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FACTORS INFLUENCING BURROWING OWL ABUNDANCE IN PRAIRIE DOG COLONIES ON THE SOUTHERN HIGH PLAINS OF TEXAS

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ABSTRACT.—Large numbers of Western Burrowing Owls (*Athene cunicularia hypugaea*) nest in black-tailed prairie dog (*Cynomys ludovicianus*) colonies in the southern high plains of Texas. Because the Western Burrowing Owl is a species of concern with an uncertain future due to widespread extirpation of prairie dogs, we examined the roles of prairie dog colony size, burrow density, proxies of prey availability, and vegetative composition and structure on owl abundance and reproductive rate. The number of nesting Burrowing Owl pairs was positively correlated to colony area ($r^2 = 0.550$, P = 0.006) and to number of prairie dog burrows in a colony ($r^2 = 0.733$, P = 0.0230). Burrowing Owl numbers and reproductive rate (maximum number of young seen per successful pair) were not related to our measures of vegetative composition and structure in prairie dog colonies, nor to indices of prey availability.

KEY WORDS: Western Burrowing Owl; Athene cunicularia hypugaea; prairie dog; Cynomys ludovicianus; population size; reproductive rate.

FACTORES QUE INFLUYEN LA ABUNDANCIA DE *ATHENE CUNICULARIA HYPUGAEA* EN COLONIAS DE *CYNOMYS LUDOVICIANUS* EN LAS ALTIPLANICIES DEL SUR DE TEJAS

RESUMEN.—Grandes cantidades de individuos de *Athene cunicularia hypugaea* anidan en las colonias de *Cynomys ludovicianus* en las altiplanicies del sur de Tejas. Dado que *A. c. hypugaea* es una especie de interés conservacionista con un futuro incierto debido a la extendida eliminación de *C. ludovicianus*, examinamos el papel del tamaño de la colonia de *C. ludovicianus*, de la densidad de madrigueras, de los indicadores de disponibilidad de presa y de la composición y estructura de la vegetación sobre la abundancia y la tasa reproductiva de *A. c. hypugaea*. El número de individuos de *A. c. hypugaea* estuvo positivamente correlacionado con el área de la colonia ($r^2 = 0.550$, P = 0.006) y con el número de individuos de *C. ludovicianus* en una colonia ($r^2 = 0.733$, P = 0.0230). Las cantidades y las tasas reproductivas (número máximo de pollos vistos por pareja exitosa) de *A. c. hypugaea* no estuvieron relacionadas con nuestras medidas de composición y estructura de la vegetación en las colonias de *C. ludovicianus*, ni con los índices de disponibilidad de presa.

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Western Burrowing Owls (Athene cunicularia hypugaea) are widely distributed across the western portion of North America from deserts to grasslands to agricultural areas (Haug et al. 1993). Declines in the range and numbers of Burrowing Owls across the species' North American distribution have been attributed primarily to habitat destruction and land conversion (Desmond et al. 2000, Korfanta et al. 2001, Martell et al. 2001, Murphy et al. 2001, Sheffield and Howery 2001). Burrowing Owls are thus considered a U.S. Fish and Wildlife Service (U.S.F.W.S.) regional conservation priority (U.S.F.W.S. 2001).

Burrowing Owls are migratory over much of their range. One region that has both summer (breeding) and winter populations is the southern high plains of Texas, although relatively little research has been done on Burrowing Owls in this region. McIntyre (2004) found a long-term decline since the 1940s in the number of wintering owls recorded in Christmas Bird Counts for this area, whereas Breeding Bird Survey data suggested that summer Burrowing Owl populations may have remained stable since the 1960s. These factors, as well as a dearth of information on nearly all aspects of Burrowing Owl ecology for this region, make this an important area in which to examine owl abundance and reproductive rate.

In this region, Burrowing Owls nest almost exclusively in burrows excavated by black-tailed prairie dogs (Cynomys ludovicianus). Published reports differ on whether Burrowing Owl numbers are related to prairie dog colony size. Orth and Kennedy (2001) in Colorado and Restani et al. (2001) in Montana found no relationship between colony size and number of Burrowing Owls, whereas Desmond and Savidge (1996) found a positive correlation between colony size and number of Burrowing Owls in Nebraska. In the southern high plains of Texas, the number of Burrowing Owls observed while surveying prairie dogs in a 12-county area was positively, but weakly, correlated to prairie dog colony size, with a >20-fold range in the number of owls seen in smaller (2 to 20 ha) prairie dog colonies (Pruett 2004). Given this preliminary information and the variation in the relationship between colony size and owl abundance in other locations, we hypothesized that: (1) prairie dog colony size (area) would be positively correlated to numbers of Burrowing Owls; moreover, since such a relationship may be driven more by the number of vacant prairie dog burrows (representing potential nest burrows for owls) than by current prairie dog population size or colony extent, we hypothesize that (2) both owl numbers and reproductive rate would be

positively correlated to burrow density. We also hypothesized that (3) Burrowing Owl abundance would be negatively associated with the amount of vegetative cover, and (4) owl abundance and reproductive rates would be positively associated with prey abundance, based on published literature (vegetation: Bonham and Lerwick 1976, Whicker and Detling 1988, Schmutz 1997, Trulio 1997, Clayton and Schmutz 1999; and prey: Gleason and Johnson 1985, Orth and Kennedy 2001). Finally, we also expected that (5) there would be fewer owls (and lower reproductive rates) in nest burrows located farther from wetlands because the latter are well-known regional foci for biodiversity (Bolen et al. 1989).

Linkages among prairie dog colony traits, vegetation, and owl prey have not been investigated in west Texas: it is currently unknown to what extent prairie dog colony size (and other factors such as vegetation changes elicited by prairie dogs, and owl prey abundance) influences owl breeding population size, nest-site (nest burrow) selection, and reproductive success of Burrowing Owls. Here, we provide information about Western Burrowing Owls from the southern high plains of Texas, a region that supports a relatively stable population of this species. Studies of Burrowing Owls in association with prairie dogs are scarce in this region, however, which is especially important in light of declining prairie dog populations and subsequent conservation concern.

METHODS

Study Sites. We selected three sites on the U.S. Department of Energy/National Nuclear Security Administration Pantex Plant in Carson County, TX, and three in the Lubbock area, Lubbock County, TX (Table 1). Study sites were chosen to have regionally representative patterns of surrounding land use (namely, agriculture and urbanization in the form of industrial use and residential development) and histories of on-site control of prairie dog numbers. The Pantex Plant is a controlled-access facility; it included two pastoral (grazed) agricultural sites and one urbanized/industrial site; two of the three Pantex sites had a known history of prairie dog control activities but primarily limited to where perimeters extended into operational areas. The Lubbock sites included three urbanized sites, one of which was on industrial property; the other two were located near housing developments. We knew from previous surveys (McCaffrey 2001, Pruett 2004) that these areas provided nesting sites for

Table 1. Data on Burrowing Owls, prairie dogs, and burrows from six intensively monitored sites from Lubbock and Carson counties, Texas, and data known prior to the start of the 2003–2004 field seasons.

SITE	County	HISTORIC TREATMENT ^a	SURROUNDING LAND USE	COLONY AREA (ha)	OWLSb	Prairie Dogs ^c	NUMBER OF BURROWS	BURROW DENSITY ^d	INDEX OF BURROW VACANCY ^e
L103	Lubbock	None	Residential/ urban	14.37	27	80	938	80.10	11.73
School	Lubbock	None	Residential/ urban	12.78	18	142	595	78.77	4.19
X-Fab	Lubbock	None/PT	Industrial/ urban	37.15	14	22	649	58.36	29.50
12-36	Carson	PT	Industrial/ urban	11.61	15	84	1179	99.39	14.04
Pantex Lake	Carson	None	Agricultural	22.63	10	145	810	107.93	5.59
Zone 4	Carson	PT	Agricultural	5.20	2	28	266	86.44	9.50

^a PT denotes known (2003–2004) prairie dog control efforts using Phostoxin.

Burrowing Owls on prairie dog colonies ranging from 3.1 to 37.1 ha.

Capture and Marking of Owls. We used bal-chatri traps, noose carpets, walk-in traps, and bow nets (Bloom 1987, Bloom et al. 2007) to capture Burrowing Owls from 2002–2004; details may be found in Teaschner (2005). We banded captured owls with one aluminum band issued by the U.S. Geological Survey Bird Banding Laboratory, and one red alphanumerically coded anodized band. We recorded captured individuals as adult or juvenile based on plumage (Haug et al. 1993). All research was conducted following methods approved by the Texas Tech University animal care and use committee (protocol # 03014-02). All owls were captured/marked under U.S.G.S. banding permit #22801 (C.W. Boal) and Texas Scientific Permit SPR-0201-137.

Owl Abundance and Reproductive Rate. We endeavored to resight banded owls in both summer (breeding season) and winter to determine site and burrow fidelity, as well as inter-seasonal and interannual movements. We monitored Burrowing Owls with spotting scopes and binoculars from parked vehicles, which we used as viewing blinds (Coulombe 1971). Identification of individual Burrowing Owls was used to determine individual nest sites, between-year area and pair fidelity as well as timing of seasonal migrations. We considered pairs of adult owls occupying a nest burrow and engaging in typical pair behaviors (e.g., allopreening, prey deliveries) as a nesting pair. However, determination of nesting success by Burrowing Owls is challenging because

nests are not directly observable inside nest burrows; quantifying productivity in Burrowing Owls is thus not straightforward, and various methods have been used, potentially confounding comparisons among studies (Garcia and Conway 2009). We assessed nesting success on the basis of "apparent productivity" determined by documenting the number of nestling or fledgling owls at a given owl pair's known nest burrow. To do so, we monitored nest burrows for three separate 10-min periods within a 2-wk period as nestlings began to emerge from nest burrows (Gleason and Johnson 1985). We defined a nesting pair of owls as successful if at least one nestling was observed outside of the pair's nest burrow, and we defined estimated productivity for each nesting pair as the maximum number of young birds seen during any one observation period for each nest burrow. Once a nestling was observed aboveground it was considered "fledged," although this term is here used in a broad sense because the owlets were not flighted and would retreat down the nest burrow. We recorded the number of Burrowing Owls, marked Burrowing Owls, nest burrows, and maximum number of young seen per nest burrow (Martin 1973, Green and Anthony 1989, Desmond and Savidge 1996). We attempted to search all six main sites ≥1 time/wk to minimize underestimations of owl abundance due to imperfect detections of this burrowing species that alters its activity according to ambient conditions (Conway et al. 2008, Manning 2011).

^b Numbers of Burrowing Owls counted during prairie dog surveys in 2002 (Pruett 2004).

^c Number of prairie dogs estimated using model based on three independent surveys (Pruett 2004).

^d Number of prairie dog burrows per hectare.

e Index of the abundance of vacant burrows, based on number of prairie dog burrows per prairie dog.

Prairie Dog Abundance and Burrow Density. We examined correlations between number of Burrowing Owl pairs and productivity to (1) prairie dog colony size (spatial area), (2) number of prairie dogs, and (3) number of vacant prairie dog burrows in 2003-2004. We conducted an average of 3.5 (±1.8) searches per mo at each of our six focal colonies between September 2003 and April 2005 to count the number of marked Burrowing Owls observed. We determined perimeters of the study colonies by walking around the exterior burrows with a handheld global positioning satellite (GPS) unit (Garmin model 12, Garmin International Inc., Olathe, KS), and uploaded the GPS track to a computer to determine colony area. We estimated the number of prairie dogs during three counts, following Pruett (2004).

During 2004, we made a complete count of all burrows on each of our sites. We recorded locations of each prairie dog burrow at the six sites, including burrows used as nest burrows by Burrowing Owls, with a GPS unit. To obtain overall burrow density per prairie dog colony, we created 50-m buffers from prairie dog colony centers using ArcView GIS and counted the number of owl nest burrows per unit area. Given the size of prairie dog colonies on our sites, all nest burrows were within three of these 50-m buffers from the colony center. We also derived an index of burrow vacancy as a function of prairie dog population per colony by dividing the number of burrows counted at each site by the estimated number of prairie dogs present (Pruett et al. 2009; Table 1). Although this index may be an overestimate (if prairie dogs used more than one burrow), we reasoned that sites with a higher index (more burrows per prairie dog; e.g., a portion of the colony with higher burrow availability) should have more vacant burrows available for Burrowing Owls to use. If true, then there may also be a positive relationship between number of owl nest burrows and prairie dog burrow spacing (i.e., the average distance among prairie dog burrows). To estimate burrow spacing, we randomly selected an equal number of prairie dog burrows as there were Burrowing Owl nests on each site, and compared distance from each nest burrow to its five closest prairie dog burrows to the distance from the random burrows to their five closest prairie dog burrows.

Indices to Prey Abundance. Distance to playas (ephemeral freshwater wetlands) containing water was used as one index of food availability, because many amphibians and insects in this area use playas

to complete their life cycle (Anderson 1997). Playas are regional foci of biodiversity (Bolen et al. 1989). The locations of playas were identified from digital layers based on hydric soils (Fish et al. 1998, Pruett 2004). We checked for the presence of water while Burrowing Owls were nesting and recorded distances to nearest playas containing water to correlate distance to playas containing water to number of Burrowing Owl nests and nest success using Pearson's product moment correlation.

We also assessed relative abundance of small mammals, a potential food source for Burrowing Owls, on the six prairie dog colonies in June–August 2003 and 2004. Trapping grids consisted of 100 Sherman live traps, 10 m apart, set for three consecutive nights during summer (Burrowing Owl nesting season). All captured mammals were identified to species and sexed, weighed, measured, and marked for identification upon recapture as part of a concurrent project (Pruett et al. 2010). We compared numbers of initial captures between sites for all species that we considered possible prey for Burrowing Owls to assess relative abundance of foods in relation to Burrowing Owl nest-burrow density and nesting success.

Vegetation Structure and Composition. We also examined vegetative data to assess characteristics of Burrowing Owl nesting sites and vegetative structure and composition. Two 25-m line intercept transects were randomly placed in each prairie dog colony. During summer in 2003 and 2004, we record the percent cover (intercept distance) of vegetation along each transect by mutually exclusive category: grass, forb, shrub, litter, bare ground, or other (Bullock 1996). Visual obstruction was estimated using Robel pole measures (n = 6/transect; Vermeire et al. 2002) taken at 5-m intervals along each 25-m transect. We modified the lowest 2 decimeters of our pole, marking off 2-cm intervals to record <1 decimeter vegetation heights. Raw data on visual obstruction scores and percent cover by site may be found in Teaschner (2005).

Statistical Analyses. We used SAS 9.4 (SAS Institute Inc., Cary, NC) to perform all statistical tests at an $\alpha=0.05$ level of significance, and we report means and standard errors for variables of interest. We used a generalized linear model analysis of variance (ANOVA) to examine differences in owl abundance and productivity by site type (agricultural vs. residential urban vs. industrial urban) and year. Pearson correlation analysis was used to explore possible relationships between owl abundance and prairie dog colony size, number of burrows, prairie dog

Table 2. Summary of Burrowing Owl captures and resightings by season for Burrowing Owls captured at six study sites in Lubbock and Carson counties, Texas, between January 2003 and May 2005, including three additional winter owls captured on adjacent Carson County sites in February 2004. More winter-marked owls were residents than summer-marked ones ($\chi^2_1 = 10.20$, P = 0.004).

SEASON	NUMBER BANDED	NUMBER COLOR- BANDED	Number Never Observed Again	NUMBER OBSERVED IN THE SEASON BANDED ^a	Number Observed in ≥1 Other Season	Number Observed in the Same Season the Next Year ^b	NUMBER OF KNOWN RESIDENTS ^c
Winter	16	9	3	4	1	0	4
Summer	123	108	51	57	2	10	4

^a Burrowing Owls seen in season they were banded (includes late-migrating owls that were no longer observed within 2 wk of the end of the season of capture).

abundance, vegetation parameters, and prey availability. A Pearson chi-square analysis was used to examine whether the distribution of prairie dog burrows (our density index) behaved according to chance (with the expected distribution of burrows equal across all portions of a prairie dog colony). We analyzed data separately for each year to determine whether pooling data across years was possible, and then subsequently pooled and re-ran our analyses on productivity.

RESULTS

We captured Burrowing Owls (n=153; 137 adults, 16 juveniles) between January 2002 and July 2004. Most owls (89%; 137 of 153) were captured during the summer breeding periods. Only 12% (n=16; three on the added sites) of all owls were captured during the winter periods. Our sites had 3–7 times more Burrowing Owls during the summer breeding period (between March and September) than they did during the winter (October through February).

There were more known resident winter-marked owls (44.4%; four of nine) than summer-marked (3.7%; four of 108) owls (Table 2). Some additional owls may have been resident, including owls that were observed the summer following the year in which they were marked (9.3%; 10 of 108). These owls may have overwintered in the region undetected at sites that we did not survey, or they may have migrated south and returned to the same sites to breed the following summer. Additionally, 2.6% of our marked owls (3 of 117) were seen in only two consecutive seasons (one seen winter and the following summer, and two seen summer and the following winter). We therefore determined that most Burrowing Owls in this area were summer residents

only, with only a small proportion (6.8–18.0%, or 8–21 of 117 total marked owls) likely remaining overwinter between consecutive breeding seasons. Furthermore, in over 406 d of searching at the six intensively monitored sites and 43 d of searching adjacent sites within 8 km of the focal colonies, no marked owl was ever observed at any site other than the one at which it was captured.

We identified 98 nesting pairs on our six sites during 2003 (n = 57) and 2004 (n = 41). The earliest date we recorded seeing young was May 19, and the last observed emergence of new young was June 25. Numbers of nesting pairs/ha ($F_{3,8} = 1.80$, P =0.2251) and productivity (number of chicks per nesting pair; $F_{3,8} = 0.87$, P = 0.4940) did not differ between years. Therefore, we pooled these data across years for analyses of owl productivity. There was an average of 1.02 (± 0.40) nesting pairs/ha on our sites, and productivity averaged 2.80 (±0.13) young per nesting pair (Table 3). There was no significant difference in overall owl abundance ($F_{2,3}$ = 5.60, P = 0.0972), number of nesting pairs ($F_{2,3} =$ 1.576, P = 0.3418), or number of young per nesting pair $(F_{2,3} = 0.78, P = 0.5321)$ by site type.

The number of Burrowing Owl pairs was positively correlated ($r^2=0.5498$, P=0.0060) to prairie dog colony size. The number of prairie dog burrows increased with colony size ($r^2=0.7006$, P=0.0377). The number of Burrowing Owl pairs was positively correlated ($r^2=0.7327$, P=0.0296) to the number of prairie dog burrows on our six sites in 2004, and mean distance between burrows of nesting pairs was 66.3 m (± 4.22). However, number of Burrowing Owl pairs was not related to either the density of prairie dogs (estimated prairie dogs per ha; $r^2 < 0.3$, P > 0.1) or the index of vacant burrows

^b Burrowing Owls seen, in this case, the summer after the summer that they were banded. These birds may have remained in the area but wintered at sites where we did not observe them.

^c Burrowing Owls seen in ≥3 consecutive seasons.

Table 3. Burrowing Owl nesting data for the six intensively monitored sites in Lubbock and Carson counties, Texas, for 2003 and 2004

YEAR	SITE	No. Pairs	No. Young/Successful Paira	Area (ha)	SPACINGb
2003	L103	13	3.3	11.71	49.03 ± 7.86
	School	8	2.0	7.55	55.91 ± 21.75
	X-Fab	13	2.5	14.48	67.22 ± 12.94
	12-36	9	3.4	11.86	62.80 ± 16.06
	Pantex Lake	11	2.9	7.50	64.75 ± 10.67
	Zone 4	3	3.7	1.57	71.85 ± 7.96
2004	L103	8	2.5	11.71	81.62 ± 21.01
	School	6	3.0	7.55	91.56 ± 26.43
	X-Fab	5	3.0	11.12	77.78 ± 25.32
	12-36	13	3.2	11.86	59.85 ± 8.28
	Pantex Lake	5	1.8	7.50	85.00 ± 3.03
	Zone 4	4	1.5	3.08	44.59 ± 7.38

^a Mean maximum number of nestlings seen aboveground for successful nesting Burrowing Owl nesting pairs.

^b Mean and standard error for distances between Burrowing Owl nest burrows in meters.

(number of burrows/estimated prairie dogs; $r^2 < 0.3$, P > 0.1) for our six intensively monitored sites. Burrowing Owls did not use more or less dense areas of burrows within the prairie dog colonies. There was no difference (P > 0.10) between distances from Burrowing Owl nests and total burrow distances, or between the five closest burrows to Burrowing Owl nests and the five closest to randomly selected burrows. There were more nest burrows in zones farther from the colony center but because buffers farther from the center also incorporated much larger areas, the number of nest burrows was not greater than expected if owls nested at equal densities in each zone from the center to the outer edges of prairie dog colonies ($\chi^2 = 2.40$, P = 0.3009).

Measures of visual obstruction and vegetative composition were not correlated to Burrowing Owl numbers or productivity ($r^2 < 0.4$, P > 0.1). Our measures of relative food abundance (distance to playas containing water and relative abundances of small mammals) did not show significant relationships to Burrowing Owl nesting pairs or productivity ($r^2 < 0.1$, P > 0.1).

DISCUSSION

As hypothesized, we found a positive relationship between prairie dog colony size and numbers of Burrowing Owl nesting pairs. We believe this is due to an increased number of burrows and, hence, nesting opportunities on larger prairie dog colonies (although Powell et al. [1994] point out that numbers of burrows may not be directly related to number of prairie dogs). Although we do not know how many burrows were actually vacant, it did

not appear that the number of vacant burrows in prairie dog colonies limited Burrowing Owls, as there were more burrows with little or no evidence of prairie dog activity than there were pairs of owls. Sidle et al. (2001) found that Burrowing Owls appear to prefer prairie dog colonies that are occupied by prairie dogs to those that are abandoned: they cited lack of burrow maintenance by prairie dogs and possible increases in predation as potential reasons. (With other prey [prairie dogs] absent, predators may focus more on Burrowing Owls.) In 2004, we found Burrowing Owl numbers particularly high on the 12-36 site, even following prairie dog control with Phostoxin just prior to the spring arrival of owls. However, this site was rapidly recolonized by prairie dogs from nearby untreated areas, so burrows were seldom vacant for very long.

Contrary to our hypothesis that Burrowing Owls should be associated with vegetative cover and obstruction, vegetative differences over all sites and years were not related to either Burrowing Owl nest density or productivity. This was unexpected, as vegetation height may negatively affect Burrowing Owls by obscuring prey or potential predators (Green and Anthony 1989). The lack of response we saw could be due to the fact that all six of our study sites were located on prairie dog colonies with low vegetation, mostly on grazed shortgrass prairie or neglected sites in an agricultural-suburban interface where there was minimal visual obstruction (2.7 \pm 0.16 cm). Similarly, although we hypothesized that there would be positive relationships among owl abundance, owl nesting success and productivity, and prey abundance, we found no such significant relationships. It is possible that there were abundant resources for both of our study years, or at least comparable prey availability across sites.

Most owls on our sites were resident in summer only (noted as a relatively stable long-term population by McIntyre 2004). Only 6.8%-18.0% of the owls we marked were observed overwintering or breeding on our sites in a second season. This was much lower than reported returns of owls in Florida (68%; Millsap and Bear 1997) or in California (20-25%; Coulombe 1971). A higher proportion of wintering owls than summering owls were sighted again in another season in our study. Our returns were similar, although somewhat higher, than those previously reported for other studies in the southern Great Plains. Butts (1976) reported <1% of the summer owl population present in late July returned to his study site in the Oklahoma Panhandle to breed in the following year, whereas in Dallam County, Texas, 2.7% of the owl population from late July returned the following year. However, all banded owls known to have overwintered at both the Oklahoma and Texas sites remained to breed the following breeding season. Our higher numbers relative to those reported by Butts (1976) may reflect a change since the 1970s, with fewer owls using the northern parts of their continental range (Clayton and Schmutz 1999) and more remaining or breeding in Texas. To date, we have had only two band recoveries from the 153 owls that we banded. One was killed by a car adjacent to its Lubbock banding site shortly after banding, and the other was recovered in Apatzingan, Michoacán, México, in January 2004, 7 mo after it was banded in Lubbock County during June 2003. This band recovery rate was similar to that of Butts (1976), who reported one banded female from the breeding season in the Oklahoma Panhandle, which was shot 17 mo later during early winter in Zapotlanejo, Jalisco, México. Another similar record was from an owl captured and banded in this region by Ross and Smith (1970) in March 1968 in Swisher County, Texas, and recaptured the following year in El Paso, Texas.

The productivity observed in our study area was comparable to reports from an urban site (grassland portion of an airport) in California (Thomsen 1971), residential-urban (Millsap and Bear 2000) sites in Florida, prairie dog colonies in Montana (Restani et al. 2001), and prairie dog colonies in New Mexico (Arrowood et al. 2001). However, productivity on our sites was less than that reported in agricultural

areas of central Argentina (Bellocq 1997), mixed grasslands-agricultural areas in Saskatchewan (Haug and Oliphant 1990, James et al. 1997, Wellicome 1997), prairie dog colonies on shortgrass prairie in South Dakota (Griebel and Savidge 2007), and prairie dog colonies on shortgrass prairie in North Dakota (Konrad and Gilmer 1984). These differences may be due in part to differences in habitat type among these studies compared to ours, with associated potential differences in predation risk and prey availability, but may also result from differing measurements of productivity.

Each prairie dog colony exists at a unique location in space, meaning that its inhabitants (prairie dogs and burrowing owls) are subject to unique forms of disturbance. All our study sites were subject to some form of anthropogenic disturbance. However, the number of nesting pairs of owls and the number of young per pair did not differ among the different forms of disturbance (agriculture vs. industrial urbanization vs. residential urbanization), possibly because all of the owls in our study were nesting in a similar sort of immediate environment (a prairie dog colony).

Prairie dogs are clearly important to Burrowing Owls in our area; however, the characteristics that make one prairie dog colony more suitable than others are largely unknown. It does seem that the lack of visual obstruction from tall vegetation and the large number of potentially vacant burrows are key elements in making good Burrowing Owl habitat. Lethal control of prairie dogs may initially reduce burrow occupancy by prairie dogs, leaving more burrows available for owls, although the quality of available burrows may be lacking, as well as the supply of future Burrowing Owl nest sites. Additionally, the lack of prairie dogs in a colony can lead to an increase in visual obstruction and potential loss of valuable nesting habitat.

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