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Authors: Chipman, Erica D., McIntyre, Nancy E., Strauss, Richard E., Wallace, Mark C., Ray, James D., et al.

Source: Journal of Raptor Research, 42(2) : 87-98

Published By: Raptor Research Foundation

URL: <https://doi.org/10.3356/JRR-07-20.1>

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EFFECTS OF HUMAN LAND USE ON WESTERN BURROWING OWL FORAGING AND ACTIVITY BUDGETS

ERICA D. CHIPMAN

Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409 U.S.A.

NANCY E. MCINTYRE¹

*Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409 U.S.A.
Natural Science Research Laboratory, The Museum of Texas Tech University, Lubbock, TX 79409 U.S.A.*

RICHARD E. STRAUSS

Department of Biological Sciences, Texas Tech University, Lubbock, TX 79409 U.S.A.

MARK C. WALLACE

Department of Natural Resources Management, Texas Tech University, Lubbock, TX 79409 U.S.A.

JAMES D. RAY

BWXT Pantex LLC, Pantex Plant, Bldg. T-9061, Amarillo, TX 79120 U.S.A.

CLINT W. BOAL

U.S. Geological Survey Texas Cooperative Fish and Wildlife Research Unit, Texas Tech University, Lubbock, TX 79409 U.S.A.

ABSTRACT.—Western Burrowing Owls (*Athene cunicularia hypugaea*) often live in close proximity to humans, yet their behavioral responses to anthropogenic land use are largely unknown. We compared the diurnal foraging and activity budgets of adult male Burrowing Owls during the breeding seasons of 2004 and 2005 at three urban and three rural sites in northwestern Texas. The owls ($N = 17$ urban, 10 rural) spent most of their time being vigilant, resting, preening, perching, and in the burrow; less time was spent hunting, eating, provisioning the mate or young, flying, or engaging in other behaviors. Activity budgets did not differ significantly with land use. There were significant differences in activity budgets among study sites and with respect to times of day, weather variables, and numbers of owlets. Although hunting success and provisioning rates did not vary between urban and rural sites, aerial insects were taken as prey more often at urban than at rural sites. More foraging attempts occurred in habitats dominated by forbs, grasses, and bare ground than in areas with woody vegetation or impervious surfaces. Urban sites generally had more human forms of disturbance, but more mammalian and avian predators of Burrowing Owls were observed at rural sites. Our understanding of the behavioral effects of urbanization is still in its infancy, but the study of urban behavioral ecology will likely increase in importance as urban development continues.

KEY WORDS: *Burrowing Owl; Athene cunicularia; behavior; land use; Texas; urban.*

EFFECTOS DEL USO ANTRÓPICO DEL SUELO SOBRE EL FORRAJE Y LOS PRESUPUESTOS DE ACTIVIDAD DE *ATHENE CUNICULARIA HYPUGAEA*

RESUMEN.—*Athene cunicularia hypugaea* vive comúnmente en cercanía a los humanos. A pesar de esto, se desconocen sus respuestas de comportamiento al uso antrópico del suelo. Comparamos el forrajeo diurno y los presupuestos de actividad de machos adultos de este taxón durante las estaciones reproductivas de 2004 y 2005, en tres sitios urbanos y tres sitios rurales en el noroeste de Texas. Las lechuzas ($N = 17$ urbanas, 10 rurales) gastaron la mayoría de su tiempo vigilando, descansando, acicalándose, perchadas y en

¹ Email address: nancy.mcintyre@ttu.edu

el interior de sus madrigueras; gastaron menos tiempo cazando, aprovisionando a la pareja o al pichón, volando o realizando otros comportamientos. Los presupuestos de actividad no difirieron significativamente entre los sitios con diferente uso del suelo. Se encontraron diferencias significativas en los presupuestos de actividad entre los sitios de estudio y con respecto a la hora del día, las variables ambientales y el número de pichones. Aunque el éxito de cacería y las tasas de aprovisionamiento no variaron entre los sitios urbanos y rurales, los insectos aéreos fueron tomados como presa más comúnmente en los sitios urbanos que en los rurales. Se registraron más intentos de forrajeo en los ambientes dominados por plantas herbáceas (no gramíneas), pastos y suelo desnudo que en áreas con vegetación leñosa o con superficies duras. Los sitios urbanos generalmente presentaron más formas de disturbio humano, pero se observaron más mamíferos y aves depredadoras de *Athene cunicularia* en los sitios rurales. Nuestro entendimiento de los efectos de la urbanización sobre el comportamiento es aún prematuro, pero el estudio de la ecología del comportamiento urbano probablemente incrementará con el desarrollo de las áreas urbanas.

[Traducción del equipo editorial]

The Western Burrowing Owl (*Athene cunicularia hypugaea*) of North America is dependent upon the burrows of fossorial mammals such as badgers (*Taxidea taxus*), ground squirrels (*Spermophilus* spp.), and especially the black-tailed prairie dog (*Cynomys ludovicianus*) (Desmond et al. 2000, Sheffield and Howery 2001, VerCauteren et al. 2001). However, the numbers of black-tailed prairie dogs have been reduced by 90–98% throughout much of the species' historical range, largely due to direct eradication and to habitat destruction from agriculture and urban development (Desmond et al. 1995, Sidle et al. 2001). As a result, Burrowing Owl populations have also greatly declined, making the owl a species of conservation concern (Haug et al. 1993).

Burrowing Owls often live in close proximity to humans, yet little is known about the effects of human activities on owl behaviors. Nesting success of Burrowing Owls in Florida (*A. c. floridana*) was influenced by the amount of the surrounding landscape that was urbanized, with the proportion of nests that failed increasing as urbanization increased (Millsap and Bear 2000). Both Florida and Western Burrowing Owls in other urban areas likewise experienced mortality or nest failure directly due to humans (Gleason and Johnson 1985, Feeney 1997, Mealey 1997, Schulz 1997). However, urban Burrowing Owls may use urban features (such as streetlights) to forage successfully (Estabrook 1999). Because they are central-place foragers (Green and Anthony 1989) and usually travel <250 m in diurnal hunting forays (Gleason 1978, Thompson and Anderson 1988, Haug and Oliphant 1990), Burrowing Owls are most strongly affected by land cover in the immediate vicinity of the burrow. Therefore, landscape context will likely affect many aspects of Burrowing Owl biology, as has been seen for other raptor species (Bird et al. 1996, Marzluff et al. 2001).

Most studies of the effects of human activity (especially land use) on raptors have focused on reproduction or survival. For example, studies have shown that many species of raptors breed successfully within urban or cultivated settings, despite anthropogenic sources of mortality such as vehicular collisions (e.g., for Northern Saw-whet Owls [*Aegolius acadicus*] in New Jersey; Loos and Kerlinger 1993) or reduced prey availability relative to natural areas (e.g., for the Lesser Kestrel [*Falco naumanni*] in Spain; Tella et al. 1996). Other species, such as the Rough-legged Hawk (*Buteo lagopus*) decrease in abundance with increasing urbanization (Berry et al. 1998). The effects of human activity on raptor behavior, however, are poorly understood.

Although researchers have quantified Burrowing Owl behaviors such as breeding, territoriality, and foraging in nonurban areas in several states, including California (Coulombe 1971, Thomsen 1971), Colorado (Plumpton and Lutz 1993), Idaho (Moulton et al. 2004), Oregon (Green and Anthony 1989), Wyoming (Thompson and Anderson 1988), and New Mexico (Martin 1973), Burrowing Owl behaviors in Texas are as yet unstudied. This represents a large gap in our knowledge because Texas, unlike many areas, hosts both breeding and overwintering populations in urban and rural habitats and is thus an important site for this migratory species (McIntyre 2004).

We compared breeding adult male Burrowing Owl behaviors (foraging and overall activity budgets) between rural and urbanized sites in the Texas panhandle. Our primary objective was to determine the effects of surrounding land use on adult male Western Burrowing Owl activity budgets. We predicted that because owls in urban areas are exposed to greater amounts of anthropogenic disturbances (e.g., pedestrians, domestic cats and dogs) than are rural owls, urban owls will experience a greater per-

ceived risk than do rural owls; thus, we predicted that resting behaviors among urban owls should be decreased relative to rural conspecifics. Foraging may also be affected if owls are forced to select different foraging microhabitats in urban compared to rural settings; this may in turn influence prey availability, hunting success, and ultimately nesting success. Therefore, we compared hunting success, provisioning rates, and diurnally captured prey between land-use types and assessed foraging habitat selection based on ground cover types.

METHODS

We identified sexes of Burrowing Owls from plumage characteristics (males tend to have paler plumage than do females) and behavior (females tend to spend more time in the burrow, and they usually receive food from the male and carry it down the burrow; Martin 1973, Haug and Didiuk 1993). We captured male owls with bal-chatri traps, noose carpets, and/or bow nets; each owl was banded with a U.S. Geological Survey Bird Banding Laboratory (Patuxent, MD, U.S.A.) band on one leg and a red Acraft (Edmonton, Alberta, Canada) aluminum color band with a unique alpha-numeric identification code on the other. We focused on male owls, because males interact directly with the landscape for a greater proportion of the breeding season, as females spend most of the early portion in the burrow incubating eggs and brooding young.

Study Sites. Our research was conducted in Lubbock and Carson counties, Texas, in 2004 and 2005. In the Texas panhandle, the local environment for a Burrowing Owl is typically a prairie dog colony. However, that colony may lie within a largely urbanized area (e.g., within the city limits of a town) or within a more rural, agricultural context. There were two urban and one rural sites in Lubbock County, and one urban and two rural sites ca. 205 km to the northeast in Carson County. We defined urban sites as those within a residential or industrial setting, with paved roads and constant human presence <1 km away; rural sites had lower human density, unpaved roads, and an agricultural landscape. Each study site was centered on a prairie dog colony. The Lubbock County sites were located in and around the city of Lubbock. The Carson County sites were located on land controlled by the Pantex plant (hereafter, Pantex), a fenced, 4047-ha U.S. Department of Energy/National Nuclear Security Administration facility with controlled access and both industrial and agricultural compo-

nents. At each study site, potential disturbance factors (abundance of humans and of mammalian and avian predators of Burrowing Owls) were quantified by counting the numbers of humans, predatory mammals, and other raptors present.

We used all six sites in 2004 but focused our research on two of the six sites (one urban and one rural, both in Lubbock County) in 2005. In 2004, two owls were monitored at site L95 (33°40'N, 101°51'W) in Lubbock County, a rural site consisting of a pasture near two dirt roads, bordered by another pasture and the Lubbock landfill. Three owls were monitored at site L79 (33°36'N, 101°49'W), an urban site within the Lubbock city limits which was near two paved roads with regular traffic flow, opposite a high school and bordered by a residential area. Three owls were monitored at site L91 (33°37'N, 101°52'W), an urban site within the Lubbock city limits, located at the X-Fab manufacturing plant near two highways with high traffic volume. The site was bordered by an athletic complex with sports fields on one side and a state school on another. The factory maintained a 3-shift (24-hr) work cycle, so there was constant traffic and human presence. In Carson County in 2004, three owls were monitored at site PL (35°22'N, 101°29'W), a rural site consisting of a pasture located off the Pantex compound, bordered by dirt roads and wheat and sorghum fields on all sides. Three owls were also monitored at site Z8 (35°19'N, 101°36'W), a rural site on the Pantex compound, bordered by a wheat field, railroad track, pasture, and dirt roads. Four owls were monitored at site TW (35°19'N, 101°33'W), an urban site on the Pantex compound, adjacent to buildings and paved roads near a high-traffic zone with an entry gate on one side and unplowed fields on the remaining sides. Pantex maintained a 3-shift (24-hr) work cycle, so there was constant traffic and human presence near this site. In 2005, only the Lubbock sites L91 (seven owls) and L95 (two owls) were used.

Experimental Design and Data Collection. We used a focal-animal approach (Altmann 1974, Lehner 1996) to observe behavior. We conducted seven 2-hr daily observation periods between 0630 and 2030 hrs (e.g., 0630–0829 H, 0830–1029 H, etc.) for 6 d/wk. Two male owls per site were simultaneously monitored during these observation periods, one owl per each of two observers per 2-hr observation period. At the start of each observation period in Lubbock, we estimated cloud cover visually and measured air temperature and mean and

maximum wind speeds with a Kestrel 3000 (Boothwyn, PA) handheld unit. Because of security restrictions at the Pantex site, however, we measured only air temperature and time of day.

We used vehicles as observation blinds while using binoculars and 15–45× spotting scopes to observe owl activities. We recorded the location of each foraging attempt, whether successful or not, on printouts of aerial photographs of study sites; these were used to determine a male's foraging distance away from the nest burrow. We attempted to identify prey type, and we categorized the cover type at each foraging location as forb, bare ground, grass, shrub, cactus, or impervious surface (e.g., asphalt, concrete).

Behaviors were recorded at 5-min intervals. We recorded owls as being in one of six mutually exclusive positions: in burrow, out-of-sight (either on or off the prairie dog colony), standing on ground, perching above the ground (e.g., on a fence post), or flying. Within the last three positions, activities could also be determined (preening, resting, hunting, eating, feeding mate or young, being vigilant), and so a hierarchical ranking based on activity rather than location was used for analysis (Lehner 1996). For example, if an owl was preening while perched, it was considered to be preening. Although some important behaviors may occur infrequently and are unlikely to be captured precisely on the 5-min mark (thereby underestimating their occurrence), this form of data collection captures overall activity patterns (Lehner 1996).

Owls were observed systematically at each study site; that is, all owls at a given site were observed before an observer moved on to another study site. The sites were thus monitored in a rotational fashion. Each study site and owl per site were systematically monitored in this order throughout the season, so that all owls were observed during all time periods. An average of 1.5 study sites was covered per day for a total of 14 observation hr per d. Ten owls were monitored at rural sites, 17 at urban ones. Observations were made daily, weather permitting, from 1 June until the last day each male was observed to feed young, which typically occurred by late August.

Because we suspected a change in activity was associated with ambient air temperature in 2004, we modified our methods slightly in 2005 to account for the effects of varying temperatures throughout the day. During the hottest part of the day, Burrowing Owls engage in thermoregulatory behaviors

such as gular fluttering and various heat-stress postures, and perching in shady areas or remaining in burrows (Coulombe 1971, Fisher et al. 2004). Based upon our observations of reduced activity during the hottest part of the day in 2004, we did not collect data from 1230–1630 H in 2005. In addition, each owl in 2005 was randomly assigned a particular block of time in which to be observed throughout the study period. Assigning each owl to a given block of time minimized variability of behaviors within individuals, thereby increasing our power to detect differences in activity budgets among individuals. Moreover, by using a given block of time per owl and having the same blocks to compare between urban and rural sites, we could make more consistent comparisons between land-use types without time of day being a potential source of bias. As in 2004, each observer focused on only one owl during any given 2-hr period. All other methods were the same between years.

Statistical Analyses. Analyses of owl behavior must allow for systematic variation in behaviors across time with changing environmental conditions. Simple descriptive statistics, or even analyses of variance (ANOVA), would tend to underestimate differences between land-use types if such systematic variation is present within study sites. In addition, because frequencies of behaviors are correlated (if an owl is engaged in one behavior, it cannot be doing other behaviors), a multivariate analysis is required. A series of separate univariate analyses of behaviors could be uninformative and perhaps even misleading if these correlations among behaviors are ignored. For these reasons, and because we had fewer owls than behaviors, a variable number of days between observations by owl, a variable number of observations per owl, and variable responses by owl (some owls were never observed to engage in some behaviors), a conventional repeated-measures multivariate analysis of variance (MANOVA) or nested MANOVA (nested by date) could not be conducted without a high Type I error rate and low power. Instead, we used MANOVA with profile (trend) analysis (Johnson and Wichern 1992), using randomization methods to assess statistical significance due to small sample sizes.

Profile analysis summarizes the responses for each subject and then uses these as the predictor variables in subsequent MANOVAs (von Ende 2001). For our study, profile analysis entailed regression of each behavior (number of times observed/total number of min observed) by Julian date for

each owl to obtain an estimated predicted value of each behavior per owl at the midpoint of the season. The predicted behavioral estimates were then used in individual MANOVAs for each main effect: site type (urban or rural), site (6 sites), number of owlets (0–5), and time of day (7 2-hr blocks in 2004, 5 in 2005). In these analyses, the individual owls are the replicates, whereas the land-use types or sites are groups. Separate analyses were performed for 2004 and 2005 because of differences in the observation methods between years. Sampling distributions of MANOVA test statistics for *P*-values were obtained from bootstrap randomizations (5000 iterations); using randomization procedures to generate assumption-free, data-based significance distributions instead of relying on a theoretical test-statistic distribution (whose form is based on assumptions about the data) eliminates potential bias from small sample size. To further increase power, 5 behaviors (flying, in burrow, out-of-sight on colony, out-of-sight off colony, and other) were omitted from analysis in 2004 and 7 (same as in 2004 with the addition of perching and feeding) were omitted in 2005. Compared to the remaining behaviors (hunting, resting, eating, preening, and vigilance), the omitted behaviors were the least observed and had the least biological significance. Those effects that were significant were further explored using discriminant function analysis (DFA) to determine the nature of the relationships between the main effects and behaviors. These analyses were performed in MATLAB v6.5 (The Mathworks Inc., Natick, MA), using programming code available at <http://www.faculty.biol.ttu.edu/Strauss/Matlab/matlab.htm>.

Selection of foraging habitats (here defined as use of a cover type in greater proportion than its availability; Manly et al. 2002) was assessed with chi-square goodness-of-fit tests. The number of foraging attempts made in each of the six cover types (forb, bare ground, grass, shrub, cactus, impervious surface) was tallied, and these frequencies were compared to cover types available at an equal number of randomly located points. Because Burrowing Owls are central-place foragers and therefore tend to select foraging locations and habitats that are near the burrow (Green and Anthony 1989), we measured habitat availability at two spatial scales: cover types within each male's average observed foraging distance from the nest burrow, and cover types within the entire prairie dog colony. Count data were square-root-transformed for analysis (Sokal and Rohlf 1981). We estimated 95% confidence inter-

vals to distinguish between habitat "selection" and "avoidance" for each of the six cover types. Data from 2004 and 2005 were analyzed separately.

A chi-square frequency test was used to determine whether the type of prey taken depended on land use; the more abundant prey taxa (arthropods as a whole, aerial insects, beetles, grasshoppers, and vertebrates as a whole) were then compared individually between urban and rural sites with Fisher's exact test (i.e., a $2 \times 2 \chi^2$) with an expected equal frequency of prey taken between land-use types compared to actual prey numbers (Sokal and Rohlf 1981). Weather data were analyzed by assessing rank correlations with the Spearman coefficient. We omitted less-common behaviors from analysis and focused on the effect of weather variables and time of day on preening, perching, hunting, eating, feeding mate or young, and time spent in burrow. Weather data from 2004 and 2005 were analyzed separately.

RESULTS

We collected 472 hr of observations for 27 owls over two breeding seasons (\bar{x} = 17.5 hr/owl/season; range = 2–78 hr/owl). Eight males were observed in Lubbock County (two owls at rural sites, six at urban sites) and 10 in Carson County (six rural, four urban) in 2004, and nine were observed in Lubbock County (two rural, seven urban) in 2005. No individuals were monitored in both years. Adult male Burrowing Owls at our sites spent most of their time being vigilant, resting, preening, perching, and in the burrow; relatively little time was spent hunting, eating, feeding the mate or young, flying, or engaged in other behaviors (Fig. 1). This was partly due to our observation technique (recording behaviors on 5-min marks); for example, only six of the 27 owls were ever observed hunting on the 5-min mark, although all were observed feeding their mate or owlets at least once. Owls at our study sites seldom left the prairie dog colony but their positions on the colony were often obscured by vegetation; prairie dog colony size ranged from 3–21 ha in 2004 and 3–12 ha in 2005.

Profile analysis revealed that surrounding land-use type did not significantly influence the activity budgets of adult male Western Burrowing Owls in either year (2004: $F = 2.09$, $P = 0.209$; 2005: $F = 2.28$, $P = 0.242$). The amount of time engaged in different behaviors varied significantly by number of owlets being provisioned in both years (2004: $F = 2.50$, $P = 0.02$; 2005: $F = 37.58$, $P = 0.04$), and by

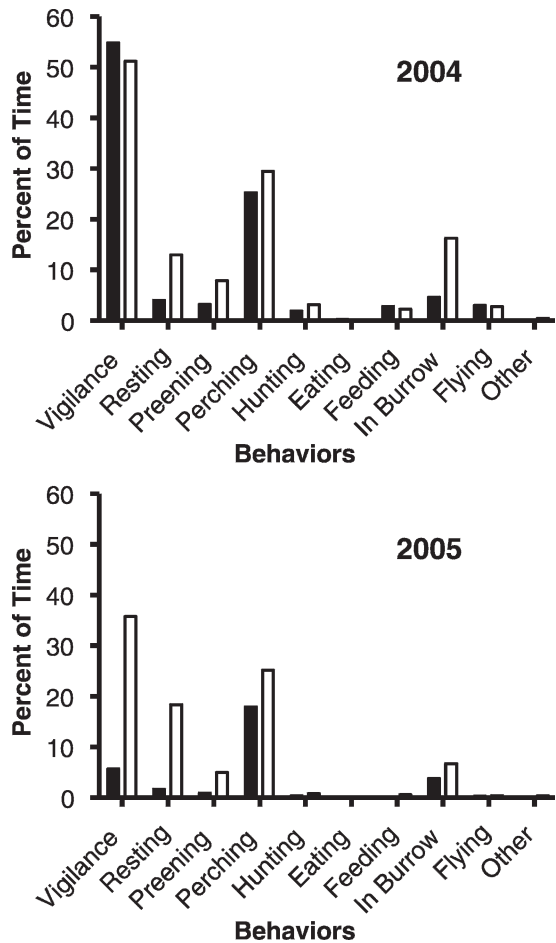


Figure 1. Activity budgets (percent of time) of rural (black bars) and urban (white bars) Burrowing Owls partitioned by year (top: 2004; bottom: 2005).

site ($F = 2.70$, $P = 0.03$) and time of day ($F = 1.57$, $P = 0.028$) in 2004 (site 2005: $F = 2.28$, $P = 0.057$; time of day 2005: $F = 2.04$, $P = 0.381$). When the portions of time owls were out of sight were omitted and comparisons were made for only times when owls were in view, we found that urban owls tended to engage in more resting, preening, perching, and staying in the burrow than did rural owls. Urban owls also spent more time than rural owls in being vigilant in 2005, but the opposite was true in 2004 (Fig. 1).

Various forms of disturbance from humans, hawks (primarily Swainson's Hawk [*Buteo swainsoni*]), and mammals (*Canis latrans* and domestic cats and dogs) were noted at both urban and rural sites. Human disturbances (human presence within

or immediately adjacent to the prairie dog colony) were greater at urban than rural sites during both years (2004: 7 at urban sites, 1 rural; 2005: 3 urban, 0 rural). However, there were no clear trends with other forms of disturbance (2004: 6 hawks and 3 mammals observed at rural sites, 0 at urban sites; 2005: 5 hawks and 1 mammal observed at the rural site, 6 hawks and 1 mammal at the urban site).

Although the type of land-use surrounding a site did not significantly influence behaviors, there appeared to be a locational effect: DFA revealed that owls tended to engage in more vigilant behavior at the Carson County sites and more of other behaviors in Lubbock in 2004 (Fig. 2). There were no clear behavioral trends by number of owlets in 2005 or by time of day in 2004 (i.e., the presence of more owlets was not associated with a consistent or linear increase in certain behaviors, nor did behaviors increase or decrease steadily with time of day). In 2004, however, owls with no owlets spent more time preening and eating than did males with chicks to provision (Fig. 2, 3).

In 2004, significant ($P < 0.05$) correlations for the Lubbock sites were noted between: amount of time spent perching and average and maximum wind speeds; hunting and temperature; time spent in burrow and temperature, average and maximum wind speed, cloud cover, and time of day; and eating and time of day (Table 1). There were no significant behavior and weather correlations for Carson County sites in 2004. In 2005, significant correlations between behavior and weather or time of day for Lubbock were observed between: preening and cloud cover; perching and temperature, average and maximum wind speeds; hunting and temperature; and feeding and temperature. All other correlations were nonsignificant (Table 1).

Foraging distances from the nest burrow ranged from 10.1–42.4 m in 2004 and 9.5–36.0 m in 2005. There was large variation in the amount of time owls spent hunting and in hunting success, with no clear trends by land-use type (Table 2). However, the frequency of the types of prey consumed varied with land use ($\chi^2 = 16.54$, $df = 4$, $P = 0.002$; Table 3): owls at urban sites tended to take more aerial insects ($F = 7$, $df = 1$, $P = 0.040$), but other prey types were taken with similar frequency at urban and rural sites (arthropods: $F = 137$, $df = 1$, $P = 0.170$; beetles: $F = 9$, $df = 1$, $P = 0.999$; grasshoppers: $F = 18$, $df = 1$, $P = 0.240$; vertebrates: $F = 5$, $df = 1$, $P = 0.350$). Provisioning rates varied as much between owls within a land-use type (coefficient of variation for

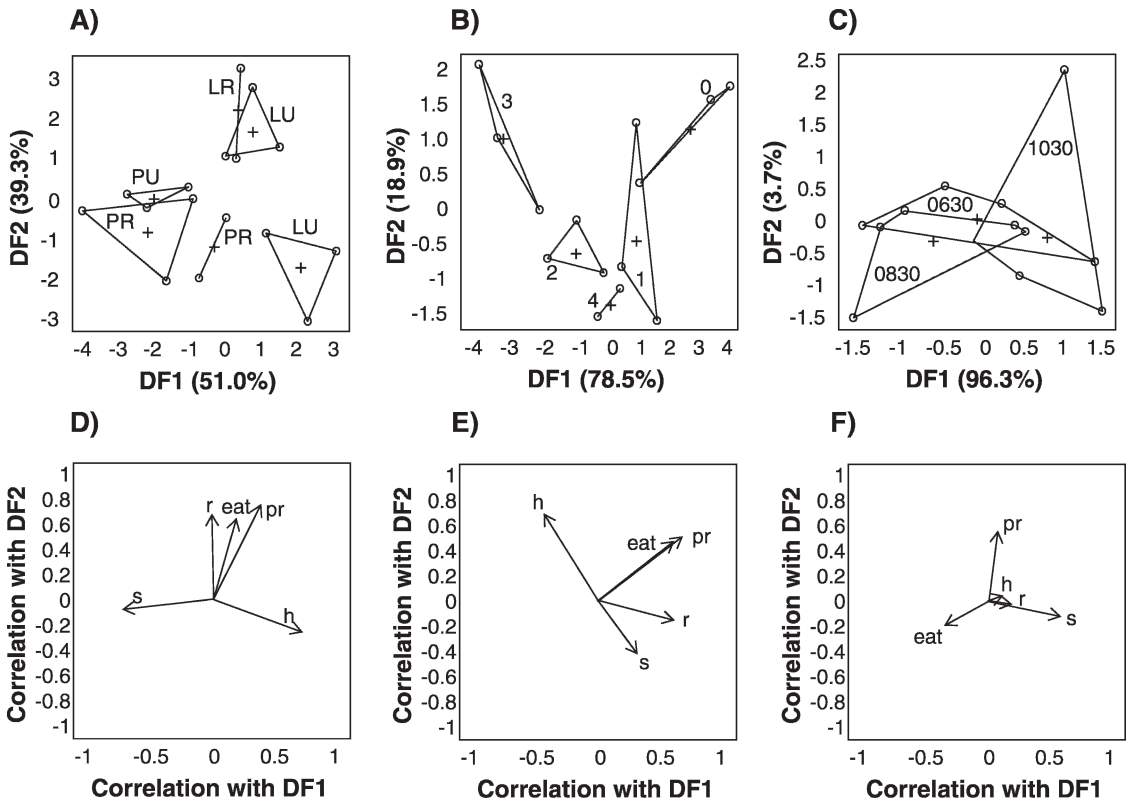


Figure 2. Results of discriminant function analysis, 2004. (A) DFA biplot for sites (LR = Lubbock rural [$N = 1$ site]; LU = Lubbock urban [$N = 2$]; PR = Carson rural [$N = 2$]; PU = Carson urban [$N = 1$]); (B) DFA biplot for number of owlets being provisioned; (C) DFA biplot for time of day (0630 indicates the two-hour block starting at 0630 H, 0830 indicates block starting at 0830 H, etc.). A plus sign (+) indicates a polygon's centroid. Behaviors that were observed fewer than twice for a given individual could not be plotted (no replication); (D) Correlation matrix for sites; (E) Correlation matrix for number of owlets; (F) Correlation matrix for times of day. Behavioral codes: s = standing vigilant; r = resting; eat = eating; pr = preening; h = hunting. In correlation matrices, the length of an arrow indicates its strength of effect.

owls within rural sites = 0.72; CV for urban sites = 0.86) as between land-use types (overall CV = 0.80; Table 4).

There was significant selection for certain foraging habitats in both years (2004: $\chi^2 = 2028.2$, $df = 8$, $P < 0.001$; 2005: $\chi^2 = 1039.2$, $df = 8$, $P < 0.001$). Most foraging attempts occurred in forbs, grasses, or bare ground cover types; areas with shrubs, cacti, or impervious surfaces were relatively rare and used in proportion to their occurrence (Fig. 4). Bare ground was particularly selected in 2004, whereas forbs were especially selected in 2005. Because the data were count data (number of foraging attempts made versus an equal number of random locations), selection for a given habitat did not result in a concomitant avoidance of some other habitat type.

DISCUSSION

Human activity is known to affect the behaviors, survivorship, and reproductive success of various raptors (see Bird et al. 1996, Marzluff et al. 2001). These effects, however, vary by the response variable examined, location, and species. This variability precludes a general prescription for how land use affects a given species in a given location, such as Burrowing Owls in the Texas panhandle. In our study, for example, we found that urban study sites generally had more human forms of disturbance, and we initially predicted that because urban owls are potentially exposed to greater amounts of human activities than are rural owls, urban owls should perceive greater risk than rural owls; thus, we expected resting behaviors among urban owls to be less frequent relative to rural conspecifics (with a

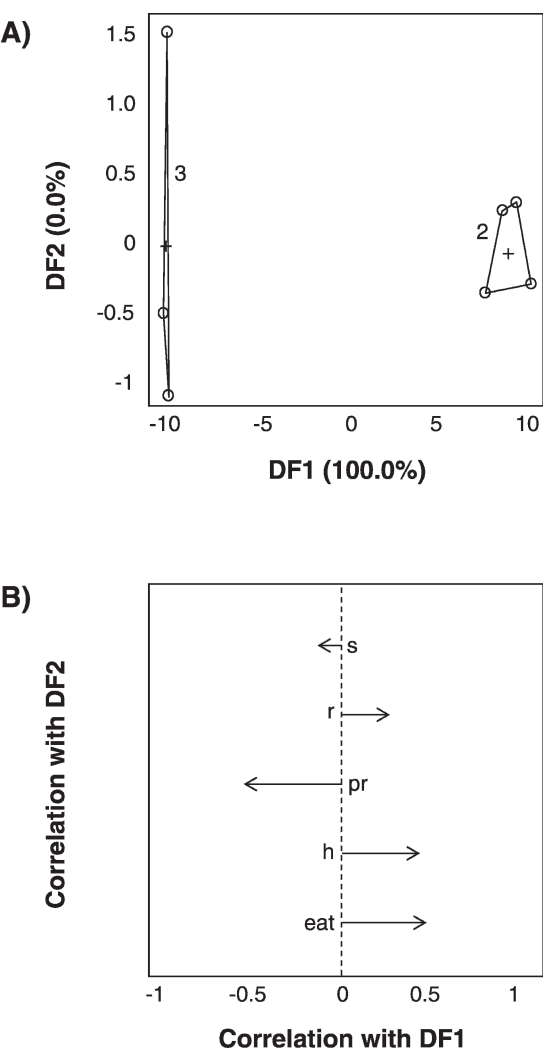


Figure 3. Results of discriminant function analysis, 2005. (A) DFA biplot for number of owlets being provisioned. A plus sign (+) indicates a polygon's centroid; (B) Correlation matrix for number of owlets. In correlation matrix, the length of an arrow indicates its strength of effect. Behaviors that were observed fewer than twice for a given individual could not be plotted (no replication). Behavioral codes: s = standing vigilant; r = resting; eat = eating; pr = preening; h = hunting).

concomitant impact on other behaviors). However, activity budgets did not differ significantly with land use, and there was high variation between owls and between sites within land-use types. Furthermore, we observed more mammalian and avian predators of Burrowing Owls at rural than at urban sites, so

Table 1. Spearman correlations (*r*) between weather variables and behaviors in Lubbock and Carson counties in 2004 and 2005. "Air" is air temperature (°C), "Avg wind" is average wind speed (km/hr), and "Max wind" is maximum wind speed (km/hr). Significant (*P* < 0.05) results are in bold font.

LOCATION AND YEAR	OWL BEHAVIORS				
	PREENING	PERCHING	HUNTING	EATING	IN BURROW
Lubbock 2004					
Air	<i>r</i> = -0.13, <i>P</i> = 0.126	<i>r</i> = -0.03, <i>P</i> = 0.757	<i>r</i> = -0.25, <i>P</i> = 0.005	<i>r</i> = -0.12, <i>P</i> = 0.169	<i>r</i> = 0.43, <i>P</i> < 0.001
Avg wind	<i>r</i> = 0.04, <i>P</i> = 0.674	<i>r</i> = -0.22, <i>P</i> = 0.011	<i>r</i> = -0.01, <i>P</i> = 0.833	<i>r</i> = 0.05, <i>P</i> = 0.565	<i>r</i> = 0.18, <i>P</i> = 0.032
Max wind	<i>r</i> = -0.03, <i>P</i> = 0.717	<i>r</i> = -0.18, <i>P</i> = 0.041	<i>r</i> = -0.08, <i>P</i> = 0.347	<i>r</i> = 0.09, <i>P</i> = 0.320	<i>r</i> = 0.20, <i>P</i> = 0.022
Cloud cover	<i>r</i> = 0.12, <i>P</i> = 0.140	<i>r</i> = -0.08, <i>P</i> = 0.366	<i>r</i> = 0.12, <i>P</i> = 0.141	<i>r</i> = -0.03, <i>P</i> = 0.732	<i>r</i> = 0.09, <i>P</i> = 0.301
Time of day	<i>r</i> = 0.11, <i>P</i> = 0.207	<i>r</i> = 0.06, <i>P</i> = 0.436	<i>r</i> = -0.10, <i>P</i> = 0.228	<i>r</i> = -0.18, <i>P</i> = 0.041	<i>r</i> = -0.11, <i>P</i> = 0.180
Carson 2004					
Air	<i>r</i> = -0.25, <i>P</i> = 0.207	<i>r</i> = 0.32, <i>P</i> = 0.099	<i>r</i> = -0.30, <i>P</i> = 0.134	<i>r</i> = 0.12, <i>P</i> = 0.534	<i>r</i> = -0.28, <i>P</i> = 0.156
Time of day	<i>r</i> = -0.19, <i>P</i> = 0.289	<i>r</i> = 0.17, <i>P</i> = 0.361	<i>r</i> = -0.004, <i>P</i> = 0.981	<i>r</i> = 0.06, <i>P</i> = 0.720	<i>r</i> = -0.18, <i>P</i> = 0.321
Lubbock 2005					
Air	<i>r</i> = -0.11, <i>P</i> = 0.345	<i>r</i> = 0.32, <i>P</i> = 0.002	<i>r</i> = 0.27, <i>P</i> = 0.009	<i>r</i> = 0.10, <i>P</i> = 0.371	<i>r</i> = 0.21, <i>P</i> = 0.042
Avg wind	<i>r</i> = 0.10, <i>P</i> = 0.409	<i>r</i> = -0.30, <i>P</i> = 0.004	<i>r</i> = 0.03, <i>P</i> = 0.820	<i>r</i> = 0.14, <i>P</i> = 0.223	<i>r</i> = -0.09, <i>P</i> = 0.442
Max wind	<i>r</i> = 0.10, <i>P</i> = 0.396	<i>r</i> = -0.25, <i>P</i> = 0.015	<i>r</i> = -0.01, <i>P</i> = 0.946	<i>r</i> = 0.14, <i>P</i> = 0.223	<i>r</i> = -0.11, <i>P</i> = 0.332
Cloud cover	<i>r</i> = 0.28, <i>P</i> = 0.014	<i>r</i> = -0.20, <i>P</i> = 0.092	<i>r</i> = -0.16, <i>P</i> = 0.171	<i>r</i> = -0.10, <i>P</i> = 0.407	<i>r</i> = -0.01, <i>P</i> = 0.908

Table 2. Outcome of every observed hunting attempt for male Burrowing Owls by site type in 2004–05. “Unknown” indicates the outcome could not be determined, and “Null” indicates the owl was performing hunting behaviors (e.g., hovering) but did not attempt to capture prey.

OWL	SITE TYPE	HOURS OF OBSERVATION	TOTAL ATTEMPTS	OUTCOME OF FORAGING ATTEMPT (%)				
				MISSED	EATEN	FED	UNKNOWN	NULL
DSB	Rural	32	53	28	9	40	21	2
SS3	Urban	24	20	10	40	20	10	20
XF2	Urban	22	57	26	16	40	11	7
XF1	Urban	11	16	19	25	19	25	12
XFC	Urban	4	11	9	18	64	9	
TOTAL		93	157	92	108	183	76	41

there may be perceived risks regardless of land-use type.

We also predicted that foraging would be affected by location. We suspected that urban owls may be forced to select different microhabitats in which to forage compared to rural conspecifics, which may in turn affect prey availability and hunting success. Hunting success and provisioning rates did not vary with land use, although the type of prey taken did differ between urban and rural sites. Some of these patterns (or the lack thereof) may have been biased by hunting success at particular sites; for example, more vertebrate prey were taken at a single rural site than at all urban sites combined (Table 3).

Weather influenced behavior in our study, with a decrease in activity during the hotter ($>26.8^{\circ}\text{C}$) portions of the day in 2004, less perching when it was windy ($>8.5\text{ km/hr}$), and more time spent in the burrow with increased temperature, wind speed, cloud cover, and time of day (in 2004). We modified our observation protocols in 2005 to control for potential negative effects that weather (as determined by time of day) had on behavior; this modification meant that our observation periods in 2005 were generally crepuscular. Therefore, it was not surprising that the negative relationship between air temperature and activity observed in 2004 was replaced by a positive correlation in

Table 3. Total observed number of prey taken by male Burrowing Owls in Lubbock and Carson counties in 2004 and 2005.

PREY TYPE	NUMBER OF PREY OF EACH TYPE					
	LUBBOCK 2004		CARSON 2004		LUBBOCK 2005	
	RURAL	URBAN	RURAL	URBAN	RURAL	URBAN
Invertebrate						
Unknown arthropod	35	27	17	36	42	66
Aerial insect	1	12	5	9	1	1
Beetle	6	1	2	2	1	4
Grasshopper	6	3	14	7	4	3
Earthworm					1	
Caterpillar	1					
Moth/butterfly			1			1
Vertebrate						
Unknown						1
Lizard	1					
Snake	1					
Small mammal	4	1				
Carion	2					
TOTALS	57	44	39	54	49	76

Table 4. Average provisioning rate (prey/hour) brought by male Burrowing Owls to mate or owlets in Lubbock and Carson counties in 2004 and 2005.

LAND-USE	AVERAGE PROVISIONING RATE (PREY DELIVERED/HR)								
	LUBBOCK 2004			CARSON 2004			LUBBOCK 2005		
	SITE	OWL	RATE	SITE	OWL	RATE	SITE	OWL	RATE
Rural	L95	DS2	0.50	PL	PL1	0.50	L95	DSB	0.66
		DS4	0.27		PL2	2.75		DSD	2.00
					PL3	1.00			
				Z8	Z81	0.50			
					Z82	2.00			
					Z83	1.60			
AVERAGE		0.38			1.39			1.33	
Urban	L79	SS1	0.36	TW	TW1	1.33	L91	XFA	0.10
		SS2	0.37		TW2	1.50		XFC	1.75
		SS3	0.17		TW3	1.83		XFD	0.50
	L91	XF1	0.27		TW4	1.75		XFE	1.63
		XF2	1.05					XFG	0.17
		XF4	0.07					XFH	0.25
AVERAGE		0.38			1.60			XFI	0.42

2005. It should be noted, however, that all of the associations between weather and behavior were relatively weak ($r < 0.43$), indicating that Burrowing Owl activity was also influenced by factors other than weather.

Burrowing Owls prey primarily on insects during the day and small mammals during the night (Haug et al. 1993, Restani et al. 2001, Poulin and Todd 2006). Thus, the correlation that we observed between decreased hunting and increased time spent in the burrow during hotter times of day makes biological sense. However, we did observe the capture and consumption of a few vertebrates during the day (Table 3), in contrast to Haug and Oliphant (1990), who observed vertebrates being taken only at night.

Our data indicate that Burrowing Owls at our study sites selectively foraged in cover types of relatively low vegetative stature; areas with taller, woody vegetation (shrubs or cacti) or with impervious surfaces were uncommon at our study areas and were used in proportion to their availability. Burrowing Owls in other locations have also been observed to select foraging and nesting areas with low vegetation (Rich 1986, Green and Anthony 1989, Haug et al. 1993, Plumpton and Lutz 1993).

Based on our research, land-use conditions at our study sites in the Texas panhandle did not have an

effect on adult male Burrowing Owl activity budgets. There has been limited research on long-term differences in survivorship or fitness by land-use type, although such data will be necessary for future Burrowing Owl management and conservation in an increasingly human-dominated world. For example, Botelho and Arrowood (1996) found that although mortality factors were higher in urban than natural sites in New Mexico, nesting success was also higher. Similarly, although nest density and nesting success were higher at agricultural than urban sites in Washington, natal recruitment and adult annual return rate were higher at the urban locations (Conway et al. 2006). Furthermore, Conway et al. (2006) found that mean clutch size and number of fledglings per successful nest did not differ with land use, suggesting that site-specific traits may be more influential than land-use context.

Activity budgets of Burrowing Owls appear to be highly variable and affected by weather, time of day, habitat, available prey, and other factors. Any determination of effects of human activities on owls will have to account for these effects and thus will likely require large sample sizes. Moreover, given that land use varies with local socioeconomic, climatic, and topographic factors, the effects on Burrowing Owls will likely vary by region. Due to the increasing levels of land conversion and the imperiled status of

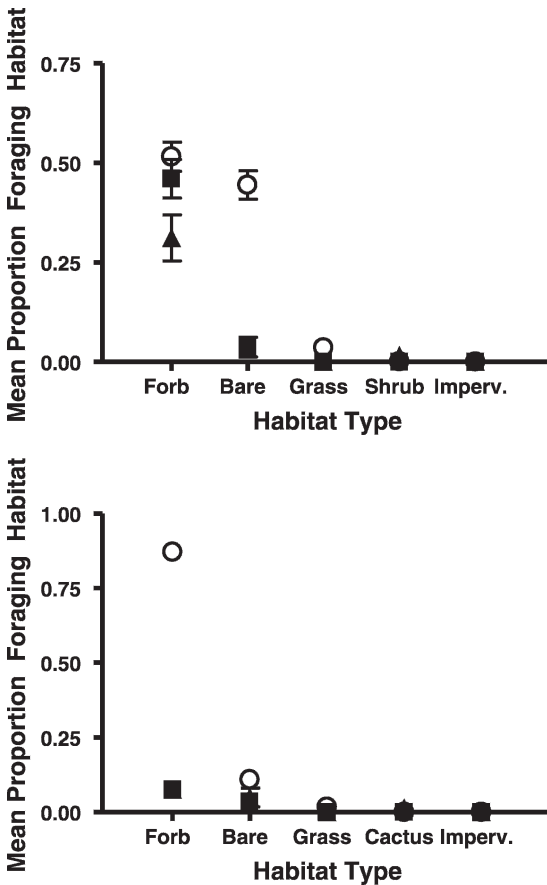


Figure 4. Mean (+95% C.I.) frequency of foraging attempts by cover type for habitat use (open circles) compared to availability (filled symbols) at two spatial scales (filled squares: average foraging distance; filled triangles: within entire prairie dog colony) for 2004 (top) and 2005 (bottom). In 2004, foraging was observed in only forb, bare ground, grass, shrub, and impervious cover types; in 2005, foraging was observed in only forb, bare ground, grass, cactus, and impervious cover types.

Burrowing Owls, further research on the effects of urbanization is clearly needed.

ACKNOWLEDGMENTS

We thank B. Beall, T. Holsombeck, K. McLaughlin, A. Teaschner, E. Thiemann, D. Tinkler, and D. Walker for field assistance. K.A. Schmidt provided helpful discussion. We thank M. Schoenhals and M. Keck for assistance with access to Pantex sites (U.S. Department of Energy/National Nuclear Security Administration in cooperation with BWXT Pantex LLC). Comments from G. Holroyd, M.K. Skoruppa, and three reviewers improved the manuscript.

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Received 17 April 2007; accepted 28 January 2008
Associate Editor: Joseph B. Buchanan