability of fixation also increases with lower migration. This is particularly true with recessive alleles, which are expressed often in the homozygous state with the concomitant increase in the efficacy of selection. (There are 100 demes with 100 diploid individuals each, $s = 0.0002$ and dots represent 10^6 simulations each.)

These results have been tested by simulation in a wide variety of models of population structure, including the island model, extinction–recolonization, stepping-stone models, and source–sink models. They work remarkably well (see Figs 7.4 and 7.5).

The probability of fixation of beneficial alleles tends to be much reduced with population structure. This is mainly a result of the fact that the effective

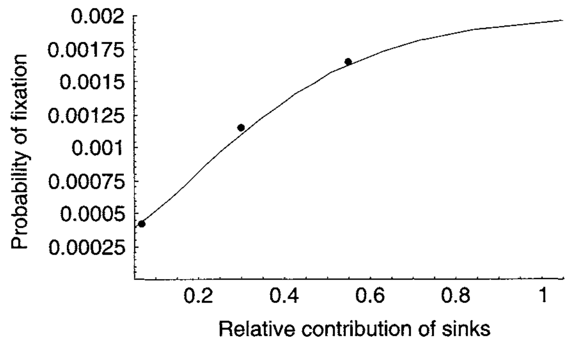

Fig. 7.5 The probability of fixation in a source–sink model. Here there are 100 demes, 20 of which are "sources" and the rest are "sinks". Each deme has 100 individuals, and the immigration rate to the sources is 0.2, whereas it is 0.25 in sinks. Demes exchange migrants by a modified island model, where each sink's contribution to the migrant pool is a fraction of that of each source. As this asymmetry increases, the effective population size is reduced and the probability of fixation of beneficial alleles drops. For these examples, $s = 0.002$ and $h = 1/2$, and dots represent results of 10^7 simulations.

population size is reduced in most models of population structure. The probability of fixation can be increased for some loci, especially for nearly recessive alleles that can be expressed more strongly in structured populations because of increased homozygosity.

Let us return to the island model. As mentioned earlier, the island model is an extreme description of population structure because it allows no variance among populations in reproductive success. For additive alleles, Maruyama and successors found the probability of fixation to be simply s in an island model, the same as in an unstructured population. The more general model predicts that the probability of fixation should be $s\ (1 - F_{ST})\ N_e/N_{tot}$ (because the island model in its basic form as used by Maruyama is also a soft selection model). Remember that the island model has the unusual property of having a larger N_e than census size: $N_e = N_{tot}/(1 - F_{ST})$. Putting this N_e into the probability of fixation equation simplifies it to simply s. The results are consistent; what is more important is that the island model is unrealistic and extreme. Most real species will have $N_e < N_{tot}$, and so most will have lower probabilities of fixation of beneficial alleles than predicted by Maruyama's formula. Probabilities of fixation are not invariant with respect to population subdivision.

Relaxing the assumption of uniform selection has been investigated using the island model by a variety of authors (Barton, 1987; Tachida and Iizuka, 1991; Gavrilets and Gibson, 2002). Population structure tends to increase the probability of fixation relative to that expected by the mean fitness of the alleles across demes. It is not yet known what effect heterogeneous selection would have with a more realistic model of subdivision.

Population structure also substantially affects the time taken for fixation of new alleles (Whitlock, 2003).

7.5 GENETIC LOAD IN SUBDIVIDED POPULATIONS

Genetic load is the reduction in the mean fitness of a population relative to an optimal genotype caused by some particular factor, such as deleterious mutation, genetic drift, and segregation (Crow, 1993). Load is sometimes strongly affected by population structure, as reviewed in this section.

Mutation Load

Mutation load is the reduction in mean fitness caused by recurrent deleterious mutations in a population. Mutation load is usually calculated at mutation–selection balance: that is, it is the mean reduction in fitness associated with an allele frequency predicted by the equilibrium between mutation and selection. In panmictic populations, the load associated with an allele that is not completely recessive is $L = 2\mu$ (where μ is the mutation rate from wild type to deleterious allele; remarkably, this is not a function of the strength of selection against the deleterious allele).

With population structure, load equations become more complicated (Whitlock, 2002):

$$L \cong -(2h(1-F_{ST})+F_{ST})s\hat{q} \tag{7.12}$$

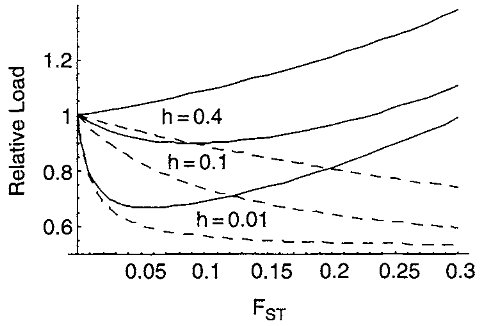

Fig. 7.6 The mutation load in a metapopulation relative to the load at a similar locus in an undivided population (~2μ). For the values of F_{ST} likely to be found within species and relatively small values of the dominance coefficient *h*, the mutation load can be reduced substantially in a subdivided population. Solid lines show pure soft selection, whereas dashed lines correspond to pure hard selection. Parameters for this example are $s = -0.1$, $\mu = 10^{-6}$, and the three pairs of curves correspond to $h = 0.4$, 0.1, and 0.01 from top to bottom.

where the value of $\hat{q}$ is given by Eq. (7.7). Note that *s* will cancel out when this substitution for $\hat{q}$ is made, but load remains a function of the dominance coefficient, unlike the panmictic case. Figure 7.6 shows the change in load as a function of population subdivision. Load is always reduced with hard selection, but with soft selection, load is increased for high values of F_{ST} and near additivity. With nearly recessive alleles, the reduction in load can be nearly 50%.

Segregation Load

Segregation load is the reduction in fitness caused by the inability of a population to be composed entirely of heterozygotes even when these genotypes are the most fit. As such, segregation load requires overdominance. With population structure, there are even fewer heterozygotes in a species than under Hardy–Weinberg conditions so the segregation load would be more pronounced. Using the same notation as in the overdominance section given earlier, the segregation load is expected to be

$$L = \frac{(1 + F_{ST})st}{s + t}, \tag{7.13}$$

which reduces to the segregation load in a panmictic population when $F_{ST} = 0$ (Crow, 1958). Therefore, the segregation load is $(1 + F_{ST})$ times as great in a subdivided population as in an undivided one, as expected by the increased number of homozygotes.

Drift Load

Drift load is the reduction in fitness caused by drift changing allele frequencies away from those favored by selection. An extreme form of drift load results from fixation of deleterious alleles by drift. Drift load has received a lot of attention in the last several years because of the possible mutational meltdown of small endangered populations (Lande, 1994; Lynch et al., 1995a,b).

The rate that deleterious alleles accumulate in a species is a function of the efficacy of selection and of the effective population size; the smaller these two values are the faster drift load will accumulate. We have seen that selection is often more effective in structured populations (although not always), but more importantly, the effective population size tends to be reduced by structure. Because the latter of these two effects turns out numerically to be more important, in most cases, population structure increases the rate of accumulation of deleterious alleles (Higgins and Lynch, 2001; Whitlock, 2003). This is most pronounced in cases with large variance in reproductive success among demes, such as with extinction and recolonization or source–sink models. Figure 7.7 shows that the change in the probability of fixation of deleterious alleles can be reasonably large (two- to three fold), although perhaps in most cases the change is less than a doubling.

Migration Load

If the local population in a deme is well adapted to local conditions and if migrants to this population come from populations adapted to other conditions, then the alleles that come into the population by migration are likely to be poorly adapted to local conditions. The reduction in mean fitness that results is called *migration load.* Migration load increases with increasing differences in the selection coefficients among populations and with migration rate. In some species, migration load is likely to be the most important type of genetic load. Migration load may be key in determining the range limits of species because migration from the species center may prohibit further local adaptation at the margins (Mayr, 1963; Kirkpatrick and Barton, 1997).

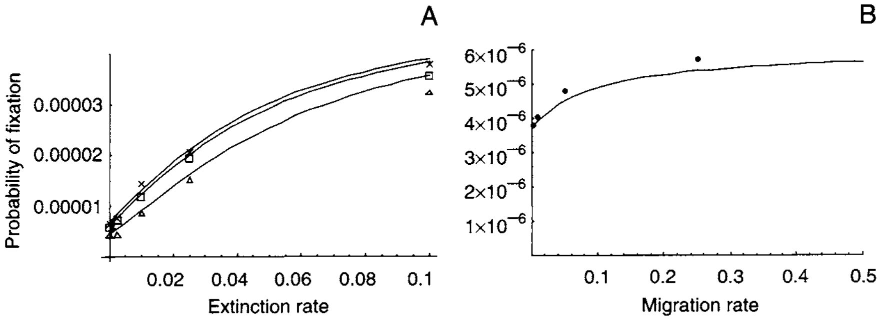

Fig. 7.7 The probability of fixation of deleterious alleles with (A) extinction and colonization or (B) a one-dimensional stepping stone model. (A) The three lines plot, from bottom to top, the predicted probability of fixation for alleles with dominance coefficients of 0.5, 0.1, and 0.01, respectively. The symbols mark simulation results over a minimum of 10^7 replicates each, with the three dominance coefficients represented by triangles, squares, and crosses, respectively. Other parameters used for these examples were $s = -0.0002$, $m = 0.1$, 100 demes of 100 diploid individuals each, and colonization by four individuals with a probability of common origin equal to 1/2. The probability of fixation is increased substantially by the reduction in N_e that accompanies extinction dynamics. (B) The parameters in these examples were $h = 0.01$, $s = -0.0002$ with 100 demes of 100 diploid individuals. Points represent the results of 10^8 simulations.

Local Genetic Load and the Consequences of Migration

In subdivided populations, weakly deleterious alleles can rise by drift to high frequencies within local populations, even if selection is effective at keeping their overall frequency low throughout the species. Crow (1948) proposed that this could be the mechanism for the commonly observed pattern of heterosis, the increase in fitness often observed in hybrids between different populations. We examined this hypothesis using Wright's distribution of allele frequencies for the island model (Whitlock et al., 2000; Ives and Whitlock, 2002) and found that Crow's hypothesis was extremely credible. We referred to the reduction in mean fitness caused by this local increase in the frequency of deleterious alleles *local drift load* and showed that reasonably large values of heterosis were consistent with what is known about mutation rates and population structure. These results have been extended by Morgan (2002) and Glémin (2003). Morgan (2002) showed that

$$\frac{\bar{w}_{hybrid}}{\bar{w}_{local}} = \left(\frac{(1-hs)^2}{1-s}\right)^{nV_{among}} \tag{7.14}$$

where V_{among} is the variance among demes in allele frequency as defined and n is the number of loci. With this we can write a prediction for the heterosis in terms of F_{ST} and $\bar{q}$:

$$heterosis = \frac{\bar{w}_{hybrid}}{\bar{w}_{local}} - 1 = \left(\frac{(1-hs)^2}{1-s}\right)^{nF_{ST}\bar{q}\bar{p}} - 1 \tag{7.15}$$

If the metapopulation itself is relatively large and at equilibrium, then $\bar{p} \cong 1$ and $\bar{q}$ is approximately $\hat{\bar{q}}$ from Eq. (7.7).

Heterosis has an interesting biological consequence. If offspring formed by crosses between demes have selective advantage, then the offspring of migrants will have increased fitness (Ingvarsson and Whitlock, 2000; Morgan, 2002). Thus the genetic effects of migration will be increased relative to the actual observed migration rate. The *effective migration rate* for a neutral locus is approximately

$$m_e = m\, e^{heterosis/\tilde{r}}, \tag{7.16}$$

where $\tilde{r}$ is the harmonic mean recombination rate between the neutral locus and all selected loci (Ingvarsson and Whitlock, 2000). For low values of F_{ST}, the magnification of the effective rate of migration can be severalfold. This can be counterbalanced or reversed by sufficient local adaptation or strong differences among populations in epistatic interactions.

Load in Subdivided Populations, a Summary

Several types of load are affected by population structure. Mutation load tends to decline at equilibrium with structure, and migration load is lowered with lower migration rates, whereas drift load, segregation load, and local drift load tend to increase. Because these different genetic loads are cumulative, the mean fitness of the population with three different types of genetic load is approximately $(1 - L_1)(1 - L_2)(1 - L_3)$. If the loads are small (they are not in general expected to be) then the overall load is approximated by the sum over the types of load. Whether population structure increases or decreases mean fitness on average depends on a large number of circumstances. If habitat conditions vary strongly, then population structure allows local adaptation (in other words, reducing migration load) and this effect can be paramount. However, if migration rates become too small and local population size is low, then local drift load will become very important and essentially the population will suffer from inbreeding depression. Species-level drift load could become important if there is a lot of variance among demes in reproductive success and if the total census size of the species was small (so that the effective size was low), but is likely not very important if the effective size of the species is over about 10,000. Mutation load may be reduced by population structure (at equilibrium), but not by more than a half. In some species, for example, those in which the genomic deleterious mutation rate is high, this could be a major effect; but for species with lower mutation rates, this could be a trivial effect. The balance of the effects of these processes will depend on the specifics of the species.

7.6 CONCLUSIONS AND INCONCLUSIONS

The course of evolution is changed quantitatively and qualitatively by the subdivision of populations over space. All of the population genetic processes that act in unstructured populations are affected, sometimes substantially, and some kinds of evolution are only possible with structured populations. This chapter focused on the former: quantitative changes in evolutionary rates from population subdivision. Even with uniform selection, the rate of genetic drift and the response to selection are changed substantially.

For some of the quantities described in this chapter (e.g., N_e, the probability of fixation of beneficial alleles), results have already been found for a special case of population structure: the island model. The island model is the oldest in population genetics, and it is rightfully the first to turn to when considering new problems because of its simplicity. Unfortunately, the very simplicity that make it appealing also makes it an aberration. The island model assumes that all demes are equal; not only do all demes have the same population size and migration and immigration rates, but more importantly, it implicitly assumes that all demes contribute exactly equally to the next generation. Clearly these conditions do not apply to most (or even all) natural populations, but this would not matter if these assumptions had no effect on our evolutionary predictions. Unfortunately, this assumption of equal reproductive success has a qualitative effect on our predictions, especially for questions that involve effective size. In this subtle but key respect, the island model is an extreme model, and some of the predictions made from the island model are extreme as a result.

Fortunately, it is possible to derive theory that predicts the necessary parameters for other models of population structure. The last couple of decades have seen a lot of development of models, including isolation by distance, local extinction, population size change, variable migration rates, and asymmetric migration. Even more fortunately, the results described in this chapter show that, at least for weak selection, most of the effects of population structure can be described in a few summary statistics, especially F_{ST} and N_e. This is extremely useful because we know a lot about how F_{ST} is changed by various demographic processes and we have the theory to predict the effective size for a broad class of models. F_{ST} in particular has been very well studied, with many empirical studies devoted to measuring it in a wide variety of species and a large number of theoretical models. These include extinction and recolonization (Wade and McCauley, 1988; Whitlock and McCauley, 1990), population fission and fusion (Whitlock, 1994), source–sink models (Gaggiotti, 1996), and stepping-stone models (Kimura and Weiss, 1964). In all of these cases, F_{ST} differs significantly from that predicted by the island model, and in most the effective population size is also substantially different (and usually much less than the census size). Moreover, it is usually straightforward to calculate F_{ST} even for a novel system.

As an aside, the reason that F_{ST} has been measured empirically so often has little to do with its importance to predict the effects of population structure on selection or drift. F_{ST} has been measured usually because of the false hope that it could be used to estimate the number of migrants coming into a population per generation (Whitlock and McCauley, 1999). It is fortunate then that this effort has not been wasted, and it is important not to throw the evolutionary baby out with the estimator bathwater. F_{ST} is an excellent descriptor of the nature of population structure and should be calculated in genetic studies of metapopulations. Unfortunately, the same cannot be said for its properties as an estimator of dispersal.

There are many unresolved questions on evolution on space. We have made some progress in understanding the effects of population structure on response to uniform selection, but we have not yet made similar progress with the heterogeneous selection case. All of the results considered here deal with discrete populations in which organisms are grouped into demes with the space between them empty. Most of the questions presented here have not solved for the spatial case in which individuals are spread continuously over space, a much more challenging topic. These results all assume weak selection, yet some of the most interesting cases involve selection coefficients stronger than migration rates.

We also need many more empirical studies on these topics. This chapter has not reviewed the empirical literature at all, but most of the theory presented here remains untested experimentally. Furthermore, we need better measures of some key parameters. The dominance coefficient has a tendency to cancel out of panmictic calculations, but this is not true for evolution in structured populations; we have very few estimates of the distribution of dominance coefficients. We desperately need more empirical studies of the effective size of structured populations. We also need to develop individual-weighted estimators of F_{ST}, as has been shown to be required by this theory.

The subdivision of a species over space can affect its evolution strongly and in a variety of ways. Because most species in nature are subdivided over space, it behooves us to understand this nearly ubiquitous feature of the natural world.

Conservation Strategy: The Effects of Fragmentation on Extinction
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CONSERVATION STRATEGY: THE EFFECTS OF FRAGMENTATION ON EXTINCTION

A recurring topic in the application of population biology theory to conservation is whether a single large nature reserve or several small reserves will protect more species (referred to by the acronym SLOSS; e.g., Simberloff and Abele 1976; Gilpin and Diamond 1980; Higgs and Usher 1980; Higgs 1981; Cole 1981). One of a variety of approaches to this problem recently explored by Simberloff and Abele (1982) considers how subdividing a population affects its probability of extinction or, more precisely, the extinction of newly created, smaller subpopulations. Simberloff and Abele discuss additional considerations bearing on SLOSS, but they only draw specific conclusions using this approach. They conclude that the probability of population extinction is not necessarily greater in several small reserves than in a single large reserve, and they also imply that fragmentation of a single large reserve should not affect extinction rates.

Our purpose is not to reexamine the SLOSS issue per se, but to discuss the assertion that effectively states that habitat fragmentation should be innocuous to most species, and therefore need not be a consideration in reserve design. This conclusion runs counter to the prevailing view that habitat fragmentation negatively affects population survival, and thus biological diversity, and therefore should be a prime consideration in conservation strategy (e.g., Janzen 1974; Picton 1979; Soulé and Wilcox 1980; Lovejoy and Oren 1981; Whitcomb et al. 1981). In view of the increasing interest in the application of biological theory to conservation and the reliance on the scientific literature for guidance in conservation decisions, we feel that this contradiction warrants examination.

This apparent contradiction arises from three sources: (1) the SLOSS problem is not equivalent to, or is at very best a special case of, the problem of habitat fragmentation; (2) the population model Simberloff and Abele (1982) employ is inadequate because it ignores key factors affecting population survival; and (3) Simberloff and Abele's treatment does not consider how the disposition of one species may affect the survival of others, because it is limited to single-species population phenomena and ignores interspecific interactions or community-level phenomena.

HABITAT FRAGMENTATION VERSUS SLOSS

The expansion of land use that accompanies human population growth results in the fragmentation of natural habitat. As fragmentation proceeds, average fragment size and total fragment area decrease and insularity of fragments increases (Moore 1962; Webb and Haskins 1980; Burgess and Sharpe 1981). Habitat fragmentation thus can be described as having two components, habitat loss and insularization, both of which contribute to a decline in biological diversity (Wilcox

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1980). This "collapse" of a biota has a temporal component which, judging from studies of land-bridge island faunas (Brown 1971, 1978; Diamond 1972; Terborgh 1975; Wilcox 1978, 1980), ranges from virtually instantaneous to 10^4 years, depending on island size and the taxon (Wilcox 1980; Diamond 1984). Not surprisingly, habitat fragmentation is rapidly becoming a central issue in conservation policy, prompting legislative and regulatory action aimed at mitigating its impacts on biotic diversity (e.g., Cooley and Cooley 1984; Harris 1984), as well as prompting long-term research on its effects (e.g., Lovejoy et al. 1983).

The SLOSS problem implicitly addresses fragmentation from a static perspective; that is, it is limited to systems of existing habitat islands supporting biotas presumed to be at equilibrium. A valid comparison of the species diversity or composition of a set of small "reserves" with that of a large "reserve" requires that the biotas either are not supersaturated as a consequence of prior fragmentation, or will not sustain what amounts to further fragmentation by additional conversion of surrounding habitat. Thus, the conservation problem posed by habitat fragmentation is understanding the collapse process that it precipitates, while the problem posed by SLOSS is determining which of two reserve configurations of equal area supports more species after the collapse. SLOSS is therefore a special case of habitat fragmentation and conclusions from its analysis have limited applicability to the more general problem of habitat fragmentation.

The appearance of "fragmentation" in the title of Simberloff and Abele (1982) and the terminology used in the text cloud this distinction between SLOSS and habitat fragmentation. Particularly misleading are the predictions about the effects of fragmenting intact habitat. These predictions are based on a theoretical analysis of a subdivided population, but the analysis fails to consider the overall reduction in population size that is a result of habitat loss. As Simberloff and Abele (1984, p. 399) correctly pointed out more recently: "subdividing an existing refuge by cutting swaths out of it simultaneously decreases its area."

EFFECTS OF POPULATION SUBDIVISION ON EXTINCTION PROBABILITY

Simberloff and Abele's 1982 analysis, even if applied only to SLOSS as a special case of habitat fragmentation (i.e., no loss of habitat area), nonetheless presents major difficulties concerning how subdivision of a population affects its likelihood of extinction. They consider how the probability of extinction is related to population size by employing a stochastic population model (RDG) developed by Richter-Dyn and Goel (1972). RDG examines the relationship between the ratio of per capita birth and death rates (λ/μ) and the time to extinction for a population. The model shows that when λ/μ is greater than about 1.5, there is a critical population size, $N_c \geq 20$, which, if exceeded, will allow persistence of a population for an immensely long time.

Citing this result, Simberloff and Abele (1982, p. 43) contended that "for most species λ/u [$\equiv\lambda/\mu$] will exceed 1.5 at low population sizes, so if a subdivided refuge had all or even one of its subrefuges with greater than a critical population size N_c for most species, the expected times to extinction for the species in both the archipelago of refuges and the original single refuge would be so large that this need not be a consideration in planning refuge configuration.'' They also list, independently of this, additional considerations not accounted for in the RDG model, but draw no general conclusions except that reserve design ultimately depends upon the idiosyncrasies of the particular natural system under consideration.

Population extinction can occur for at least four basic reasons: demographic stochasticity, environmental variation, genetic stochasticity, and natural catastrophes (Shaffer 1981). Demographic stochasticity, upon which RDG is based, is the main cause of extinction only for very small populations. Leigh (1981) has shown that for larger populations, environmental variation is the main cause of fluctuations in size that lead to extinction. Since RDG overlooks the main cause of extinction for population sizes greater than 20, its conclusion that the survival time for a population is independent of its size when it exceeds 20, in effect, is meaningless from a practical standpoint. Even if it is otherwise correct, RDG alone is insufficient to assess the effects of reduced population size on extinction probability in terms of either SLOSS or habitat fragmentation. Shaffer and Sampson (1985) discussed additional shortcomings of the Richter-Dyn and Goel model and presented empirical evidence that suggests that the above values of λ/μ and N_c may not be applicable even for small populations.

The above application of RDG assumed that the survival of each subpopulation is entirely independent of others. Yet for any population or previously occupied habitat patch there is some probability of either recruitment or reestablishment via migration from other populations (if they exist). Richter-Dyn and Goel (1972) extended their model to incorporate this probability. Simberloff and Abele also cited these results, pointing out that, depending on the migration rate between the subpopulations, the probability of survival ''might well be increased by subdivision'' of a population (Simberloff and Abele 1982, p. 43).

Unfortunately, this is an inappropriate application of Richter-Dyn and Goel's subdivided-population model. Their unsubdivided population relates the average time to extinction, T_1, to the carrying capacity, K^* (see their fig. 3); they do not, however, extend this constraint to their model of an ensemble of populations. Thus, Richter-Dyn and Goel's analysis does not (nor was it apparently intended to) realistically describe alternative conservation strategies when habitat area is constrained, or even an issue.

To our knowledge, only Wright and Hubbell (1983) have developed a model that specifically addresses this problem. Their results show that a single area supports more species than two smaller areas of the same total size, in the presence or absence of migration. This approach is especially promising in that it avoids uncertainty about the value of λ/μ and is supported by data on the frequency of extinction in some insular bird populations. (Also promising from a practical standpoint is that critical population sizes may be estimated from year-to-year abundance data without resorting to speculation about λ and μ.)

An additional difficulty with the practical application of RDG is the model's assumption of the lack of complexity in population structure or habitat. Most populations are naturally subdivided, consisting of ''populations of populations,'' or ''metapopulations'' (Levins 1970). Furthermore, environmental heterogeneity normally exists within and among suites of habitat patches supporting metapopulations. This consideration renders the development and application of realistic theoretical models more problematical yet. That these factors increase the risk of extinction from fragmentation, however, is both logical and supported by empirical evidence.

Consider, for example, the currently endangered checkerspot butterfly *Euphydryas editha bayensis,* whose populations have been monitored for 25 yr by P. R. Ehrlich and colleagues. During this time, population structure, dynamics, and regulation have been described and extinctions observed (Ehrlich et al. 1975; Ehrlich et al. 1980). Ehrlich (1965) showed that a purported population supported by three nearly contiguous habitat patches on Jasper Ridge Preserve actually consisted of three demographic units whose sizes fluctuated independently in response to annual changes in rainfall. One of these demographic units became extinct, was reestablished by immigration, and again became extinct several years later. A second is now on the verge of extinction. Meanwhile, populations within dispersal distance (Murphy and Ehrlich 1980) have been increasingly isolated or extirpated by habitat fragmentation.

The case for regarding such local extinctions as ''normal'' ecological events is strengthened by mounting empirical evidence (e.g., den Boer 1981; Blaustein 1981; Parker and Root 1981; Schoener 1983; Diamond 1984). Natural populations of many species are therefore frequently at a ''critical size,'' even though they may consist of hundreds or thousands of individuals during the years prior to extinction, as in the case of *Euphydryas*. Metapopulations of such species undoubtedly persist via interpatch migration which offsets local extinction. Yet, the apparent capacity of even relatively sedentary species to disperse among habitat patches does not suggest that habitat fragmentation will be inconsequential. Metapopulation survival requires a mean extinction rate less than the immigration rate (Levins 1970). The modification or conversion of natural habitat will more probably impede dispersal than will isolation caused by unsuitable natural habitat.

The risk of fragmentation is thus threefold: (1) demographic units may be destroyed outright, reduced in size, or subdivided (thus increasing their rate of extinction); (2) potential sources of immigrants may be lost (as a consequence of risk 1); and (3) immigration may be impeded by conversion of natural habitat between habitat patches. Note that even though risk 3 occurs without a loss of critical habitat per se, the probability of extinction is potentially increased.

The existence of habitat heterogeneity within and among habitat patches casts further doubt on the validity of predictions concerning the effects of fragmentation based solely on conventional population models. Many workers have shown that within-habitat (microhabitat) heterogeneity has a significant effect on the population dynamics of insects (Andrewartha and Birch 1954; Birch 1957; Ehrlich et al. 1975, 1980; Singer and Ehrlich 1979; den Boer 1981; Murphy et al. 1983) and mammals (Anderson 1970; Birney et al. 1976; Stenseth et al. 1977; Rosenzweig and Abramsky 1980; Cockburn and Lidicker 1983). *Euphydryas* butterflies again provide an apt illustration. Local population extinction, particularly in response to drought, is a rather common occurrence in coastal California habitats of *Euphydryas editha* (Ehrlich et al. 1980; Murphy and Ehrlich 1980). Especially dry years result in high larval mortality in microhabitats with southern exposures where host plants senesce relatively early. Survival occurs exclusively in north-facing microhabitats under such conditions. The pattern of survival, however, is effectively reversed in particularly wet years. Thus, only habitat patches consisting of a variety of microhabitat exposures sustain populations for more than a few years.

The relationship between the size or number of habitat patches and the probability of extinction for their associated species therefore is not a simple matter of relating population density to habitat area, even accounting for within-habitat differences in carrying capacity. The risk of extinction from habitat fragmentation (or mere subdivision) may not be linearly proportional to the associated reduction in habitat or fragment area and may well increase disproportionately, particularly on the geographic scale at which remedial conservation action is taken.

Simberloff and Abele touch on the genetic implications of population subdivision. We concur that assessing the role of genetic stochasticity is problematic; what was not pointed out, however, is the inconsistency between N_e as predicted by RDG and as predicted by population genetic theory. Along with environmental variation, genetic stochasticity can increase the probability of extinction for populations of far greater size than estimated by RDG on the basis of the effect of demographic stochasticity. An order of magnitude larger could be required to maintain genetic variability and, hence, the capacity of populations to adapt to extreme environmental changes. By the most conservative genetic criteria (Franklin 1980), the effective population size, N_e, must be > 50, which probably translates to an actual population size in the hundreds for most species. Several different approaches currently produce estimates of N_e in this range and higher (Franklin 1980; Soulé 1980; Shaffer 1981).

COMMUNITY-LEVEL EFFECTS AND SECONDARY EXTINCTIONS

The potential effects of habitat fragmentation on extinction go beyond the sole consideration of population-level phenomena. Even if survival of relatively few species is directly jeopardized by fragmentation, the loss of those species may precipitate multiple extinctions through community-level effects. Terborgh (1976) raised this point previously, arguing that some primary extinctions may represent the loss of species in "keystone" positions in communities. More recently, Gilbert (1980) described cases of elaborate mutualistic relationships in neotropical forests which, if disrupted as a consequence of a single extinction, will result indirectly in a cascade of extinctions amounting to the loss of entire food webs.

Community-level effects caused by the loss of species on land-bridge islands have been demonstrated recently in an extensive study of two mutualistic guilds of hummingbird pollinators and plants (Feinsinger et al. 1982). These workers found that as a result of a decrease in the number of hummingbird species, plants were visited more erratically and with less fidelity. Although further consequences were not documented, Feinsinger et al. suggested, as have Futuyma (1973) and Janzen (1974) previously, that tightly coupled systems would exhibit more drastic effects, including extinctions. Such potentially negative consequences of habitat fragmentation through the disruption of mutualistic guilds are not limited to tropical forests. Most higher plants, for example, are entirely dependent upon mycorrhizal (root-associated) fungi, which in temperate forests may be in turn largely dependent upon small mammals for their dispersal (Maser et al. 1978). Harris (1984) indicates that the extent to which old-growth forests can sustain further fragmentation without jeopardizing their diversity, functional integrity, and ability to contribute to the regenerative capacity of surrounding logged forests may depend on the minimum habitat sizes and degrees of insularity required for small mammal populations. This and other empirical evidence (see Campbell and Clark 1981; Karr 1982; Lovejoy et al. 1984) suggests that such ripple effects ought to be given serious thought when the effects of habitat fragmentation are considered.

Finally, if there is any doubt that fragmentation of existing nature reserves is not a prudent policy, it is dispelled by empirical data on mammalian population densities in a wide range of national parks and similar protected areas. In separate studies East (1981, 1983) and Schonewald-Cox (1983) have both shown that the sizes of many such populations are less than 100, and more than half are in the range of 100–1000. Thus a substantial proportion of the large-mammal faunas of comparatively large and intact reserves already may be at risk without further fragmentation. These observations lend support to predictions, based on island biogeographic theory, that faunal collapse will occur in (intact) reserves (Soulé et al. 1979; East 1983).

Large mammals might be considered a somewhat biased example since they constitute only a tiny fraction of a biota and are especially vulnerable to fragmentation because of their large body size and trophic needs. The growing list of invertebrates endangered as a result of habitat fragmentation (Wells et al. 1983) suggests otherwise, however. Furthermore, for success, conservation strategy must not be based on *how many* species are maintained given hypothetical reserve strategies; rather, the criterion should be *which* species of those that are rare, threatened, or endangered can be preserved given real options.

When one assesses the risk of extinction associated with fragmentation, one must begin by considering all potentially relevant population-level and community-level factors, as well as physical, or edge, effects (e.g., Brittingham and Temple 1983; Lovejoy et al. 1984; Janzen 1983), whether or not fragments already exist (i.e., SLOSS). That current ecological theory is inadequate for resolving many of the details should not detract from what is obvious and accepted by most ecologists: habitat fragmentation is the most serious threat to biological diversity and is the primary cause of the present extinction crisis.

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