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NESTING ECOLOGY OF BURROWING OWLS OCCUPYING BLACK-TAILED PRAIRIE DOG TOWNS IN SOUTHEASTERN MONTANA

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ABSTRACT.—Detailed investigations of the relationship between Burrowing Owls (*Athene cunicularia*) and black-tailed prairie dogs (*Cynomys ludovicianus*) are rare, but such information is necessary to manage the population declines of owls reported throughout much of the western United States. In 1998 we studied nest-site selection, productivity, and food habits of Burrowing Owls breeding on prairie dog towns in southeastern Montana. We located 13 breeding pairs, seven of which nested on private land. Nesting density (1 pair/110 ha) on prairie dog towns was low compared to densities in other regions. Few habitat characteristics differed between nest sites and random points, but power in statistical tests was low. Nesting density and habitat use suggested the population of owls was well below carrying capacity. Productivity was 2.6 young/pair. Owls fed on invertebrates (mainly grasshoppers and beetles), mammals (mice and voles), birds (blackbirds and buntings), and amphibians (frogs). Plague (*Yersinia pestis*), poison, and habitat conversion have fragmented prairie dog habitat and potentially threaten owl persistence in our study area.

KEY WORDS: *Burrowing Owl;* Athene cunicularia; *black-tailed prairie dog;* Cynomys ludovicianus; *plague;* Yersinia pestis; *food habits; habitat selection; Montana.*

Ecológia del anidamiento de Búhos Cavadores ocupando poblados de perros de la pradera de cola negra en el sudeste de Montana

RESUMEN.—Investigaciones detalladas de la relación entre Búhos Cavadores (*Athene cunicularia*) y perros de la pradera de cola negra (*Cynomys ludovicianus*) son raros, pero tal información es necesaria para manejar el descenso de la población de búhos reportado en la mayoría del occidente de los Estados Unidos. En 1998 nosotros estudiamos la selección de sitios nido, productividad, y hábitos alimenticios de Búhos Cavadores reproduciéndose en colonias de perros de la pradera en el sudeste de Montana. Localizamos 13 parejas reproductoras, siete de las cuales anidaban en terrenos privados. La densidad de anidamiento (1 pareja/110 ha) en los poblados de perros de la pradera fue baja en comparación a densidades de otras regiones. Pocas características del hábitat diferían entre los sitios nido y puntos al azar, pero el poder de las pruebas estadísticas fue bajo. La densidad de anidamiento y el uso de hábitat sugiere que la población de búhos estaba bien por debajo de la capacidad de carga. La productividad fue 2.6 jóvenes/pareja. Los búhos se alimentaron de invertebrados (principalmente saltamontes y escarabajos), mamíferos (ratones y campañoles), aves (mirlos y verderones), y anfibios (ranas). La peste (*Yersinia pestis*), el veneno y la transformación del hábitat ha fragmentado el hábitat de los perros de la pradera y potencialmente ha puesto bajo amenaza la persistencia de los búhos en nuestra área de estudio.

[Traducción de Victor Vanegas y César Márquez]

The recent finding that the petition to list the black-tailed prairie dog (*Cynomys ludovicianus*) under the U.S. Endangered Species Act is "warranted but precluded" draws national attention to the status and management of a declining species subjected to poisoning campaigns, recreational shooting, and introduced plague (*Yersinia pestis*). Decreases of prairie dog populations and their

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habitat are thought to be responsible for similar declines of closely associated species (Miller et al. 1994, Samson and Knopf 1994), most notably the black-footed ferret (*Mustela nigripes*) and mountain plover (*Charadrius montanus*). Burrowing Owls (*Athene cunicularia*) in the Great Plains south of Canada also rely on prairie dog habitat (Butts and Lewis 1982, Plumpton and Lutz 1993a, Desmond et al. 1995), and many states report recent declines in owl abundance (James and Ethier 1989, Marti and Marks 1989, James and Espie 1997).

Although Burrowing Owls nest extensively in prairie dog burrows, few studies have reported habitat characteristics important in nest-site selection or factors influencing owl density within prairie dog towns. In Colorado, differences between nest burrows and random burrows in surrounding burrow density, town size, and distance to road varied from year to year (Plumpton and Lutz 1993a); however, owls favored areas with lower vegetation than was available at random on prairie dog towns. In Nebraska, owls nested in loose colonies within larger prairie dog towns, but spaced themselves randomly within smaller towns (Desmond et al. 1995). Density of prairie dog burrows did not affect spacing patterns of nesting owls, and a positive relationship existed between town size and number of nesting pairs (Desmond and Savidge 1996).

Plague, poisoning, and habitat conversion have reduced and fragmented prairie dog towns across the Great Plains, including Montana (Flath and Clark 1986), but how these processes affect nest-site selection and population ecology of Burrowing Owls remains unknown. In 1998 we initiated a study in southeastern Montana to elucidate nest-site selection of Burrowing Owls occupying black-tailed prairie dog towns. We also estimated productivity and quantified food habits. We selected a study area previously mapped for prairie dogs because presence/absence of Burrowing Owls had been recorded during visits (R. Richardson, D. Tribby, K. Wittenhagen, Jr. unpubl. data). Thus, some data were available to determine the population trend of owls.

STUDY AREA AND METHODS

The study area in southeastern Montana (Custer and Prairie counties; 46°44′N, 105°38′W) encompassed approximately 400 km^2, of which 1425 ha (3.6%) was occupied by black-tailed prairie dogs. We surveyed the prairie dog complex within the Custer and Harris Creek watersheds, areas being considered for black-footed ferret reintroduction. The badland topography was gently rolling to flat (elevation 680–865 m). Vegetation was dominated by grasses (*Agropyron smithii*) and shrubs (*Artemisia tridentata* and *A. cana*). Riparian areas supported scattered cottonwood (*Populus tremuloides*) and willow (*Salix* spp.), while open stands of ponderosa pine (*Pinus ponderosa*) and juniper (*Juniperus scopulorum*) dominated hilly terrain. Climate was semi-arid. The study area was an even mixture of public (federal and state) and private land that supported livestock grazing. Recreational shooting of prairie dogs occurred year round, but was concentrated during spring and early summer.

Beginning in mid-May 1998, we used spotting scopes (15–45×) and binoculars (10×) to survey prairie dog towns for Burrowing Owls. We made no attempt to search for owls off of prairie dog towns. We scanned towns from a vehicle or on foot, concentrating effort in early morning (0500–1000 H) or late afternoon (1700–2200 H), the daytime periods when owls are most active and visible (Haug and Oliphant 1990). Presence of territorial pairs, whitewash, cast pellets, molted feathers, and prey remains were used to identify nest burrows. We used a GPS receiver (Garmen XL 12) to plot the locations of nest burrows on USGS 7.5 min topographic maps. Individual towns were visited repeatedly (every 2 wk) throughout the field season (May–August) to minimize the possibility of overlooking secretive or non-breeding owls and to monitor nesting success.

At nest burrows (N = 13), we measured elevation (nearest m with a GPS receiver) and percentage slope with a clinometer. From the nest burrow, we used a tape to measure distance to the nearest active and inactive prairie dog burrows (±0.05 m), nearest edge of the prairie dog town (±0.5 m), and nearest road (±0.5 m). We also counted active (presence of fresh diggings and/or scat) and inactive prairie dog burrows within a 30-m radius of the nest burrow (0.28 ha circle) to index prairie dog activity (Biggens et al. 1993). Size of prairie dog towns was obtained from habitat mapping with a GPS receiver conducted from July–September 1996 (K. Wittenhagen, Jr. and D. Tribby unpubl. data). We used a GPS receiver to measure distance (±50 m) from the nest burrow to the nearest neighboring nest burrow.

We also measured these same habitat variables at 13 burrows selected haphazardly from prairie dog towns not occupied by nesting owls. We selected burrows by dividing randomly selected prairie dog towns into progressively smaller quadrants bisected by the cardinal directions (numbered 1–4, chosen using a random numbers table). The number of quadrants required to narrow down to a single potential nest burrow depended upon the size of the prairie dog town. We picked only those burrows with openings large enough for nesting owls.

Terminology describing reproductive success and productivity of Burrowing Owls followed Steenhof (1987). successful pairs fledged at least one young, and productivity estimates included both successful and failed pairs We assumed every owl pair attempted to breed (i.e., laid eggs). Multiple visits (10–20) to individual nest sites throughout the breeding season permitted accurate determination of nesting success (young fledged per pair). We estimated nesting chronology from age of emerged young based on plumage (Priest 1997), assuming an in-

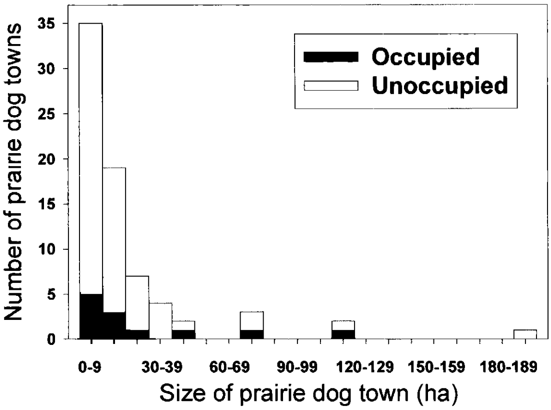

Figure 1. Size (ha) of black-tailed prairie dog towns occupied and unoccupied by Burrowing Owls in southeastern Montana, 1998.

cubation period (first egg to first hatch) of 30 d and fledging at 40 d (Haug et al. 1993).

We collected pellets and prey remains opportunistically from May–August while visiting nest sites and surrounding perching and feeding areas. Entomologists at Montana State University, Bozeman, used a dissecting scope (6.4–10×) to sort and identify invertebrate remains to family, and relied on museum specimens and Borror et al. (1989) for classification to genus. To save space, we have presented invertebrate taxa to only the family level. We checked remains of vertebrate prey against pellet contents collected during subsequent visits to the same nests to minimize duplication. We used a dissecting scope (7–30×) to identify vertebrate prey, and relied on museum specimens and Hoffman and Pattie (1968) for classification to species. Number of both invertebrate and vertebrate prey were determined conservatively by presence of diagnostic body parts (e.g., legs, mandibles, skulls). We calculated percentage biomass using estimates from Marti (1974), Rodriguez-Estrella (1997), and museum specimens.

We log transformed data prior to analyses (SPSS 1998) to achieve normal distributions (Kolmogorov-Smirnov test) and homogeneity of variances (Levene's test). However, we have presented untransformed data ($\bar{x} \pm$ SE) in this paper to facilitate interpretation. Because of the relatively small number of nesting pairs ($N = 13$) and concerns of low statistical power, we opted to reduce Type II errors by assigning statistical significance at $P \leq 0.10$ when comparing habitat variables between occupied and random sites.

RESULTS

Prairie dog towns on our study area averaged 19.5 ± 3.6 ha (range = 0.4–198.3 ha, $N = 73$). Most occupied prairie dog habitat surveyed was on private land (65%), followed by federal (30%) and state (5%) lands. Prairie dog towns averaged 11.0 ± 1.9 ha on private lands ($N = 30$) and 17.3 ± 5.3 ha on public lands ($N = 19$; $t = 0.64$, df = 47, $P = 0.53$).

Burrowing Owls nested on 12 of 73 (16%) prairie dog towns that we surveyed in 1998. We found 13 breeding pairs of Burrowing Owls on ca. 1425 ha (1 pair/110 ha) of prairie dog towns within the 400 km^2 study area. No single adult owls were observed. Size of prairie dog towns did not differ between towns occupied by owls and towns unoccupied by owls ($t = 1.24$, df = 71, $P = 0.22$; Fig. 1). Burrowing Owls neither preferred nor avoided nesting on prairie dog towns subjected to recreational shooting ($\chi^2 = 0.00$, df = 1, $P = 1.00$) or to grazing ($\chi^2 = 0.16$, df = 1, $P = 0.69$). Seven pairs nested on private land, with three pairs each on federal and state land.

Most habitat characteristics did not differ for occupied Burrowing Owl nest sites and random points (Table 1). Occupied nests were closer to ac-

Table 1. Habitat characteristics ($\bar{x} \pm$ SE) of Burrowing Owl nest sites ($N = 13$) and random sites ($N = 13$) on black-tailed prairie dog towns in southeastern Montana, 1998.

HABITAT VARIABLE	OCCUPIED SITE	RANDOM SITE	t	P
Elevation (m)	749 ± 51	752 ± 58	0.15	0.88
Percentage slope	2.6 ± 0.5	2.3 ± 0.4	0.27	0.79
Nearest active burrow (m)	14.6 ± 7.1	21.8 ± 6.4	1.81	0.08
Nearest inactive burrow (m)	6.7 ± 1.9	7.7 ± 2.8	0.68	0.50
Number of active burrows	11 ± 2	9 ± 2	0.74	0.47
Number of inactive burrows	32 ± 3	30 ± 3	0.56	0.58
Distance to town edge (m)	111 ± 36	73 ± 17	0.85	0.40
Town size (ha)	27.3 ± 10.1	25.4 ± 7.1	0.96	0.35
Nearest road (m)	227 ± 98	280 ± 110	1.29	0.21
Nearest neighbor (km)	2.2 ± 0.5	3.3 ± 0.7	1.28	0.21

Table 2. Prey of Burrowing Owls based on remains found at nest and perch sites on black-tailed prairie dog towns in southeastern Montana, 1998. Prey are expressed in number of items (*N*), percentage frequency, and percentage biomass. Unidentified items were not included in biomass estimates. Invertebrates were identified to family, vertebrates to genus or species.

TAXON	*N*	PERCENT FREQUENCY	PERCENT BIOMASS
Chilopoda			
Scolopendromorpha	1	<1	<1
Arachnida			
Scorpiones	2	<1	<1
Araneae	6	<1	<1
Non-insect arthropod	2	<1	<1
Insecta			
Odonata			
Family undetermined	1	<1	
Orthoptera			
Acrididae	311	26	9
Gryllacrididae	4	<1	<1
Gryllidae	8	<1	<1
Hemiptera			
Belostomatidae	3	<1	<1
Reduviidae	1	<1	<1
Coleoptera			
Carabidae	337	28	3
Silphidae	72	6	<1
Hydrophilidae	3	<1	<1
Histeridae	1	<1	<1
Scarabaeidae	127	11	<1
Elateridae	1	<1	<1
Tenebrionidae	81	7	<1
Meloidae	1	<1	<1
Cerambycidae	42	3	<1
Chrysomelidae	5	<1	<1
Curculionidae	12	1	<1
Diptera			
Asilidae	1	<1	<1
Muscoidea	1	<1	<1
Lepidoptera			
Sphingidae	1	<1	<1
Hymenoptera			
Sphecidae	7	<1	<1
Eumenidae	4	<1	<1
Formicidae	16	1	<1
Undetermined Hymenoptera	2	<1	
Amphibia			
Rana pipiens	28	2	10
Scaphiopus bombifrons	2	<1	<1
Aves			
Sturnella neglecta	18	1	25
Calamospiza melanocorys	22	2	11
Undetermined	1	<1	
Mammalia			
Spermophilus richardsonii	6	<1	18
Perognathus fasciatus	4	<1	<1
Peromyscus spp.	36	3	11
Onychomys leucogaster	2	<1	1
Microtus spp.	12	1	8
Zapus hudsonius	2	<1	<1
Unknown rodents	16	1	
Total	1202	100	100

tive prairie dog burrows than were random points. Neither number of active prairie dog burrows nor total number of burrows (inactive + active) correlated with town size ($P > 0.30$, $N = 26$). Statistical power was 0.35 for each of the two contrasts with low and nonsignificant *P*-values (i.e., nearest road and nearest neighbor).

Burrowing Owls produced 2.6 ± 0.4 young/pair ($\bar{x} \pm$ SE, $N = 13$ pairs). Twelve pairs (92%) each produced at least one fledgling. One pair failed for unknown reasons. Productivity did not correlate with number of active or inactive prairie dog burrows ($P > 0.30$, $N = 13$) within a 30-m radius of the nest. Productivity also did not correlate with size of prairie dog towns ($P = 0.57$, $N = 13$). Owls nesting on prairie dog towns subjected to recreational shooting ($N = 6$) had productivity similar to those nesting pairs not exposed to shooting ($N = 7$) (2.3 young/pair versus 2.9 young/pair, respectively; $t = 0.65$, df $= 1$, $P = 0.54$). By backdating from young of known age ($N = 7$ nests), we estimated a $\bar{x}$ laying date of 20 May (±1 d), $\bar{x}$ hatching date of 19 June (±1 d), and $\bar{x}$ fledging date of 29 July (±1 d).

We identified 1053 invertebrate and 149 vertebrate prey remains (Table 2). The most common invertebrate prey were grasshoppers (Orthopotera) and beetles (Coleoptera). Amphibian prey included northern leopard frogs (*Rana pipiens*) and plains spadefoot (*Scaphiopus bombifrons*). Only two species of birds were taken: Lark Bunting (*Cala-*

mospiza melanocorys) and Western Meadowlark (*Sturnella neglecta*). Mice (*Peromyscus* spp.) and voles (*Microtus* spp.) were the most common mammalian prey. Most important prey items in terms of biomass were meadowlarks (25%), mice + voles (20%), and Richardson's ground squirrels (*Spermophilus richardsonii*; 18%).

DISCUSSION

Burrowing Owl Use of Prairie Dog Towns. Two observations suggested the Burrowing Owl population was well below carrying capacity of nesting habitat on black-tailed prairie dog towns within our study area. First, density of Burrowing Owls (1 pair/110 ha) was low compared to densities in Oklahoma (1 pair/0.19 ha, Butts 1971), and $\bar{x}$ nearest-neighbor distance on our study area (2.2 km) greatly exceeded that in Nebraska (0.11–0.13 km, Desmond and Savidge 1996). In fact, only one prairie dog town supported more than one pair of owls. Second, the habitat characteristics we measured did not differ between nest sites and random points. Prairie dog towns unoccupied by owls were vacant apparently for reasons other than habitat suitability, perhaps indicating an owl population in decline (Schmutz 1997). However, conclusions regarding habitat suitability remain preliminary because some comparisons lacked adequate statistical power to detect differences between occupied and random sites.

The only habitat attribute that appeared to differ between nests and random points was distance to the nearest burrow occupied by prairie dogs, which was less for nest sites. Why owls nested near active prairie dog burrows remains unknown, but two previously noted patterns imply an anti-predator benefit. Owls nesting in areas of highest burrow density in Nebraska suffered less badger (*Taxidea taxus*) predation than did other nesting owls (Desmond et al. 2000). Badger predation on black-tailed prairie dogs also correlated positively with town size in Wyoming (Campbell and Clark 1981). Density of prairie dog burrows did not correlate with town size in both Wyoming and southeastern Montana. The relationships between badger predation and (1) burrow density and (2) town size imply that highest predation of owls should occur on large towns with low burrow density, assuming badger predation on owls occurs under the same conditions as predation on prairie dogs.

Prairie dog towns occupied by Burrowing Owls in southeastern Montana were half the size of occupied towns in Nebraska (Desmond et al. 1995). Burrow densities of prairie dog towns in southeastern Montana and Colorado (Plumpton and Lutz 1993a) were similar, but were 3× higher than in Nebraska (Desmond et al. 1995). Therefore, prairie dog towns occupied by nesting owls in southeastern Montana were relatively small and active, habitat conditions that should have minimized the probability of badger predation. Badger predation of owls did not occur during our study, supporting this hypothesis.

Historically, Burrowing Owl occupancy of prairie dog towns on our study area was highest in 1978–79 (27%, 15 of 55 towns; C. Knowles pers. comm.), intermediate in 1991 (14%, nine of 66 towns; R. Richardson and D. Tribby unpubl. data), and lowest in 1996 (4%, three of 73 towns; K. Wittenhagen, Jr. and D. Tribby unpubl. data). We recorded an increase to 16% (12 of 73 towns) occupancy in 1998. Fluctuating population size of Burrowing Owls over the past 20 yr may have reflected the impact of plague. Plague was first confirmed on our study area in 1986, and by the late 1980s had significantly reduced prairie dog populations in southeastern Montana (C.J. Knowles unpubl. data). Owl occupancy should lag behind fluctuating prairie dog populations (which it did) if towns decimated by plague provide nesting habitat for 3–4 yr before inactive burrows collapse or fill in with soil (Butts and Lewis 1982, Desmond et al. 2000).

In this study area, rodents and birds composed most of the Burrowing Owl diet by percent biomass, whereas insects dominated percent frequency. Owls nesting on prairie dog towns in Colorado and Wyoming exhibited similar prey use (Marti 1974, Thompson and Anderson 1988, Plumpton and Lutz 1993b). Use of prey varied seasonally, as mammalian prey were most important to owls early in the nesting period before insects became available (Marti 1974, Green and Anthony 1989, Schmutz et al. 1991). Owls appeared to forage for mammals mostly at night and concentrated on insects during daylight. In Saskatchewan home range size decreased significantly once insects became abundant (Haug and Oliphant 1990).

Management Implications. Productivity and juvenile and adult survivorship act in concert to determine the trend of Burrowing Owl populations (James et al. 1997, Johnson 1997, Clayton and Schmutz 1999). Some of the mechanisms that affect demography included habitat availability, predation, and food availability. Productivity and population size of Burrowing Owls in southeastern Montana during 1998 was low and we did not estimate survivorship. Populations in neighboring Saskatchewan and Alberta with similar or higher productivity showed significant annual decreases over the past decade (Hjertaas 1997, Wellicome 1997b). Our preliminary results suggested the owl population in Montana may have increased within the past 5 yr as prairie dogs rebounded from plague epizootics. However, future monitoring is warranted because productivity and density were both low, and because significant owl declines continue nearby in Canada.

Management of Burrowing Owls in southeastern Montana must consider population ecology and habitat selection of black-tailed prairie dogs. Managing plague is the greatest challenge to prairie dog conservation, and has similar potential to challenge management of Burrowing Owls in the Great Plains. Plague moved through prairie dog towns in southeastern Montana during the mid-1980s (C. Knowles unpubl. data), and reduced prairie dog populations to a level where plans to reintroduce black-footed ferrets were halted. Whether size or distribution of prairie dog towns influences epizootic severity or movement of plague remains unknown. However, because Burrowing Owls select the best, not the largest, remaining habitat patches (Butts and Lewis 1982, Warnock and James 1997), plague may severely reduce owl populations in Montana.

Burrowing Owls did not avoid nesting on prairie dog towns subjected to recreational shooting, and productivity of pairs nesting on or off shooting areas was similar. Although owls have been shot in other areas (Butts 1973), we found no evidence of shooting mortality in our area. Nonetheless, recreational shooting may have disrupted daytime foraging by adults and thus produced subtle negative effects. For example, owls fed extensively on diurnal prey (e.g., birds and grasshoppers) when the food demand of owl broods in southeastern Montana was highest, in mid- to late-July (see also Haug and Oliphant 1990). Food limits Burrowing Owl productivity during the nestling stage (Wellicome 1997a, 2000), so aboveground counts of juveniles in Montana would have underestimated nestling mortality if starvation had occurred belowground. In addition to maintaining nesting habitat, resource managers must ensure that grasslands and shrublands support the primary prey species taken by owls during the nesting season (e.g., mice and voles, meadowlarks, grasshoppers, and beetles).

Finally, management to benefit Burrowing Owls should consider historically-based negative attitudes toward prairie dogs because nesting owls were evenly distributed across both public and private lands. Many state agricultural agencies, including Montana's, continue to consider prairie dogs "vertebrate pests" requiring systematic "suppression" (Sections 7-22-2207 [6] and 80-7-1101 Montana Code Annotated). The acrimonious debate between agricultural and conservation interests impedes effective wildlife management. Conservation of prairie dog habitat can only proceed through partnerships between private citizens and government (Samson and Knopf 1994, Holroyd et al. 2001). To address both economic and conservation concerns, the Montana Prairie Dog Working Group is developing and implementing a statewide conservation plan for black-tailed prairie dogs. Incentives to maintain prairie dog habitat on private lands are an important component of the plan, as is the goal to maintain viable populations of associated species, such as the Burrowing Owl.

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