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PATTERNS OF OCCURRENCE AND ABUNDANCE IN COLONY COMPLEXES OF THE MEXICAN PRAIRIE DOG (*CYNOMYS MEXICANUS*) IN PRODUCTIVE AND UNPRODUCTIVE GRASSLANDS

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RESUMEN

El perro llanero mexicano (*Cynomys mexicanus*) vive en una pequeña área (500-600 km^2) del noreste de México. La especie está considerada en peligro de extinción debido principalmente a la fragmentación del hábitat, al reciente desarrollo y expansión agrícola en la porción norte de su limitada distribución geográfica y a la invasión de arbustos en el sur de su área de distribución. En este trabajo estudiamos el papel ecológico del perro llanero mexicano en la ecología de los pastizales en el sur del desierto Chihuahuense. Muchas colonias de esta especie, particularmente en la parte más sur de su área de distribución, están actualmente asentadas en pastizales cortos que se desarrollan en suelos de productividad baja derivados de yeso, donde la tasa de invasión de los arbustos es reducida. Un estudio de la región de los alrededores de las colonias sureñas indicó que esto no siempre ha sido el caso y hay evidencias de que en el pasado estuvo presente en los suelos aluviales profundos más productivos. Se evaluaron la producción de biomasa y las densidades estacionales de la especie en suelos baja productividad del sur de su área de distribución actual y sobre suelos aluviales ricos y profundos en la parte norte. En los suelos aluviales profundos la producción de biomasa total fue siete veces mayor y las densidades de los perros llaneros fueron tres veces y media más grandes. Las densidades estacionales de adultos no fueron significativamente diferentes por tipo de suelo durante el período del monitoreo, en cambio las densidades de juveniles aumentaron significativamente en los censos de verano debido al nacimiento de las crías. La similitud en densidades estacionales por sitio sugiere que la especie está limitada por alimento. Un estudio inferencial del desarrollo de una colonia aislada sobre los suelos aluviales más productivos en el norte del área de distribución de la especie, mostró densidades bajas en el centro y en el borde de la colonia de reciente expansión, en comparación con la zona periférica al centro. La cobertura vegetal también fue escasa en el centro de esa colonia. Las áreas periféricas al centro y la zona de expansión de la colonia mostraron menor cobertura de pastos y juncias en comparación con el pastizal aledaño no utilizado por la colonia, mientras que la especie de pasto *Bouteloua gracilis* estuvo ausente en el centro y periferia de la colonia, y aumentó significativamente en cobertura desde la zona de expansión de la colonia hacia el pastizal que la circunda.

Los pastizales de productividad baja pudieron haber funcionado como refugios para el perro llanero durante episodios previos de invasión de arbustos en el Holoceno. La fragmentación natural de esos pastizales, sugiere que el perro llanero mexicano puede estar funcionando como una metapoblación. Se

registraron colonizaciones y extinciones en áreas monitoreadas en cada tipo de suelo. La diferencia principal entre los dos complejos se debió a la productividad mayor de los suelos aluviales de la porción norte. En consecuencia, se producen tres veces mas juveniles por hectárea en esos suelos, lo que aumenta mucho la probabilidad de que la especie mantenga una colonia establecida o de fundar con éxito nuevas colonias en esos suelos. La probabilidad de extinción del perro llanero mexicano es mas alta en el sur de su área de distribución debido a estas densidades mas bajas y su conservación ahí deberá de incluir el trasplante sistemático de individuos desde las colonias de los suelos aluviales productivos de la parte norte.
Palabras clave: *Cynomys mexicanus*, pastizales del desierto, especie en peligro, metapoblación, perro llanero mexicano.

ABSTRACT

The Mexican prairie dog lives in a small (500-600 km^2) area of northeastern Mexico. The species is listed as endangered due to habitat fragmentation from recent large-scale agricultural development in the northern part of its limited geographical range and from shrub encroachment in the south. In this work we aim to study the role of Mexican prairie dog in the ecology of grasslands in the southern Chihuahuan Desert. Most of the species' colonies, particularly in the far south of its range, occur today in short grasslands that grow on low productivity, gypsum-derived soils where the rate of such shrub encroachment is reduced. A survey of the region surrounding these southern colonies indicated that this has not always been the case as evidence of the species' occurrence on more productive alluvial soils in the past is apparent. Biomass production and seasonal prairie dog densities were measured on these low productivity soils in the south of its range and on richer and deeper alluvial soils to the north. Total biomass production was seven times greater and densities were three-and-one-half times greater on the deeper alluvial soils. Adult seasonal densities were not significantly different within a soil type during the period monitored while juvenile densities increased significantly in the summer censuses due to the birth of young. The similar seasonal densities at each site suggest that the Mexican prairie dog is resource limited. An inferential study of the development of one isolated colony on the more productive alluvial soils in the north of the species' range showed lower prairie dog densities in the center of the colony and at the edge of the colony in the zone of recent expansion than in the area peripheral to the center. Vegetation coverage was too scarce in the center of the colony to quantify. The areas peripheral to the center and in the zone of expansion were reduced in coverage of grasses and sedges in comparison to the unutilized surrounding grassland while the palatable grass, *Bouteloua gracilis*, was absent in the center and periphery of the colony and increased significantly in coverage from the zone of expansion to the adjoining grassland.

Such low productivity grasslands may have served as refuges for the species during previous episodes of shrub encroachment in the Holocene. In addition, the natural fragmentation of such grasslands suggested that the Mexican prairie dog might function as a metapopulation. Colonizations and extinctions were recorded at monitored areas on each soil type. The major difference between the two complexes was due to the greater productivity of the alluvial soils in the north. Consequently, three times as many young per hectare are produced on these soils, greatly increasing the probability of the species maintaining an extant colony or successfully founding new colonies there. The probability of extinction of the Mexican prairie dog is higher in the south of its range due to these lower densities and conservation of the species there should involve the systematic transplantation of individuals from colonies on the richer alluvial soils to the north.
Key words: *Cynomys mexicanus*, desert grasslands, endangered species, metapopulation, Mexican prairie dog

INTRODUCION

The Mexican prairie dog, a late Pleistocene isolate of the black-tailed prairie dog, *Cynomys ludovicianus* (Baker 1956), is found in a 500-600 km² area on the altiplano of the south-central Chihuahuan Desert of north-eastern Mexico where the states of Coahuila (north), Nuevo Leon (east), San Luis Potosi (south) and Zacatecas (west) converge (Ceballos *et al.* 1993). Most of its colonies occur at altitudes of 1000 to 2000 m in the large valleys of the region (Ceballos *et al.* 1993), which are characterized by short grasslands growing on low productivity, gypsum soils (Meyer & Garcia-Moya 1989, Meyer *et al.* 1992). However, some large colonies are found at higher elevations (2000-2500 m) in the northern mountains adjacent to these valleys where they occur on more productive alluvial soils (Valdéz-Ortega 1986, Ceballos *et al.* 1993, Treviño-Villareal & Grant 1998). The species is listed as endangered due to its limited geographical distribution and to large-scale agricultural development in the north of its range (IUCN 1990, USFWS 1991a, CITES 1992, SEDESOL 1994). As are all prairie dog species, the Mexican prairie dog is highly social, forming colonies in which family groups live together (*e.g.* King 1955, Hoogland 1995). They are active diurnally and are subjected to predation by a wide range of aerial and terrestrial species. As a result, they live in and maintain open areas from which predators are more easily detected (Hoogland 1995). The establishment or expansion of a colony and its maintenance requires that prairie dogs either select open areas or remove vegetation in the area (Weltzin *et al.* 1997).

Currently, the southern section of the Chihuahuan Desert is losing its grasslands because of shrub encroachment. Estimation from aerial photographs of the loss of grasslands in the north of the state of San Luis Potosi due to this invasion (primarily *Larrea tridentata*; leguminous genera such as *Acacia, Mimosa* and *Prosopis*; and various species of *Opuntia*) has been approximately 1% per year over the last 35 years. It is in this region that the southernmost colonies of the Mexican prairie dog occur. There, their distribution is highly fragmented, many colonies are abandoned and those, occupied, have few prairie dogs living within them. These observations caused us to begin a study of the Mexican prairie dog and its role in the ecology of grasslands in the southern Chihuahuan Desert. We hypothesized, due to the low numbers of prairie dogs in the southern part of its range, that each colony there had a relatively high probability of extinction. We also hypothesized that the Mexican prairie dog's continued existence in the region was dependent on its ability to disperse to previously abandoned areas or to open areas suitable for the successful establishment of a new colony. Because of these hypotheses and the endangered status of the Mexican prairie dog, we considered the following questions:

Why is the Mexican prairie dog so strongly associated with soils of low productivity? Has this association always been the case or is it of more recent origin related to some event in the past?

What are the differences in population dynamics between colonies found on low productivity gypsum soils and those that occur on deeper, higher productivity alluvial soils? Are patterns of colonization and extinction in the south of the species' distribution similar to those on richer soils to the north?

What are the actual dynamics within a prairie dog colony that determines its use of resources in an area? In other words, how does a colony of prairie dogs develop over time, what impact does it have on the vegetation and is the species resource limited?

STUDY SITES AND METHODS

Study sites. Two complexes of colonies of the Mexican prairie dog were studied. One complex (*sensu* Scott-Morales *et al.* 2004), El Manantial, occurs on shallow, low productivity gypsum soils in the region of San Vicente, Vanegas, San Luis Potosi in the south of its range (23º 56' - 24º 15'N, 100º 50' – 100º 57' W). The second complex occurs on more productive and deeper alluvial soils at Rancho Los Angeles, Coahuila (25º 04' - 25º 08' N, 100º 58' - 101º 03' W), 230 km to the north of San Vicente. The closest weather station at a similar elevation (1815m) to the El Manantial complex (hereafter EM = El Manantial complex) is Vanegas, San Luis Potosi, 60 km to the south. Mean average daily temperature at Vanegas for an unspecified 16-year period was 17.7ºC with the coldest month January (12.2ºC) and the hottest months May and June (21.6ºC; Garcia 1973). Mean annual rainfall over the same 16-year period was 291.8 mm with 82% falling during the months of May through October. Soils in the EM complex are similar to those described by Meyer and Garcia-Moya (1989) and Meyer *et al.* (1992) with either exposed gypsum soils or with gypsum subsoil overlain by shallow fine-calcareous alluvial surface soils. Cattle, horses, goats and sheep belonging to the surrounding «ejidos» (*i.e.* collective farms) heavily graze this area. San Antonio Alazanas, Coahuila is the closest recording station (90-km northeast) to the Rancho Los Angeles complex (hereafter RLA = Rancho Los Angeles complex) at a similar elevation (2138 m) and surrounding topography. Mean average daily temperature for an unspecified 15-year period was 13.3ºC with the coldest month being January (9.0ºC) and the hottest months May and June (16.1ºC; Garcia 1973). Mean annual rainfall for an unspecified 22-year period was 498 mm with 76% falling during the months of May through October. Actual rainfall at Rancho Los Angeles, as measured by two researchers over the periods 1975-1982 and 1984-1989 was 304.2 mm (Garcia-Elizondo & Lopez-Trujillo 1997), approximately 39% lower than at San Antonio Alazanas and roughly equal to that recorded at Vanegas. Soils at the RLA complex are deep (2-15m), alluvial limestone deposits derived from Mesozoic marine sediments (COTECOCA 1979, Valdéz-Ortega 1986). Prior to the 1960's, grazing pressure by cattle, horses, goats and sheep at Rancho Los Angeles was high. In the early 1960's, the ranch was fenced to exclude small domestic grazers and stocked with Charolais and Hereford cattle. Their grazing impact varied from moderate to heavy during the years 1998-2004 (RIY, personal observation).

Association with low productivity soils. In general, the Mexican prairie dog occurs now on low productivity gypsum soils throughout much of its range (Ceballos *et al.* 1993, Mellink & Madrigal 1993, Treviño-Villarreal & Grant 1998). We used a strong inference approach (Platt 1964) to determine the relationship between soil type and use by the Mexican prairie dog. For example, our observations of the species on these soils at the EM complex indicated that animals tended to live adjacent to the more productive lower-lying areas, where water and nutrients are concentrated after rainstorms and where most of their daily foraging activity occurred**.** We reasoned that long-term changes in the vegetation, resulting from shrub encroachment on soils with higher levels of fertility, might have been responsible for the Mexican prairie dogs present association with gypsum grasslands. We quantified previous usage by the Mexican prairie dog along eight line transects in the EM complex; four in the vicinity of the large El Manantial colony, three from the La Trueba 2 colony and one from the San Vicente east colony (for location of these transects see footnote of Table 1). Transects started approximately 100m from these active colonies and points, where changes in the vegetation occurred, were recorded using a GPS. A typical sequence of vegetation changes began at the edge of an inactive area of a prairie dog colony (a relatively open expanse of sparse grassland with occasional clumps of shrubs) with entry into a zone of short (<1 m-tall), invasive *Larrea tridentata.* The next vegetation zone encountered was a taller (1-2 m-tall) mixed stand of *L. tridentata* and *Lycium berlandieri* often with an understory of *Opuntia leptocaulis*. This vegetation zone would continue until a drainage line (usually indicated by the presence of mesquite, *Prosopis laevigata*) was encountered. Exiting the drainage line, the sequence of vegetation changes would be reversed until an open, elevated grassland (Fig. 1a) with clumps of shrubs and small trees (usually either *L. berlandieri* or aggregations of the latter species with either *Condalia mexicana, Rhus trilobata* or both) was encountered. This pattern along would repeat itself several times along the transect. In general, soils of the raised grassland areas were gypsum-derived while lower areas, dominated by shrubs and small trees, were more alluvial in nature. Additional vegetation encountered along transects were low areas where water had accumulated previously (characterized by *Flourensia cernua, Atriplex* sp. or both), and abandoned agricultural lands. In each vegetation zone intersected by a transect, evidence of previous use or non-use by the Mexican prairie dog was noted. For the EM complex, such evidence consisted of still visible but heavily eroded mounds (M), many of which had growing on them individuals of *L. tridentata* or *L. berlandieri*; obvious groups of rings (R), which are the remnants of raised «caliche» layers that form a collar around the base and sides of the mounds (Fig. 1b), and curved fragments (F) of the «caliche» layers (Fig. 1c,d) embedded in or lying on the surface. It is impossible to determine the exact time since an area was last used by the Mexican prairie dog but the erosion sequence of areas with M only (youngest), followed by areas combining M, R and F, areas with R and F and finally areas with F only (oldest) is indicative of the relative ages between areas since abandonment. Each transect was continued until either a ridge-top, a large area of abandoned agricultural lands or a barrier to the natural drainage patterns of the valley reached (*i.e.* the embanked main road going north to Zacatecas or the railroad line) was encountered. The GPS readings for each transect were mapped to scale and the distances for each segment (vegetation category) determined. In addition, the presence or absence of evidence of previous usage by the Mexican prairie dog in these segments of the map was noted, treating each segment as a distinct data point. Analysis of the occurrence of evidence of previous usage was done using a Chi-square test for a 2 X 2 contingency table (Siegel & Castellan 1988). One row heading for this table was a grouping of segments consisting of abandoned agricultural lands, drainage lines and seasonally flooded areas while the other row heading were segments that occurred on predominantly gypsum soils overlain by shallow alluvium. Column headings were evidence of presence or absence of previous prairie dog colonies in the segments.

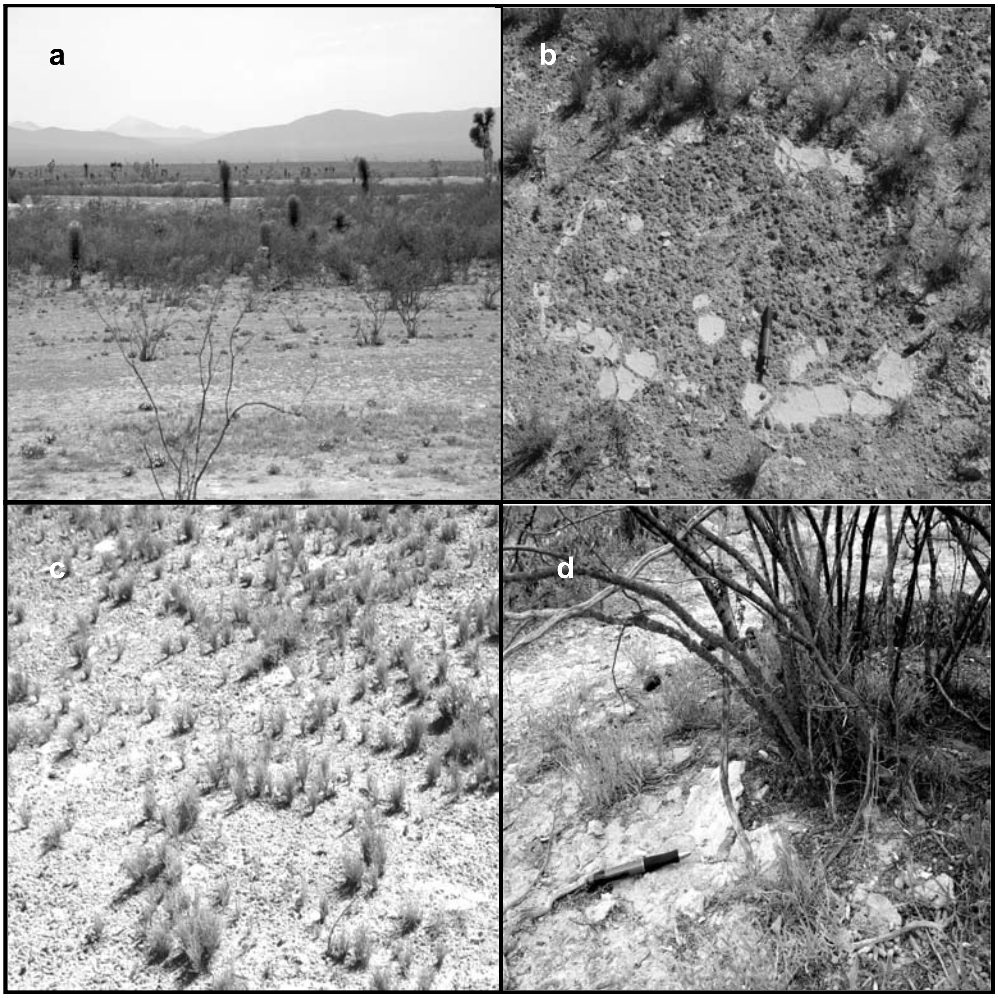

Figure 1
a) A view of one line transect in the El Manantial complex near the La Trueba 2 colony showing a series of raised open grassy areas on low productivity, gypsum soils intersected by bands of *Larrea tridentata, Opuntia leptocaulis* and young *Yucca filifera* on richer alluvial soils, b) a caliche ring on an eroded surface in gypsum grasslands indicating the previous presence of a prairie dog mound, c) fragments of caliche rings scattered on the surface of heavily eroded gypsum grasslands, d) curved fragments of an eroded caliche ring that formed around an abandoned prairie dog mound, the burrow entrance of which was later colonized by *L. tridentata.*

It was also necessary to determine how rapidly the vegetation was changing in the EM complex. The rate of vegetation change in the El Manantial region was measured by comparing quantitatively two series of aerial photographs taken in 1965 and 1999. Scale differences between the photo series were determined by measuring distances between identifiable points on the aerial photos. Then, a scaled quadrat (divided into 100 sub-quadrats and covering an area equal to 6.25 km² on the aerial photo) was used to quantify the vegetation for 25 areas in the two series. Each area selected had to have reference points in common to ensure that the same physical area was quantified and had to include areas currently in use or which had been used previously by the Mexican prairie dog. From the aerial photographs, five categories of vegetation or land-use were distinguishable; grassland, shrub-land (areas with bush encroachment by small shrubs such as *L. tridentata* and *Flourensia cernua*), mesquite (*Prosopis laevigata*) woodland, land used for agriculture, and man-made facilities such as roads and buildings. All five categories were ground-truthed. The percent cover for each category within an aerial photo series was calculated and percentage changes from 1965 to 1999 were determined using a Wilcoxon signed ranks test (Siegel & Castellan 1988). A similar study at the RLA complex was not undertaken. The vegetation dynamics in grasslands there are very different and consist of the relatively slow invasion of *Yucca carnerosana* followed by a suite of woody shrubs, dispersed by birds that use the yuccas as perches (author's unpublished data). To determine how different the soils in the EM complex were from those in the RLA complex, plant biomass production was measured for one year on 0.25 m^2 quadrats in each of the two complexes. These clipping experiments involved three treatments; no exclusion, exclusion of domestic animals only, and exclusion of both domestic animals and small indigenous mammals, mainly prairie dogs. The three treatments were grouped with ten (RLA) and eight (EM) repetitions. At the RLA complex, eight repetitions were located across the main central valley of the ranch and two repetitions were placed in the southern valley of the ranch. At the EM complex, the eight repetitions were established randomly across the large central area occupied by the relatively continuous El Manantial and Rancho Santa Ana colonies. The biomass production data were tested for differences between the two prairie dog complexes for each exclusion treatment and, within sites for differences between exclusion treatments, using Wilcoxon-Mann-Whitney tests (Siegel & Castellan 1988).

Population densities. Population densities of the Mexican prairie dog were measured at the EM and at the RLA complexes over the period of 10/1999-7/2002 (a spring census was not taken in 2002). Population densities were measured at four critical times in the annual cycle of the Mexican prairie dog (early spring before the birth of pups, early summer after the pups emerged, late summer after dispersal of second-year juveniles, and late fall). Animals were counted on twelve, permanent one-hectare quadrats each at the main colony at the EM complex and in the two large colonies found in the north valley of the RLA complex over the period. Each quadrat was observed for 15 min at 1hr intervals beginning about one hour after sunrise (usually 8:00AM Central Standard or Daylight Saving Time) until animal activity began to decrease three to four hours later. These daily censuses were repeated twice during each of the four annual monitoring periods, during which the maximum number of adults and juvenile animals active were recorded during the fifteen-minute interval. The maximum number of animals recorded for a quadrat over the two-day period of study was used in the final calculations of density (Severson & Plumb 1998). These data were tested for seasonal differences in adult and juvenile densities within each complex using Kruskal-Wallis one-way analysis of variance (Siegel & Castellan 1988). Seasonal differences in adult and juvenile densities between complexes were tested using Median tests (Siegel & Castellan 1988). Differences in the three summer censuses for juveniles, the majority of which are newborn pups, at the two complexes were tested using ANOVA and Tukey's multiple range test (Steel & Torrie 1960).

Because the numbers of individuals were variable between quadrats and years within a complex, due either to lack of success in reproduction or to animals using sections of the 1-ha plots when actually resident off the plot, average seasonal densities (for three fall and summer counts and two spring and late summer counts) were also calculated for the EM and RLA complexes for the 2.5-year period in which censuses were, instead of with taken. These data were used to calculate crude measures of the rates of *per capita* growth as well as to determine differences in dispersal and over-winter survival for the two complexes.

Seven areas each were monitored in the EM and RLA complexes from November 1998-November 2004 to determine if extinction and colonization as well as non-local dispersal (>1 km) were occurring. Initially, these areas were either occupied, but with low numbers of animals (3-30 total), or abandoned and, with the exception of the two southernmost colonies at the EM complex (La Trueba 1 and 2), were located 0.1-4.0 km from larger active colonies. Changes in numbers in each area occupied were estimated by counting all animals active above ground and scoring them as growing, diminishing or remaining the same from the previous year.

The number of animals using a 100 X 100 m quadrat (1 ha) located in the colony center, the peripheral area, the expansion zone and the adjacent grassland were counted over three consecutive days in late August, 2000. The four quadrats were located along the valley floor in a sequence beginning in the colony center and ending in the grassland. Each quadrat was located at least 100m from a neighboring quadrat and was similar to the other quadrats in terms of elevation, slope aspect and inclination and accessibility to grazers. The data collected consisted of the number of animals active during a ten-minute period within a quadrat at one-hour intervals beginning at 8:00 AM and ending at 12:00 PM. Four measures of numbers of animals active in a quadrat were obtained daily for each of the four areas. As no prairie dogs were recorded using the grassland during this study, these data were analyzed for the three areas in which prairie dogs were present using the Friedman two-way analysis of variance by ranks test (Siegel & Castellan, 1988) in which each sample, taken within an hour interval, was ranked with respect to the others in that sampling period. Also, in each area, the number of prairie dog mounds on twenty 5 X 5 m (0.0025 ha) were counted. In addition, the ten largest mounds in each area were measured. Mounds were roughly elliptical in shape. Thus for each mound, the long axis and the longest axis perpendicular to that axis were measured and their areas calculated using the formula for an ellipse. These data for number and size of prairie dog mounds were analyzed using one-way ANOVA (Steel & Torrie 1960).

Vegetation was sampled on a series of 20 X 20 cm quadrats in the Grassland (n = 50), Expansion (n = 100) and in the Periphery (n = 100). The Colony zone was not sampled as it was largely devoid of perennial plant cover and the species that did occur there corresponded with those of the Periphery. A piece of clear plastic, upon which one-hundred, 4-cm^2 quadrats were drawn, was laid over randomly determined points in each of the three zones and the identity and number of quadrats occupied by a species counted to give an estimate of its percentage cover. These data were analyzed using one-way ANOVA (Steel & Torrie 1960). Species, whose percentage covers were less than 1% in each of the three areas studied, were excluded from these analyses.

RESULTS

Association with low productivity soils. Seventy-three percent of the 9.92 km of line transects measured in the El Manantial complex showed evidence of previous occupation by the Mexican prairie dog (Table 1). More importantly, 100% of the segments of the line transects measured that were on gypsum soils overlain with alluvium showed evidence of previous occupation by the Mexican prairie dog (Table 2). In contrast, 52% of the line segments on abandoned agricultural lands, drainage lines or flooded areas with deep alluvial or saline soils showed no evidence of prairie dog usage.

Table 1

Means (± standard error) and ranges for transect length (km) and percentage of the line transects falling in categories with various levels of usage in time by the Mexican prairie dog. Numbers in parenthesis indicate sequence of relative time since abandonment with 1 = shortest and 4 = longest. Sample size was 8 transects[1]

	Mean ± S.E.		**Range**
Length (km)	1.21± 0.21	%	0.44-2.07
Mounds only (1)	12± 6		0-47
Mounds, Rings, Fragments (2)	22± 11		0-66
Rings, Fragments (3)	27± 8		0-64
Fragments only (4)	16± 7		0-47
No evidence	27± 11		0-76

[1] Transect locations are available from authors upon request.

Table 2

Number of segments in line transects with presence and absence of evidence for previous occupation by the Mexican prairie dog. Evidence = presence of mounds, rings, or fragments or some combination of the latter. Sample size was 112 transect segments.

	No eveidence	**Evidence**
Abandoned agricultural lands, drainage lines, flooded areas with deep alluvial or saline soils	27	25
Gypsum soils overlain by shallow alluvium	0	60

Areas in the El Manantial complex experienced a 38% loss of grassland as a result of increases in shrub-lands and mesquite woodlands during the period 1965 to 1999 (Z = 4.13, p <<0.001, Table 3). For each 625-hectare area measured on the aerial photographs, grasslands made up an average of 106.5 ha in 1965 decreasing in area to 65.5 ha in 1999, a loss of 1.17 ha per year during this thirty-five year period. This loss was due to increases in shrub-lands by 34.5 ha and mesquite woodlands by 4 ha during the same thirty-five year period (for the latter two categories combined, $Z = 3.47$, $p < 0.001$).

Table 3

Percent of change in vegetation (mean percentage + standard error) on twenty-five quadrats (625 ha) located in the vicinity of areas utilized by the Mexican prairie dog as determined from a series of aerial photographs from 1965 and 1999 of the Vanegas valley of San Luis Potosi where the El Manantial complex is located. % Change = (1999 per cent cover – 1965 per cent cover)/ 1999 per cent cover for each category.

Land cover (use) class	Year		% Change
	1965	1999	
Grassland	17.04±3.11	10.48±2.20	- 38
Shrub-land	71.08±4.67	76.60±4.64	+ 8
Mesquite woodland	7.60±2.20	8.24±2.23	+ 8
Agriculture	3.80±1.71	4.14±1.66	+ 9
Roads, etc.	0.48±0.22	0.54±0.41	+ 12

Biomass production for each treatment (total, partial and no exclusion) was significantly higher on the more productive soils at the Rancho Los Angeles complex than on the poorer soils at the El Manantial complex (Table 4, Wilcoxon-Mann-Whitney tests, $p < 0.005$ in each case). Additionally, within a site, significant differences (Wilcoxon-Mann-Whitney U-tests, $p < 0.05$ or lower) between the different levels of exclusion were recorded. Overall, production of standing crop biomass was seven times greater at the Rancho Los Angeles complex with exclusion of livestock and small mammals and five times greater with exclusion of livestock only than at the El Manantial complex. No standing crop biomass was measurable at the El Manantial complex for the no exclusion treatment.

Table 4

Comparison of the biomass production (g/0.25m²±standard error) with complete exclusion, partial exclusion or no exclusion during the period 8/2000 until 7/2001 in the El Manantial and Rancho Los Angeles complexes. Sample size was 10 (RLA complex) and 8 (EM complex) replications for each treatment.

Treatment	El Manantial	Rancho Los Angeles
Total Exclusion	8.1±1.2	59.3±15.1
Partial Exclusion	2.8±0.7	15.2±5.8
No Exclusion	0±0	3.5±1.2

Table 5

Average densities (+ standard errors) for Mexican prairie dogs active on twelve, one-hectare quadrats in the El Manantial and Rancho Los Angeles complexes for the period 10/1999-7/2002. N.C. = no census taken.

Date	El Manantial		Rancho Los Angeles	
	Adults	Juveniles	Adults	Juveniles
Fall 1999	2.58±0.48	0.25±0.18	12.25±1.46	1.08±0.23
Spring 2000	2.50±0.36	0.83±0.83	8.42±1.08	0.58±0.19
Summer 2000	2.50±0.36	2.17±0.61	10.00±1.20	2.08±0.38
Late Summer 2000	2.50±0.42	1.42±0.56	10.17±1.27	1.75±0.28
Fall 2000	3.00±0.80	1.58±0.66	10.50±1.26	1.25±0.28
Spring 2001	3.25±0.64	0.25±0.25	10.25±1.07	0.58±0.23
Summer 2001	2.33±0.56	0.92±0.31	12.50±1.94	4.25±0.35
Late Summer 2001	2.67±0.47	1.08±0.31	16.00±1.79	3.08±0.61
Fall 2001	2.17±0.37	0.17±0.17	11.75±1.71	1.83±0.53
Spring 2002	N.C.	N.C.	N.C.	N.C.
Summer 2002	3.41±0.63	1.17±0.64	9.67±0.79	2.00±0.58

Population densities. Population densities of adults did not vary significantly seasonally within a complex during the period of study. However, juvenile densities did vary significantly seasonally within a complex due to the birth of pups during the summer seasons (Table 5, $p< 0.005$ in each complex). Population densities of the Mexican prairie dog were significantly greater at the Rancho Los Angeles complex than at the El Manantial colony during the study (for juveniles, $c^2 = 30.2$, $p< 0.005$; for adults, $c^2 = 169.7$, $p<< 0.001$). Finally, each complex had one reproductive season during the three reproductive periods studied which was significantly higher that the other two, the 2000 season for El Manantial and the 2001 season for Rancho Los Angeles (Table 6).

Table 6

Average seasonal densities (+ standard errors) for Mexican prairie dogs active on twelve, one-hectare quadrats in the El Manantial and Rancho Los Angeles complexes for the period 10/1999-7/2002.

Season	El Manantial	Rancho Los Angeles
Spring	3.04±0.41	9.92±0.81
Summer	4.17±0.48	13.50±0.91
Late Summer	3.83±0.50	13.00±1.20
Fall	3.25±0.46	12.89±0.89

The percent seasonal increments in density (*e.g.* [Summer mean density-Spring mean density]/Spring mean density multiplied by 100%) at a site are the same from Spring to Summer (+37% and +36% for EM and RLA complexes respectively) suggesting similar reproductive efforts by the species at the two sites (Table 6). However, differences vary after the reproductive season (Summer/Late Summer = -8% EM, -4% RLA; Late Summer/Fall = -15% EM, -1% RLA; Fall/Spring = -6% EM, -23% RLA) indicating differences in either dispersal of second-year young or over-winter survival between the two complexes. Overall, population growth in the El Manantial colony as represented by the *per capita* growth rate is similar (0.37) to that for the RLA complex (0.32). These growth rates were calculated from the differences between the spring average density and the summer average density, which gives the number of young produced per ha. This result divided by the average number of animals observed in the fall and in the spring count gives an estimate of the average density that a 1-ha area can support. For example, if 11.4 animals/ha can produce 3.6 young/ha, the *per capita* growth rate per ha is 0.316.

Table 7

The history of monitored areas occupied (or previously occupied) by the Mexican prairie dog from the late fall of 1998 until the end of 2002. Size is the approximate open area of the colony, distance is how far away is the nearest colony from which the species could disperse and year represents the status of the colony in November of each year in comparison with preceding year (E = extinct, O = occupied or no change, - = decreasing population, + = increasing population).

Location	Size (ha)	Distance (km)	Year 1998	1999	2000	2001	2002	2003	2004
El Manantial Complex									
La Trueba (south)	25	3.6	O	-	O	O	O	+	+
La Trueba (north)	40	3.6	O	O	O	O	O	O	+
Rancho Santa Ana	60	0.2	O	+	+	+	+	+	+
Santa Ana (east)	72	3.5	E	O	O	O	O	O	O
El Manantial (east)	5	2.9	E	O	E	E	E	O	O
San Vicente (south)	20	1.2	O	+	+	+	+	O	O
San Vicente (north)	50	1.2	E	E	E	E	O	+	O
Rancho Los Angeles Complex									
Ejido	2	0.5	O	O	E	O	+	+	+
North valley 1	0.5	0.5	E	E	E	E	O	+	+
North valley 2	40	1.0	E	O	+	+	+	+	+
North valley 3	32	0.5	O	+	+	+	+	+	+
South valley 1	36	0.8	E	O	+	+	+	+	+
South valley 2	36	1.2	O	+	+	+	+	+	+
South valley 3	50	1.2	E	E	E	E	E	E	E

(Co-ordinates of the colonies listed above – La Trueba (south) N 23º 56.98', W 100º 58.48'; La Trueba (north) N 23º 59.07', W 100 54.73; Rancho Santa Ana N 24º 09.01', W 100º 53.44' ; Rancho Santa Ana (east) N 24º 10.36', W 100º 53.84'; El Manantial (east) N 24º 09.63', W 100º 53.97'; San Vicente (south) N 24º 12.96', W 100º 52.24'; San Vicente (north) N 24º 13.46', W 100º 51.90'; Ejido N 25º 05.95', W 101º 02.84'; North Valley (1) N 25º 07.40', W 101º 02.00'; North Valley (2) N 25º 07.18', W 101º 01.95'; North Valley (3) N 25º 07.30', W 100º 01.67'; South Valley (1) N 25º 05.16', W 101º 00.37'; South Valley (2) N 25º 04.77', W 100º 59.89'; South Valley (3) N 25º 04.71', W 100º 59.41'.)

The areas monitored in 1998, that were occupied or had been used previously by the Mexican prairie dog, showed patterns of extinction and re-colonization at each complex over the six-year monitoring period (Table 7). In the fall of 1998, four of the monitored colonies were occupied at the EM complex and three were occupied in the RLA complex. No extinctions were recorded for these occupied colonies at the EM complex while one of the occupied colonies (Ejido) in the RLA complex went extinct in the late summer of 2000 but was re-colonized by four individuals in the late summer of the following year. In 2002, this colony had increased to fourteen animals through reproduction by a breeding pair and by further immigration. In the fall of 2004, the Ejido population consisted of approximately fifty prairie dogs. Of the three extinct colonies at the EM complex, all were colonized during the monitoring period with minimum dispersal distances ranging from 1.2-3.5 km. However, one re-colonization was unsuccessful (El Manantial east) and that area remained empty until 2003 when one animal took occupancy. The San Vicente north colony was colonized in 2002 by four prairie dogs (a pair plus two solitary animals), increased to fourteen animals in 2003, and remained at the number in 2004. A new colony was also established at some time during the years 2002-2003 to the east of the San Vincente south colony and all migrants most certainly came from the latter. At the RLA complex, three of the four areas, listed as extinct in 1998, were re-colonized (dispersal distances ranging from 0.5-1.2 km). The fourth area (South Valley 3) has remained unutilized throughout the study. General population trends within the monitored areas, as determined by estimates of total population size, expansion of the area utilized by the Mexican prairie dog or both, suggest that little change is occurring at the EM complex. In contrast, the colonies monitored in the RLA complex show an overall increase in numbers as well as size of area utilized (RIY, pers. obs.).

Dynamics of a prairie dog colony. The average number of animals active was significantly greater in the Periphery of the colony than in its Center (Table 8). In addition, both the Center and Periphery of the colony had significantly more animals active than did the zone of Expansion. Significantly more burrows occurred in the Periphery than in the zone of Expansion (Table 5). No differences were apparent in mean burrow density between the Center of the colony and the latter two zones. This was primarily because mound size was significantly larger in the Center and declined sequentially into the zone of Expansion (Table 5).

There were major differences between the Periphery of the colony, the zone of Expansion and the adjacent grassland in the percentage cover and relative abundance (R.A.) of the vegetation (Table 9). Grass cover was twice as great in the adjacent Grassland as it was in the Periphery of the colony and in the zone of Expansion. This difference was mainly due to the decrease in cover of palatable *Bouteloua gracilis* from the Grassland (44.4% R.A.) to the zone of Expansion (19.7% R.A.) to its absence in the Periphery. The absence of *B. gracilis* in the Periphery of the colony was made up in part by the presence of three species of low palatability grasses and sedges not recorded in the Grassland site as well as increases in the percentage cover of two other species present in the grassland. There were no differences between the three sites in total percentage cover of forbs. However, individual species did change from site-to-site. With the exception of *Euphorbia prostrata* and, to a lesser extent, *E. dentata*, the majority of the other forb species increased their percentage covers relative to the grassland in the Periphery of the colony. The most notable of these species were *Dyssodia acerosa* (0% to 29.4 R.A.), *Dyschoriste decumbens* (0% to 10.4% R.A.) and *Ambrosia artemisifolia* (0% to 8.8% R.A.), all of which have low palatability to livestock.

Table 8

Mean numbers (+ standard errors) of active animals during the sampling period, of Mexican prairie dog mounds and of the sizes of the ten largest mounds found in the centre of the far western colony of the north valley of Rancho Los Angeles, Coahuila, its peripheral zone, its zone of expansion and its adjacent, un-colonized grassland. For the number of animals active and the ten largest mounds present, data were collected from 1 ha quadrats and for the number of mounds present from twenty quadrats, 0.025 ha in size, located in each zone. N.P. = not present. Different letters in the superscripts indicate significant differences (p < 0.05) in a column.

Site	Number of animals active	Number of mounds	Size of Mound (m²)
Centre	$8.63^{b}\pm0.51$	$4.55^{ab}\pm0.37$	$13.2^{a}\pm1.2$
Periphery	$12.75^{a}\pm0.70$	$5.30\ ^{a}\pm0.38$	$8.1^{b}\pm0.3$
Expansion	$4.92^{c}\pm0.66$	$3.70^{b}\ \pm0.42$	$4.9^{c}\pm0.5$
Grassland	N.P.	N.P.	N.P.

DISCUSSION

Association with low productivity soils. It is fairly clear from the literature and from mapping extant colonies that the Mexican prairie dog is now strongly associated with low productivity grasslands occurring throughout much of its range (Treviño-Villarreal & Grant 1998, Scott-Morales *et al.* 2004). These grasslands are found in the bottoms of the larger valleys in the four-state area where they form one phase of a mosaic with semi-arid shrub-lands. They are underlain by gypsum rock, originating from eroded marine sediments that were deposited during the Pleistocene (DETENAL 1981). Soils formed from the gypsum support the grassland phase while areas, overlain by a fine-textured calcareous alluvium of varying thickness, support shrub-lands (Meyer & Garcia-Moya 1989, Meyer *et al.* 1993). The plants found on these gypsum soils are slow-growing endemics, such as *Muhlenbergia purpusii* and *Bouteloua chasei*, and their plant communities show no decrease in basal cover and are not subjected to woody shrub encroachment under grazing pressure from domestic animals (Meyer & Garcia-Moya 1989). The results show that production of standing crop biomass on these soils in the

Table 9

Percent cover ($\overline{X}$ + standard error) and relative abundance (%) of plant species encountered in the periphery, zone of expansion and the adjacent grassland of the far western colony of the Mexican prairie dog in the north valley of Rancho Los Angeles. n = 50 quadrats each in the periphery and zone of expansion and 25 quadrats for the adjacent grassland. Different letters in the superscripts indicate significant differences (p < 0.05) in a row.

	Periphery			Expansion			Grassland		
	$\overline{X}$	S.E.	%	$\overline{X}$	S.E.	%	$\overline{X}$	S.E.	%
Grasses and Sedges									
Bouteloua gracilis	0^{a}	0	0	4.32^{b}	0.63	19.7	11.32^{c}	1.56	44.4
Buchloë dactyloides	1.76^{a}	0.50	6.9	0.04^{b}	0.04	0.3	0^{b}	0	0
Carex sp.	1.07^{a}	0.35	4.2	0^{b}	0	0	0^{b}	0	0
Erioneuron avenaceum	0.75	0.50	3.0	0	0	0	0	0	0
Muhlenburgia arenicola	0.42	0.25	1.7	1.24	0.34	5.7	1.52	0.87	6.0
M. villosa	3.00^{a}	0.91	11.8	0.62^{b}	0.28	2.8	0.04^{b}	0.04	0.1
Scleropogon brevifolius	*0.94*	*0.44*	*3.7*	*0.21*	*0.19*	*1.0*	*0.20*	*0.20*	*0.8*
Total Community	7.94^{a}	1.25		6.43^{a}	0.77		13.08^{b}	1.51	
Herbs									
Acourtia nana	1.06	0.31	4.1	0.55	0.16	2.5	0.20	0.10	0.8
Ambrosia artemisifolia	2.22^{a}	0.70	8.8	0.18^{b}	0.10	0.8	0^{b}	0	0
Dyschoriste decumbrens	1.64^{a}	0.54	10.4	0.26^{b}	0.26	1.2	0^{b}	0	0
Dyssodia acerosa	7.46^{a}	1.67	29.4	0^{b}	0	0	0^{b}	0	0
Euphorbia dentata	0^{a}	0	0	0^{a}	0	0	0.44^{b}	0.27	1.7
E. prostrata	3.78^{a}	0.83	14.9	13.52^{b}	1.70	61.9	11.48^{b}	2.25	45.1
Krascheninnikovia lanata	0	0	0	0.36	0.36	1.6	0	0	0
Sphaeralcea hastulata	0.28	0.11	1.1	0.55	0.27	23.5	0.28	0.15	1.1
Total Community	16.44	1.90		15.42	1.71		12.40	2.30	_
Total	**24.38**	**2.06**	**100**	**21.85**	**1.98**	**100**	**25.48**	**3.16**	

El Manantial colony and the average density of the Mexican prairie dog is low in comparison to that produced on deeper alluvial soils in the RLA complex. To survive on these gypsum soils, particularly in the drier parts of the year, the Mexican prairie dog excavates and consumes the roots of perennial forbs occurring there. So, while these grasslands may be of low productivity, the Mexican prairie dog can maintain a viable population, which in one or two above average rainfall years could provide yearlings for dispersal and colonisation of other sites. Such sites may be either in areas used previously by the Mexican prairie dog or abandoned agricultural lands. The large numbers of unoccupied burrows and mounds, in various stages of erosion, within the El Manantial colony suggest that the area has been in existence for some time. Archer *et al.* (1987) found for the black-tailed prairie dogs that burrow density is a better indicator of colony age than is the density of prairie dogs. A reasonable estimate of the minimum length of time that the EL Manantial has been occupied would be three-to-four hundred years based on the shapes of the chalcedony arrowheads found there which indicate that the earliest ones were made sometime in the period of 1200-1550 AD (Rodriguez 1985).

However, the Mexican prairie dog has not always been associated with these low productivity soils. It was very clear from explorations of areas adjacent to these grasslands with extant colonies or that had been occupied by prairie dogs previously and that were now invaded by shrub-land and mesquite woodland, that all had been used previously by the species at some time in the past as remnants of their mounds were still detectable. More importantly, we found evidence of colonies of the Mexican prairie dog on the more productive, deeper alluvial soils along the sides of the valley where stands of tree yuccas now exist with a dense understory of shrubs. Such sites used to be grassland similar to that at the RLA complex, as indicated by the occasional remnant patches of *Bouteloua gracilis* in the midst of dense stands of shrubs. The only places, where no evidence of prairie dog colonies was found, were areas subjected to periodic flooding which are dominated by dense stands of the shrub *Flourensia cernua* or in large drainage lines covered with a dense mixture of tall shrubs and dwarf trees such as *Acacia schaffneri, Condalia mexicana, Prosopis laevigata, Rhus trilobata* and *Ziziphus mexicana*. At Rancho Los Angeles and in the adjacent perched mountain valleys, the Mexican prairie dog maintains high-density populations on deep alluvial soils, very similar to those described regionally for the closely related black-tailed prairie dog throughout its range in North America. There, its habitat is described as occurring in swales and bottomlands where soils are deep and finely textured (*e.g.* Bishop & Culbertson 1976, Dalsted *et al.* 1981, Weltzin *et al.* 1997, Stapp 1998). Apparently, the Mexican prairie dog has survived within its current distributional range by using these gypsum grasslands, upon which shrub encroachment is severely limited, as refuges during episodes of shrub invasion. The current episode of shrub encroachment began about 150 years ago because of overgrazing, agriculture and severe drought (Branson 1985). However, at least three previous shrub expansions have occurred (approximately 3,900, 2,500 and 990 years ago) in the desert grasslands of North America (Van Auken 2000) which probably affected prairie dog colonies as well as associated species such as bison, which graze disproportionately and more efficiently within prairie dog colonies (Coppock *et al.* 1983, Kruger 1986, Whicker & Detling 1988). For example, at archeological sites in the southern plains of Oklahoma, Texas and New Mexico, bison populations were at low abundances during these earlier episodes of shrub expansions (Dillehay 1974). The absence of bison bones in middens from these periods suggests that prairie dog abundances may have also been affected by shrub encroachment at that time. Because of the latest shrub invasions, the Mexican prairie dog appears to be associated now with low productivity, gypsum grasslands.

Population densities. Seasonal differences in the numbers of young prairie dogs produced within each complex were recorded during the 2.5-year period that censuses were taken. However, adult seasonal densities were not affected, indicating a limit to the numbers of animals that could be sustained per hectare by the vegetation. Differences in the densities of adults and young between the two complexes occurred, with the RLA complex having roughly three-to-four times as many Mexican prairie dogs active seasonally on the census plots than at El Manantial. These numbers are the same order of magnitude as those measured for the differences between the two complexes for biomass production (five-to-seven), suggesting that population densities are food limited and that the species is near its carrying capacity in each site. Reproductively, the Mexican prairie dog has approximately, the same *per capita* growth rates (0.37 EM, 0.32 RLA) which are slightly less than that of 0.41 recorded by Knowles (1986) who studied the rate of recovery of a black-tailed prairie dog colony after poisoning in Montana. Those populations returned to pre-poisoning levels within three to five years due to immigration and reproduction. An attempt to control the Mexican prairie dog population by poisoning all colonies on Rancho Los Angeles in 1972 was unsuccessful and the population had recovered by 1975 to pre-control levels (de la Cruz, personal communication). Similar observations of the rapid recovery of animal numbers in colonies of black-tailed and Gunnison's prairie dogs extirpated by plague, cessation of control measures or abandonment of agricultural lands have been cited by various authors (e.g. Cincotta *et al.* 1987, Fagerstone & Ramey 1996, Roach *et al.* 2001).

Dynamics within a prairie dog colony. It is important to understand the dynamics of prairie dog colonies and their impact on the landscape as well as the effect that natural fragmentation of the landscape has on colony development. Growth of prairie dog populations is limited by the amount of resources available to them in the immediate area of their burrows. Venturing farther a field to forage puts them at risk, particularly from aerial predators (*e.g.* Michener & Michener 1977, Hoogland 1995). In both the EM and RLA complexes, Mexican prairie dogs have a tendency to excavate a series of 4-7 short and shallow escape burrows approximately 8-10 m from and encircling their nest burrows, increasing the area in which they can forage safely (authors', personal observation). Such behavior suggests limits to the area that can be occupied by a social group, to the number of animals that can be members of a social group and to the numbers of social groups that can occupy areas suitable for a colony.

The prairie dog colony in the west of the north valley at Rancho Los Angeles most probably began with a small group of animals colonizing a low-lying area along a shallow drainage line on the valley floor. As the population increased in number, the quality and quantity of the forage available to the animals was not sufficient to sustain the population increase and the colony began to expand into areas adjacent to the colony center. Such patterns and processes have been recorded by other investigators for prairie dogs (*e.g.* Weltzin *et al.* 1997). First, there are differences between the vegetation within a colony and in the adjacent unused areas. Areas within a prairie dog colony are dominated by annual forbs while palatable perennial grass species are prevalent in the adjacent, unutilized grasslands (Bonham & Lerwick 1976, Dalsted *et al.* 1981, Garrett *et al.* 1982, Coppock *et al.* 1983, Uresk 1984, Archer *et al.* 1987, Whicker & Detling, 1988). In addition, Archer *et al.* (1987) and Whicker and Detling (1988) put their results in a temporal context in which they found that the displacement of palatable perennial grass species within the colony is rapid, occurring within 2-3 years after colonization of an area and that an unpalatable annual component of forbs became dominant after 4-6 years. Finally, Garrett *et al.* (1982) studied the demography of a newly established prairie dog colony with room for expansion and an old colony with little room for expansion, both colonies suffering similar low rates of predation. They found that in the younger colony there were more pregnancies that are successful, larger litters, faster juvenile growth and yearlings more likely to reproduce, greater survivorship of young and adults, and a density two times greater than that of the old colony. These investigators attributed the differences in the two colonies to the availability of food resources. Distinct vegetation zones were visible in the old colony but were not evident in the young colony. Highly preferred species, such as *Bouteloua gracilis* and *Agropyron smithii*, dominated the grass component in the young colony while unpalatable grass species, such as *Aristida oligantha* and *Schedonnardus paniculatus*, were dominant in the old colony. In our study, *B. gracilis* was not recorded in the center and periphery of the far western colony, had reduced cover in its zone of expansion and was the dominant grass species in the adjacent unutilized grassland. We can estimate roughly from our data on seasonal prairie dog densities (Table 4) and the sizes of the colony center (3.5 ha) and the peripheral zone (37.5) ha, the minimum time the peripheral zone has been occupied at carrying capacity using the following assumptions: the differences between the spring average density and the summer average density gives the number of young produced per ha (3.6) while the average of the number of animals observed in the fall and in the spring count (11.4) gives an estimate of the average density that a one ha area can support annually. If 11.4 animals/ha can produce 3.6 young/ha, the *per capita* growth rate per ha is 0.316. Using the equation, $N_t = N_0 e^{rt}$, it would take a minimum of 8 years, after the two-to-three years necessary to deplete the preferred forage species in the colony's center, for the peripheral area to be occupied at a capacity of 11.4 prairie dogs per ha. The far western colony has been in existence for a much longer period of time than that and has not grown at the rate we measured in our study due to natural predation, human disturbance (poisoning, recreational shooting) and torrential rainstorms (de la Cruz, personal communication). Of these factors, only natural predation and torrential rainstorms serve now as a control on the growth of the Mexican prairie dog population in the north valley at Rancho Los Angeles, where there are presently four large colonies, separated from one another by receding *B. gracilis* grassland, each of which have expanded during the course of the study. The group of colonies currently extant should fill the north valley at Rancho Los Angeles within the next eight years there. The effect then on the population characteristics of the Mexican prairie dog in this valley should be similar to that for the old colony studied by Garrett *et al.* (1982).

Endangered status. Many authors have described the patchy distribution of colonies of the Black-tailed prairie dog group, attributing it to fragmentation of the landscape by variation in topography, soils and land-use history (e.g. Halpin 1987, Stapp 1998, Ceballos *et al.* 1999). The literature also suggests that this fragmentation of habitat is of relatively recent origin due to the alteration of habitat, recreational shooting and agricultural control from the late 1800's and exacerbated by the arrival of sylvatic plague during the 1920's (USFWS 1991b, Roach *et al.* 2001). However, the ancestors of the prairie dogs separated from the ground squirrels (*Spermophilus*) 2-to-3 million years ago during the Pliocene and began appearing regularly in the fossil record during the Pleistocene (Hoogland 1995), occurring disharmoniously with small mammalian species typical of tall grasslands interspersed amidst wooded areas (Graham & Lundelius 1984, Guthrie 1984). Throughout the Pleistocene, climatic fluctuations caused as many as 15 to 20 glacial periods which had major effects on the grasslands of North America (Van Devender 1995). During the Ice Age(s), these grasslands were highly fragmented with regions of the central Great Plains covered by parklands (*i.e.* grasslands with clumps of trees and shrubs) of *Pinus, Picea* and *Betula* while to the south, on the Llano Estacado of Texas, pollen records indicated the presence of open pine parkland where today there is found short-grass prairie. While present day North American grasslands have only been in existence for the last 9,000-10,000 years (Wedel 1983, Van Devender 1995), they too have experienced fragmentation in the form of multiple woody shrub invasions (Van Auken, *op. cit.*). Thus, populations of the black-tailed prairie dog group have had a long history of habitat fragmentation. Coupled with this fragmentation would be isolation of prairie dog colonies, with smaller ones having a high probability of extinction, particularly at the limits of its distribution (Lomolino and Smith 2001). Their survivorship as a species probably depended on the evolution of long-distance dispersal, examples of which have been reported by Cincotta *et al.* (1987), Halpin (1987), Hoogland (1995) and this study. Long-distance dispersal gives prairie dogs the opportunity to re-establish periodically in areas where previous colonies had gone extinct. Hence, members of the black-tailed prairie dog group probably function as a metapopulation in which the processes of extinction and colonization of patches of habitat suitable for the species are more important than the species' birth and death rates (Hanski & Gilpin 1997, Harrison & Taylor 1997, Hanski 1998). The term «metapopulation» has only been applied recently to prairie dogs (Lomolino and Smith 2001, Roach *et al.* 2001) but the concept needs to be considered carefully by conservationists in terms of the development of a recovery and management plan for the Mexican prairie dog.

Is the endangered status of the Mexican prairie dog warranted? This study was based on the preliminary work of Ceballos *et al.* (1993) in which they reported finding only twenty active and two extinct Mexican prairie dog towns in the four-state region. In contrast, this study recorded fifty-six active colonies in a two-state region (San Luis Potosi and Coahuila) in 1999. At that time, Treviño-Villarreal and Grant (1998) reported finding eighty-eight active and six inactive colonies in the four state region. A comparison of the two records showed that there were more than one hundred active colonies of the Mexican prairie dog. Later Scott-Morales and Estrada (1999) visited fifty-five of these colonies measuring their area and, using visual counts, estimated that there were more than 118,000 Mexican prairie dogs in existence. Considering that only about one half of the extant colonies were visited in their study, this species is comprised of between 200,000 and 250,000 animals. It is difficult to state with assurance what these numbers of animals indicate about the endangered status of the Mexican prairie dog. The only other species of prairie dog that has been listed as endangered in the past is the Utah prairie dog (*C. parvidens*). This species was estimated to have a total population of around 20,000 animals in 1920, which decreased to about three thousand animals in 1972 as a result of agricultural development, hunting, poisoning and sylvatic plague (USFWS 1991b). The species was listed as endangered in 1973 and maintained that status until 1984, when it was reclassified as threatened because its numbers had begun to increase, reaching nearly 8000 animals by 1989.

In contrast, the Mexican prairie dog has more than 200,000 individuals in over 100 colonies of varying sizes. The species is supposedly in danger of extinction due to large-scale agricultural development in the northern part of its range. However, in the eastern part of Coahuila, where Rancho Los Angeles is located, and in the adjoining western parts of Nuevo Leon, such development appears to have peaked due to limited supplies of water for irrigation. The Mexican prairie dog (authors', personal observation) rapidly repopulated lands in the region that had been cleared for agriculture and later abandoned.

The Mexican prairie dog is most likely to become more limited in its distribution due to extinction of colonies in the southern part of its range than in the north. In the southernmost complex, El Manantial, colonies are much more isolated from one another than in the north (Scott-Morales *et al*, 2004). In the El Manantial colony, one is struck by the large area covered by abandoned prairie dog mounds in various states of deterioration and by the paucity of prairie dogs. An initial impression is that something is drastically wrong ecologically. However, it is a false impression. During this study, prairie dog populations at the EM and RLA complexes maintained relatively constant densities while overall numbers in each region were increasing. This change in overall numbers is more apparent in the colonies occupying the more productive soils at the RLA complex. There, population growth appears to be dynamic because of the greater number of animals present and of young produced, the combination of which resulted in yearly increases in the area used by the species. In contrast, population growth in the El Manantial colony appears to be static due to its lower (but constant) densities and numbers of young produced annually, all of which are more widely spaced within the available area due to the low productivity of the soils there. The main difference between the two complexes is that the metapopulational dynamics functions better at the RLA complex because the density of the prairie dogs is higher there, which leads to the annual production of more long-distance dispersers. Thus, the probability of the establishment of new colonies in the region or the re-colonization of areas where prairie dogs colonies had previously gone extinct is higher in the north. In contrast, prairie dogs in the El Manantial complex have a lower probability of establishment because there are fewer dispersers produced by the population. There, colonization events are not an annual occurrence but are most likely to occur only after a series of above average rainfall years, which increase the standing crop biomass and augment the population size of the Mexican prairie dog.

Finally, there is no dispute that the numbers of colonies and individuals of the black-tailed prairie dog group have decreased during the last century. Nor is there an argument against the reasons put forward to explain these reductions in numbers. However, such decreases have occurred previously in the long history of the group. Prairie dogs may have evolved as metapopulations because of earlier events that caused fragmentation of their habitats, their rapid population growth within those fragments, and the impact of resource limitation and disease on those animals that inevitably lead to the evolution of long-distance dispersal. As a result, the Mexican prairie dog does not appear to be in immediate danger of extinction. Populations of the species in the southern part of its range could begin to function more effectively with an infusion of animals from the north transplanted into areas previously used by the Mexican prairie dog in the El Manantial complex.

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