J. Raptor Res. 52(2):178–190

HOME RANGES, HABITATS, AND ROOSTS OF WINTERING BURROWING OWLS IN AGRICULTURAL LANDSCAPES IN CENTRAL MEXICO

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ABSTRACT.— The winter home ranges, foraging habitats, and roost characteristics of migrant Burrowing Owls (*Athene cunicularia*) have not been described in central Mexico. This information is needed to prioritize habitat conservation measures because the species is in decline across much of western North America. We used VHF telemetry to describe the foraging range, habitat use, and roost sites of 17 Burrowing Owls in two study areas: Irapuato and Zapopan, Mexico. Burrowing Owls did not forage in the daytime. Cropland and grasslands made up the majority of the owls' foraging ranges, which averaged 70 ha. Burrowing Owls responded quickly and opportunistically to changes in land uses that removed tall dense vegetation, such as the harvest of tall crops, and fires. Distances from foraging areas to roost sites averaged 514–751 m, but varied widely from 32–1981 m. Roost characteristics were highly variable between study sites. Overall, Burrowing Owls incorporated anthropogenic land uses into their winter habitat needs.

KEY WORDS: *Burrowing Owl*; Athene cunicularia; *foraging range*; *habitat*; *Mexico*; *roost*; *winter*.

ÁREAS DE CAMPEO, HÁBITATS Y MADRIGUERAS DE *ATHENE CUNICULARIA* INVERNANTES EN PAISAJES AGRÍCOLAS DEL CENTRO DE MÉXICO.

RESUMEN.— El área de campeo invernal, los hábitats de alimentación y las características de las madrigueras de individuos migratorios de *Athene cunicularia* no han sido descritos en el centro de México. Esta información se necesita para priorizar las medidas de conservación del hábitat, dado que la especie está en declive en gran parte del oeste de América del Norte. Utilizamos telemetría VHF para describir el área de alimentación, el uso del hábitat y las madrigueras de 17 individuos de *A. cunicularia*, en dos áreas de estudio: Irapuato y Zapopan, México. Los búhos no se alimentaron durante el día. El área de alimentación estuvo conformado en su mayoría por cultivos y pastizales, promediando 70 ha. Los individuos de *A. cunicularia* respondieron rápida y oportunistamente a los cambios en el uso del suelo donde la vegetación alta y densa fue eliminada, como la cosecha de cultivos altos y en las quemas. Las distancias de las áreas de alimentación a las madrigueras promedió 514-751 m, pero varió ampliamente entre 32-1981 m. Las características de las madrigueras fueron muy variables entre las áreas de estudio. En general, *A. cunicularia* incorporó usos del suelo antropogénicos a sus necesidades de hábitat invernal.

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The western Burrowing Owl (*Athene cunicularia hypugaea*), which breeds across the Great Plains of North America is classified in Mexico as "subject to special protection" (Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT] 2010), in the USA as a species of special concern (Klute et al. 2003), and in Canada as an endangered species (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2006). The western subspecies has experienced drastic population declines and range contraction in Canada (an estimated 90% decrease) and in various regions of the United States (Wellicome and Holroyd 2001, COSEWIC 2006, Sauer et al. 2017), making it a species of concern on a continental scale (Holroyd 2005). Consequently, the conservation of this species depends on the management of habitats across western North America (Holroyd et al. 2001). Individuals from northern portions of the range spend about half of the year away from their breeding grounds. Telemetry studies indicate some make stops in the USA during migration, likely to complete molt of the flight feathers, before arriving to winter in central and coastal Mexico and coastal Texas (Woodin et al. 2008, Holroyd et al. 2010, Holroyd and Trefry 2011).

The breeding habitats of Burrowing Owls in western North America have been broadly characterized as treeless grasslands where Burrowing Owls are associated with nest burrows made by prairie dogs, badgers, or other fossorial mammals (Poulin et al. 2011). In Mexico, two studies of the breeding habitats of Burrowing Owls have taken place in arid regions. Rodríguez-Estrella and Ortega-Rubio (1993) studied owls nesting in shrubby habitats dominated by *Larrea* spp., *Prosopis* spp., *Fouquieria* spp., and *Agave* spp. in Mapimi, Durango, north-central Mexico. Cruz-Nieto (2006) found Burrowing Owls nesting in Mexican prairie dog (*Cynomys mexicanus*) colonies in Galeana, Nuevo León, northeastern Mexico. Burrowing Owl habitat use has not been previously studied in central Mexico, where Burrowing Owls are present only during winter.

Radio telemetry has been commonly used to study home ranges, habitat selection, and dispersal of Burrowing Owls in reproductive and post-reproductive periods in Canada (Haug and Oliphant 1990, Shyry 2005, Scobie et al. 2013), as well as to document winter destinations of migratory Burrowing Owls (Holroyd et al. 2010). A telemetry study identified northern Great Plains Burrowing Owls wintering in a wide range of agricultural and natural habitats in Mexico and Texas, utilizing anthropogenic burrows as diurnal roost sites. (Holroyd et al. 2010). In southeastern Texas, Williford et al. (2007, 2009) described Burrowing Owls' winter roost habitats on agricultural lands composed of 61.5% bare soil, 15.5% pasture, 11.5% shrub, and the remainder other cover types. We hypothesized that winter habitat in central Mexico would be similar to winter habitat in Texas despite broad differences in land covers in these regions. In this study, we tested that hypothesis by quantifying foraging habitat use for Burrowing Owls in two study areas in central Mexico, and comparing our results to those of previously published studies of Burrowing Owl wintering habitats. To do so, we used radio-telemetry to document winter foraging ranges, foraging habitats, and roosts of migrant Burrowing Owls in central Mexico. We also used telemetry to determine changes in habitat uses in response to anthropogenic changes in land uses.

METHODS

We studied Burrowing Owls in central Mexico near the cities of Irapuato, Guanajuato; and Zapopan, Jalisco, 300 km apart (Fig. 1). We chose these two study areas after extensive searches between 1989–2000 for concentrations of wintering Burrowing Owls in Mexico (Holroyd et al. 2010, G. Holroyd and H. Trefry unpubl. data).

Study Areas. *Irapuato.* This study site was a heavily grazed hillside bisected by a dirt road, and adjacent to lowland agricultural areas, located 9 km north of Irapuato, Guanajuato, in a region of intensive seasonal crops, and livestock agriculture. The town of Valencianita, with a population of 2500 inhabitants, bordered the eastern portion of the study area. This lowland (*Bajio Guanajuatense*) was a semiarid region formed by alluvial plains with deep, well-drained limestone soils separated by ridges of sedimentary rock (Instituto Nacional de Estadística Geografía e Informática [INEGI] 1998). Native vegetation was composed of dry tropical forest (Rzedowski and Calderón 1987). Intensive grazing on the hillside resulted in the removal of most vegetation, leaving a few scattered trees (<6 m in height) such as mesquite (*Prosopis laevigata*) and acacias (*Acacia farnesiana*, *A. schaffneri*), as well as prickly pear cacti (*Opuntia* spp.). The overgrazed hillside (44 ha) had been scarified with a large single plow, upturning linear furrows of limestone bedrock plates to catch water and soil for planting shrubs, small trees, and cacti in a revegetation project. These upturned plates created small cavities underneath

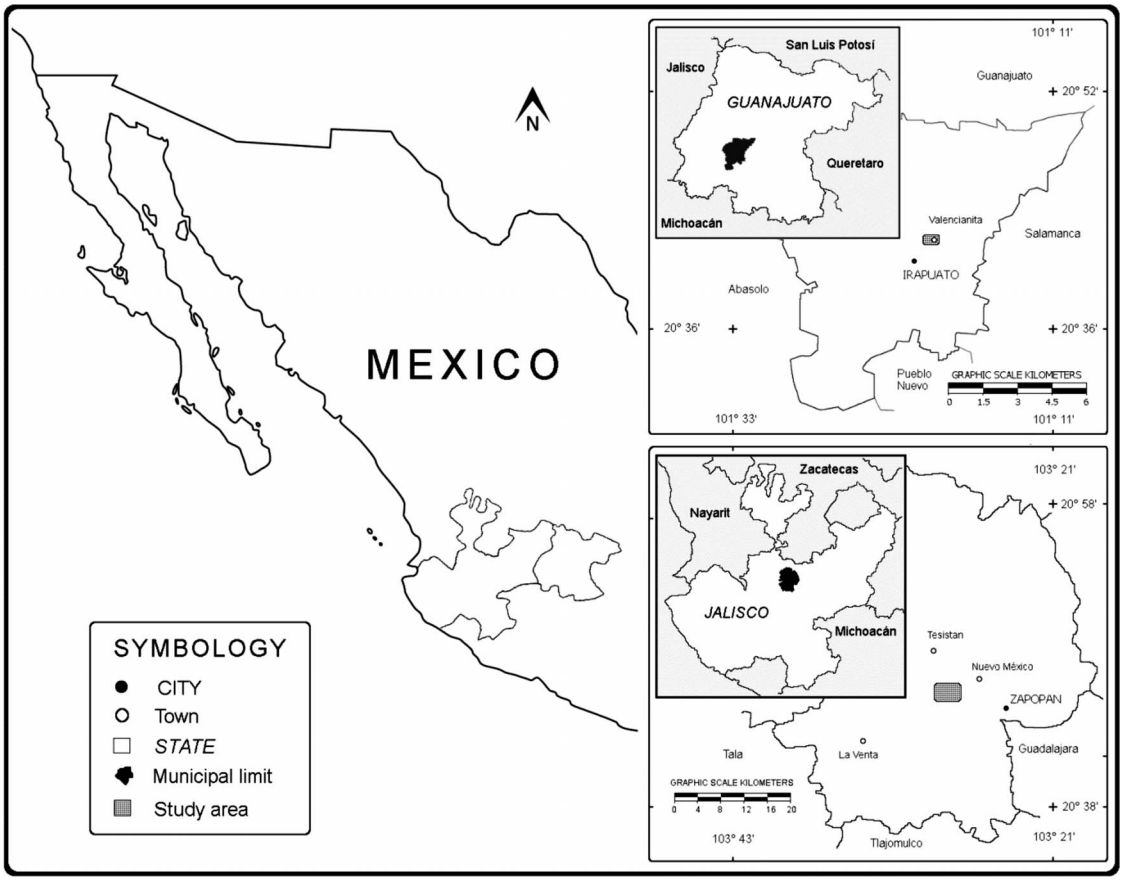

Figure 1. Locations of the Irapuato and Zapopan study areas in central Mexico, where we studied foraging range, habitat used, and roosts of wintering Burrowing Owls.

that were used as roost sites by wintering Burrowing Owls (Valdez-Gómez and Holroyd 2000). Between the rows, the ground was covered with a mixed herbaceous layer dominated by the genera *Andropogon, Aristida, Bouteloua, Gaudichaudia, Heteropteris, Lycurus, Matelea, Nissolia, Panicum*, and *Pisoniella*. Below the hillside, small fields of seasonal dryland and irrigated crops were cultivated on level, alluvial lands. Abandoned fields covered with a mixed herbaceous layer were dominated by *Andropogon*, *Aristida*, *Bouteloua*, *Lycurus,* and *Pisoniella* (INEGI 1998).

Zapopan. Our second study site was located in the Valley of Tesistán, in the northwest corner of Guadalajara, 300 km west of Irapuato. This secure study site comprised the entire 8-km^2 footprint of Zapopan's Mexican Military Airbase No 5. Crop fields lay to the west of the airbase; the rest of the airbase was surrounded by urban development and a chicken (*Gallus gallus domesticus*) farm to the north. The soils were Regosol eutric (INEGI 1999), with small arroyos and quarries cut into the limestone bedrock (Curiel et al. 1995). The resultant soil banks above the bedrock created vertical slopes within which fossorial mammals dug burrows that were subsequently used by Burrowing Owls as diurnal roost sites. Seasonal crop farming was the main agricultural activity in this region, where the original pine-oak (*Pinus* spp., *Quercus* spp.) forest was largely replaced by introduced trees including eucalyptus (*Eucalyptus globulus*), casuarinas (*Casuarina cunninghamiana*) and *Ficus* spp., which formed wind barriers between fields. Shrubs (*Ricinus communis, Nicotiana glauca,* and *Verbesina* spp.) grew along field edges and ditches. Open fields were dominated by mixed grasses, including species in the genera *Aegopogon,*

Aristida, Chloris, Eragrostis, Panicum, Paspalum, Melinis, Muhlenbergia, and *Sporobolus* (López-Coronado and Guerrero-Nuño 2004).

Trapping and Telemetry. We used bow nets with live house mice (*Mus musculus*) as lures in triggered cages. We set bow nets about 30 min before sunset and checked nets every 30 min for 4–6 hr. We trapped Burrowing Owls at Irapuato by setting bow nets near roost sites on the hillside and on dirt trails in the bordering lowland agricultural fields. Within the Zapopan airbase, we set bow nets along dirt trails around the runway in the grasslands. We banded Burrowing Owls with lock-on US Geological Survey aluminum bands and butt-end black anodized alphanumeric bands (ACraft Sign and Nameplate Co., Edmonton, AB, Canada). We used VHF radio transmitters (Holohil Systems Ltd, Newmarket, ON, Canada) mounted in a backpack configuration with 4-mm-wide Teflon® webbing (Bally Ribbon Mills Inc., PA, USA), with a combined mass of 6.2 g, which was less than the maximum of 5% recommended by Kenward (2001). We detected radio signals with R-1000 receivers (Communication Specialists Inc., Orange, CA, USA), and three-element Yagi antennas. We began telemetry on the night after each Burrowing Owl was trapped and continued until the last Burrowing Owl left both study areas in mid-March.

We tracked Burrowing Owls to diurnal roosts with telemetry. During the day, Burrowing Owls remained in their roost burrows unless disturbed, causing them to fly to an alternate roost. We never saw them foraging during the day, so we assumed that night locations included foraging sites. We located Burrowing Owls with telemetry from when they arrived at their foraging sites after dark until first light before dawn when they left the foraging sites to return to their roosts. At twilight and dawn, we were able to see the Burrowing Owls near the roosts and recorded their activity at these times.

In Irapuato, we conducted telemetry from the end of November 1999 to mid-March 2000. During this period, we visited the area every 2 wk, and spent at least two consecutive nights during visits tracking Burrowing Owls. We initiated telemetry at Zapopan in late November 2000 and continued until mid-March 2001, and from mid-December 2002 until mid-March 2003. Our schedule largely depended on the access allowed by the military. On average, we spent four nights per week tracking Burrowing Owls in Zapopan. We determined nocturnal locations by triangulation on medium to strong signals from at least two positions with angles near 90° ± 12°. We included sequential readings from two (or more) positions using a single receiver only when the transmitting source remained stationary and a minimal amount of time was spent to reach a different position. We recorded changes in local land uses, such as crop harvests and fires, and noted the responses of foraging Burrowing Owls to these land-use changes.

Land-cover Classification. We used the regional system of major land-cover types (Carey et al. 1990, Martínez and Zubergoitia 2004, Trulio and Chromczak 2007) to define eight discrete land-cover classifications: (1) seasonal crops of corn (*Zea mays*), sorghum (*Sorghum bicolor*), sugarcane (*Saccharum officinarum*), and agave (*Agave tequilana*), grown in small fields with a maximum area of 20 ha; (2) irrigated crops, cultivated yearlong including alfalfa (*Medicago sativa*), and a variety of market vegetables such as radish (*Raphanus raphanistrum*) and cauliflower (*Brassica oleracea*); (3) farms, comprised of orchards and livestock; mostly chickens and cattle (*Bos taurus*); (4) military infrastructure including the training airport with asphalt runway, 36 ha of buildings, and 16 ha of conifer forest surrounded by large mowed and un-mowed grassland; (5) urban, including single family, multifamily, commercial, and industrial development and undeveloped urban lands sparsely vegetated with introduced grasses such as *Chloris gayana, Cynodon plectostachyus* and *Melinis repens*; (6) quarry and natural arroyos, with bare ground or scattered patches of grasses and shrubs; (7) shrubland, a medium-height, dense stratum dominated by shrubs and trees (<4 m high) with presence of mixed grasses; (8) grassland, mixed stratum dominated by grasses with scattered shrubs. We then determined the extent of land-cover types within the two study areas from ground observations, aerial photos, and Google Earth using the software Arc View GIS version 3.2, (Haug and Oliphant 1990, Framis et al. 2011).

Vegetation Structure at Roosts and Nocturnal Foraging Sites. We used a Robel pole to characterize the density and height of vegetation (Robel et al. 1970). We made at least 20 measurements at random sites within each habitat where a Burrowing Owl spent the night and four measures in cardinal compass directions in a 3-m-radius of diurnal roosts. We determined ground cover using a 1-m × 1-m Daubenmire frame to estimate percentage of bare ground, organic matter, grasses, herbs, and forbs (Connelly et al. 2003) at a minimum of 25 random

sites for each habitat type and at four sites in cardinal compass directions in a 3-m-radius for each roost.

We described roosts using four variables: width, height, interior diameter (where the burrow entrance is narrowest), and depth (from the entrance to the immediate first curvature). We recorded the orientation of the roost's entrance in compass degrees. We described roosts based on their origin: (1) natural roosts shaped by the interaction between the environment and physical landscape elements, such as rocks, soil, and plants; (2) anthropogenic roosts, including limestone slabs resulting from a plow overturning soil and bedrock for revegetation purposes, and concrete structures such as culverts and pipes; (3) mammalian burrows excavated by fossorial mammals such as ground squirrel (*Spermophilus variegatus*), opossum (*Didelphis virginiana*), and rabbit (*Sylvilagus floridanus*). We measured the dimensions of roost entrances, determined their location using a GPS, and calculated the distance (m) to the nearest neighbor roost (Mrykalo et al. 2007, Williford et al. 2007).

Statistical Analysis. We used Arc View GIS (version 3.2, Home Range Extension; Jennrich and Turner 1969, Anderson 1982, Environmental Systems Research Institute [ESRI] 1999) to calculate the foraging range for each individual owl, using all nocturnal telemetry fixes to generate the 100% Minimum Convex Polygon (MCP). We also generated a study area MCP for all nocturnal locations for all Burrowing Owls for each study area, to define the size and total habitat availability in each study area. We determined overlap of the foraging ranges among Burrowing Owls at each study site and for each study year. Overlap was expressed as the amount of common land in both ranges divided by the average amount of land in the two ranges, multiplied by 100.

We identified the habitat type for each nocturnal telemetry fix for each Burrowing Owl during daytime visits. We compared the proportions of habitat types present in each individual's foraging range with what was available in the entire study area. We then compared the proportion of each Burrowing Owl's telemetry fixes in each habitat to the proportion of each habitat within each foraging range (then averaged for all Burrowing Owls in each study site) by performing a chi-square test of goodness-of-fit, and also by using a one-way ANOVA test. In both cases, our statistical null hypothesis was that the proportions in each category were the same. We evaluated the randomness of entrance orientation by performing a Rayleigh test of circular uniformity (Fisher 1993, Zar 1999), which implies a null hypothesis that roosts are evenly distributed in compass orientation.

RESULTS

Overall, the circadian cycle of wintering Burrowing Owls in central Mexico was defined by two periods separated by twilights; diurnal-passive, where the owls remained hidden in or at the entrance to a roost, and nocturnal-active in nearby fields. Within 15 min after local sunset, transmitter signals increased in intensity when the owls left their roosts. During that time ($\bar{x} = 14.8$ min after local sunset, SD $\pm$ 12.6, $n = 22$ instances), owls remained active, with relatively short movements ($\bar{x} = 55.8$ m, SD $\pm$ 18.0, $n = 42$ instances), around their roosts. We frequently observed Burrowing Owls hover-hunting for terrestrial prey at this time. These local crepuscular foraging sites appeared to be used exclusively by each Burrowing Owl in the immediate vicinity of their roost. The owls then flew longer distances to their nocturnal foraging sites. Owls returned to their roosts at the first hint of light of dawn ($\bar{x} = 14.6$ min before local sunrise, SD $\pm$ 8.4, $n = 10$), moving in segments of varying distances, shortening as they approached the roosts. We never observed foraging activity prior to roost re-entry at sunrise. The ranges discussed below were strictly from the nocturnal telemetry fixes and did not include any crepuscular and diurnal locations, and so represent foraging ranges.

Foraging Ranges. At Irapuato, from 14 to 24 November 1999, we captured six Burrowing Owls. One Burrowing Owl was never relocated despite searches within an 8-km radius from where it was caught. The remaining five transmitters generated a total of 79 locations that we used to delineate a foraging range for each of the five owls. At Zapopan, from 26 November to 7 December 2001, and from 8 December 2002 to 17 January 2003, we captured seven and five owls, and determined 165 and 85 positions, respectively. We used a total of 165 positions during the two winters to determine each owl's foraging range. At Irapuato, individual ranges averaged 67.9 ha. At Zapopan, individual ranges averaged 69.1 ha in 2001–2002 and 85.7 ha in 2002–2003 (Table 1). Foraging ranges varied from 20.3–194.5 ha and were not significantly different between years and study areas (one-way ANOVA $F_{0.05\ (1)\ 2,\ 14} = 0.180$; $P = 0.84$).

Table 1. Foraging range size of Burrowing Owls wintering in central Mexico at two study areas. Ranges calculated as Minimum Convex Polygons MCPs (ha).

			Foraging Range Size (ha)		
Study Areas	Year	*n*	Mean	Range	SD
Irapuato	1999–2000	5	67.9	20.3–116.1	45.1
Zapopan	2001–2002	7	69.1	28.1–194.5	61.7
Zapopan	2002–2003	5	85.7	15.8–170.1	62.5

Habitat. The study area MCP enclosing all telemetry positions collectively incorporated 1002.8 ha at Irapuato and 1207.8 ha at Zapopan (HABI and HABZ, respectively; Fig. 2), which we used to define the boundaries of our study areas. HABI was dominated by grasslands (31.1%) and seasonal crops (31.5%). Other habitats covered 37.4% of the study area MCP, including shrubland (16.3%), irrigated crops (12.5%), urban (6.7%), and quarry (1.9%). HABZ was dominated by grasslands (53.0%) and seasonal crops (22.4%, Fig. 2). Other habitats covered 24.6% of the study area MCP, including military infrastructure (14.2%), urban (5.1%), farm (5.0%), and quarry (0.3%). The proportion of habitats within the Irapuato and Zapopan study areas were significantly different (HABI vs. HABZ: $\chi^2 = 87.3$, df = 3, $P < 0.01$) due to the more extensive shrubland and irrigated crop at Irapuato, and more extensive grasslands and military infrastructure at Zapopan.

At Irapuato, habitats within Burrowing Owl's foraging ranges consistently incorporated irrigated cropland and seasonal crops, but grasslands were

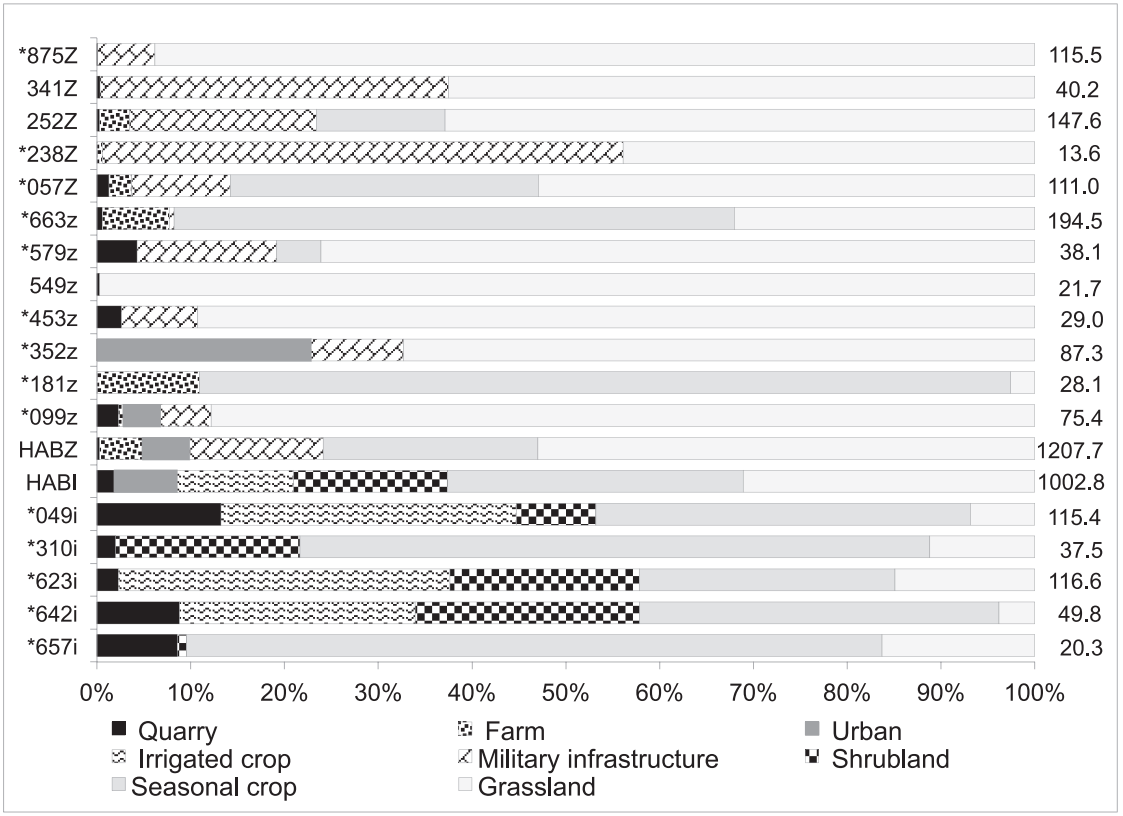

Figure 2. Habitat types present in individual Burrowing Owls' foraging ranges at Irapuato (i), and at Zapopan for the winters 2001–2002 (z) and 2002–2003 (Z), and in the total study areas at Irapuato (HABI) and Zapopan (HABZ). The labels on the left axis are the owls' transmitter numbers and the study area identifiers, and on the right are the number of hectares in the MCP. The habitat percentages in an owl's foraging range differed significantly from its corresponding study area for transmitter numbers marked with an asterisk (*), based on chi-square tests.

Table 2. Comparison of habitat used by wintering Burrowing Owls to habitat available in two study areas (Irapuato and Zapopan in Central Mexico). Telemetry locations for all Burrowing Owls within each study area/year were combined. Study area was defined as the Minimum Convex Polygon (MCP) that enclosed all telemetry fixes for all Burrowing Owls in that study area/year. Statistical results in text.

	IRAPUATO 1999–2000		ZAPOPAN 2001–2002		ZAPOPAN 2002–2003	
HABITATS	FORAGING RANGES (%)	OWL LOCATIONS (% OF TOTAL) ($n = 79$)	FORAGING RANGES (%)	OWL LOCATIONS (% OF TOTAL) ($n = 165$)	FORAGING RANGES (%)	OWL LOCATIONS (% OF TOTAL) ($n = 85$)
Quarry	7.0	3.8	1.5	10.1	0.4	3.5
Seasonal Crop	49.4	38.0	21.6	17.0	9.3	24.7
Military	0	0	5.5	3.6	25.8	5.9
Farm	0	0	2.7	6.7	1.2	11.8
Urban	0	0	3.8	5.5	0	0
Grassland	10.6	29.1	65.0	56.4	63.2	54.1
Irrigated Crop	18.4	27.8	0	0	0	0
Shrubland	14.6	1.3	0	0	0	0

underused relative to availability. At Zapopan, the proportion of habitats in the foraging ranges varied, with most foraging ranges dominated by grassland, but two dominated by seasonal crops and one by military infrastructure (Fig. 2). Overall, the proportion of habitats in 14 of 17 individual foraging ranges differed significantly from that in the respective study area (HABI or HABZ).

For each Burrowing Owl, we determined the proportion of each habitat in its foraging range and the frequency of telemetry fixes within each habitat. We then compared the average of them for each study area and winter (Table 2). The proportion of telemetry fixes in each habitat differed significantly from the proportions in the foraging ranges, showing that habitat use was selective within foraging ranges. In the Irapuato study area, irrigated crop was occupied more than expected, and grasslands and seasonal crop were used less than expected ($\chi^2 = 185.0$, df $= 4$, $P < 0.001$). In the Zapopan study area, Burrowing Owls occurred more frequently than expected based on availability in seasonal crop (2002–2003), quarry, and farm habitats, and less frequently than expected in grassland and military infrastructure (for 2001–2002 $\chi^2 = 65.0$, df $= 5$, $P < 0.001$; for 2002–2003 $\chi^2 = 120.4$, df $= 4$, $P < 0.001$).

Within the Irapuato study site, the foraging ranges of two pairs of owls overlapped 82.5% and 12.9%, whereas eight pairwise comparisons of foraging ranges did not overlap. The average overlap of foraging ranges was 9.5% (SD ± 26.0%). In the first winter at Irapuato, 16 of 21 pairwise comparisons of overlap of individual Burrowing Owls' foraging ranges were zero; the maximum overlap was 28.6% ($\bar{x}$=4.4%, SD ± 9.4). In the second winter, four of 10 overlaps were zero; the maximum overlap was 44.0% ($\bar{x}$=12.2%, SD ± 14.7).

Five land-cover types were within the five foraging ranges at Irapuato (Fig. 2). On average, seasonal crop was the most dominant habitat in all foraging ranges at 49.4% (SD ± 20.2), whereas irrigated crop composed 18.4% (SD ± 17.2). Shrubland and grassland made up 17.9% (SD ± 5.8) and 7.4% (SD ± 5.9), respectively. Lastly, quarries and arroyos composed 7.0% (SD ± 4.8) of all foraging ranges (Fig. 2). We found significant differences between habitats in all five individual foraging ranges and the proportions in the total study area (HABI). At Zapopan, six habitat types were within Burrowing Owls' foraging ranges during the two winters, although urban was only used in 2001–2002 and its occurrence was minimal (3.8%). Grasslands covered the largest area (63.2–65.0%) in the foraging ranges followed by crops (21.6% in 2001–2002) and military infrastructure (25.8% in 2002–2003). The Burrowing Owls demonstrated considerable variability, with one Burrowing Owl foraging almost exclusively in seasonal crop (86.5%) and five in grasslands (>75%).

At Irapuato, within seasonal and irrigated crops, organic matter (litter) dominated the ground (68.4%, 76.0%, respectively), whereas grasses dominated quarries, shrubland, and grasslands (42.2%, 65.4% and 51.8%, respectively). Bare ground appeared repeatedly in all habitats (37.1% in quarries) in addition to herbaceous cover, although in minor proportions (<10%). Both vegetation maximum

height and average height were higher in shrubland (113.2 cm, 56.5 cm) and grassland (66.8 cm, 22.0 cm), and lower in seasonal crops (19.8 cm, 7.7 cm) and irrigated crops (8.3 cm, 4.0 cm). At Zapopan, grasses were the dominant ground cover in the grassland (73.6% cover), quarry (57.5%), and military infrastructure (54.2%). Bare ground dominated in urban areas (68.2%), and secondarily in military infrastructure (32.7%) and seasonal crops (28.5%), and organic matter, forbs, and shrubs were present in most habitats, although in smaller proportion (<20%). The maximum and average heights of vegetation were greater in grasslands (maximum 68.2 cm, and average height 33.5 cm), quarries (63.5 cm, and 20.7 cm) than in urban (23.3 cm, and 12.4 cm), harvested crops (21.0 cm, and 7.3 cm) and military infrastructure (13.9 cm, and 5.6 cm).

Some owls had specific nocturnal movements to foraging areas that had been recently modified by human activity. Tall dense standing crops such as corn and sorghum were not used by the owls until the crops were harvested. The Burrowing Owls foraged in the short (< 30 cm) stubble, sometimes as soon as the night following the harvest. After a sugarcane field was burned, owls spent the night in that field, presumably foraging for the recently exposed prey. At Zapopan, one Burrowing Owl routinely flew over Aviación Avenue, a four-lane road, to undeveloped burned lands and to a 2-ha plot designated for composting of organic matter from parks and gardens managed by the City of Zapopan. The uses of military facilities by the Burrowing Owls were primarily associated with mowed grass at the edges of paved and dirt roads, runways, and lawns and not in the unmodified, tall grasslands. We observed Burrowing Owls hawking insects attracted to nocturnal lighting in illuminated areas associated with the military buildings. In January 2002 and 2003, three fires burned 290–340 ha of grassland adjacent to the runway and fuel storage areas. Immediately following the fires, three or four owls spent the nights on the edges of the burned grasslands and visited the grasslands again once the new grasses appeared. An adjacent chicken farm attracted six owls apparently because it had illuminated production units, and open chicken manure compost that could be an important source of prey, but the area made up only 1.1–11.2% of the foraging ranges of the owls we studied. In all the observations, the Burrowing Owls were foraging in the short (< 30 cm) vegetation and on un-vegetated lands.

Roosts. At the Irapuato study site, the distances between diurnal roosts and nocturnal foraging sites were highly variable, ranging between 32 m and 1981 m ($\bar{x}$ = 751 m, SD ± 426 m, n = 114). At Zapopan, the mean distances between roosts and foraging sites were similar between winters but showed considerable variability among owls: 2001–2002 ($\bar{x}$ = 514 m, SD ± 493, n = 133) and 2002–2003 ($\bar{x}$ = 612 m, SD ± 423, n = 102). One Burrowing Owl consistently roosted away from the airbase, traveling almost 3 km over urban environments to its roost in a golf course ($\bar{x}$ = 2962 m, SE ± 304, n = 27). We treated this as an outlier and did not include it in the previous means.

During the two winters, we studied 37 roosts on the hillside at Irapuato and 36 roosts of 17 owls at Zapopan. At Irapuato, all roosts used during the two winters were under flat limestone rocks that had been exposed and lifted. At Zapopan, 25 roosts had fossorial mammal origins, seven were anthropogenic, and four were natural cavities. The majority (58%) were located in arroyos and quarries. One unmarked Burrowing Owl roosted for a month in a tunnel formed by tall dense bunchgrass. One Burrowing Owl roosted in a tall casuarina tree (*Casuarina cunninghamiana*) on at least two occasions. Another Burrowing Owl roosted in a culvert under a sidewalk by a fuel storage patio.

At Irapuato, the nearest neighbor roost distances were small, due to the abundance of upturned rocks on the hillside ($\bar{x}$ = 78 m, range 17–188 m, SD 44 m). At Zapopan, the distance to the nearest neighbor's roost averaged 290 m (range 29–1021 m, SD ± 356 m).

At Irapuato, two Burrowing Owls used the same roost all winter, the other three used two roosts and moved between 74–112 m ($\bar{x}$ = 87 m, SD ± 22). At Zapopan, five owls used the same roosts all winter. The other seven owls moved between roosts 12–1596 m apart ($\bar{x}$ = 182 m, SD ± 361; n = 18), with a maximum of four roosts for a single Burrowing Owl in one winter. Average number of roosts used per Burrowing Owl per year was 1.6 (SD ± 0.6) at Irapuato and 2.3 roosts per year (SD ± 0.6) at Zapopan.

At Irapuato, the width of roost entrances varied greatly from 15–104 cm ($\bar{x}$ = 41.5 cm, SD ± 19.3), the heights from 14–40 cm ($\bar{x}$ = 24.0 cm, SD ± 6.7) and depth from 46–131 cm ($\bar{x}$ = 81.4 cm, SD ± 26.2). At Zapopan, roost entrances were usually an oval shape, slightly wider ($\bar{x}$ = 21.2 cm, SD ± 7.0) than

high ($\bar{x}$ = 18.9 cm, SD ± 3.6) but not very deep ($\bar{x}$ = 40.6 cm, SD ± 16.0). The interior diameters ($\bar{x}$ = 14.0 cm, SD ± 1.7) were considerably smaller than the entrance.

Entrances of roost burrows were not oriented in any particular direction (value of concentration 0.14 at Irapuato and 0.18 at Zapopan; Rayleigh uniformity test $Z = 0.69$ and 0.78 at Irapuato and Zapopan respectively). The results supported the null hypothesis, that roosts were evenly distributed in compass orientation (Irapuato $Z_{0.05,\ 25} = 2.98$, $P > 0.50$; Zapopan $Z_{0.05,\ 25} = 2.97$, $P > 0.50$).

DISCUSSION

Overall, the winter circadian cycle of Burrowing Owls in central Mexico was confined to two periods of activity separated by twilights; diurnal passive and nocturnal active. This contrasts to the pattern of both diurnal, crepuscular, and nocturnal foraging and prey deliveries of adult Burrowing Owls during the nesting period when they are feeding young (Rodríguez-Estrella and Ortega-Rubio 1993, Sissons 2003, Poulin and Todd 2006). Some references, such as Köning et al. (1999), incorrectly state that this species is "largely diurnal, but most active at dusk, sometimes at night." The data reported here indicate that Burrowing Owls should be considered largely nocturnal with increased activity at dusk, and active diurnally only in the breeding season.

Foraging Ranges. Summer home ranges described by other researchers include the nest burrow and roost sites, but these are within the foraging range of each owl. Thus, including burrow and roost sites should not affect the estimated size of the foraging range in summer. In winter at our study areas, all Burrowing Owls roosted away from their foraging ranges; thus, we calculated ranges of the nocturnal foraging areas. Average winter foraging ranges were variable in size between study sites and years, averaging approximately 70 ha per owl, but were consistently smaller than home ranges of nesting Burrowing Owls reported in Saskatchewan ($\bar{x}$ = 241 ha, range 14–481 ha; Haug 1985, Haug and Oliphant 1990), in Alberta ($\bar{x}$ = 328 ha, range 34–756 ha; Sissons et al. 2001, Sissons 2003), and in California ($\bar{x}$ = 183 ha, 52–302 ha; Gervais et al. 2003). These home ranges were vastly larger than winter and summer home ranges ($\bar{x}$ = 6.6 and 9.3 ha respectively) of similar-sized Little Owls (*A. noctua*) in Spain in a market gardening habitat (Framis et al. 2011). The overall pattern was that home ranges were smaller in intensive agricultural landscapes, especially with irrigation, than in native rangeland. Winter home ranges were smaller on average than summer ones, which contrasted with the pattern of nonmigratory Little Owls in Europe that moved farther from nest sites for food (Van Nieuwenhuyse et al. 2008, Grzywaczeski 2009).

A similar number of Burrowing Owls tagged with transmitters yielded similar-sized study area MCPs (Irapuato = 1002.8 ha in one winter vs Zapopan = 1207.8 ha in two winters). This landscape size may be a function of the optimal distance between roosts and foraging areas, and of the size of the agricultural landscapes in central Mexico. The low degree of overlap of nocturnal foraging ranges suggested that Burrowing Owls tend to space themselves on the landscape. However, not all Burrowing Owls in the study areas were tagged, so overlap with untagged birds could have gone undetected.

Habitat. The foraging habitats in both study areas were similar, with crops and grassland comprising most of the foraging ranges. The high use of cropland may be related to the abundance of prey, as suggested by Moulton et al. (2006). However, Burrowing Owls showed variability in the proportion of habitats used in both study areas (Fig. 2). In the Zapopan study area, Burrowing Owls generally avoided urban development, farm buildings, and military facilities. Although limited in extent, the bare ground in the quarry and arroyos provided immediate foraging options at dusk (Scobie et al. 2013).

The habitats used by Burrowing Owls in this study were similar to those described for Burrowing Owls around their winter roosts in south Texas and in central Mexico (Williford et al. 2007, 2009, Holroyd et al. 2010). Holroyd et al. (2010) found Burrowing Owls that originated from Canada, where they nested mainly in mixed grass native prairie, wintered in cultivated land, grassland, and shrubland. Cultivated habitats are important to breeding Burrowing Owls in Montana (Restani et al. 2008) and to year-round residents in Arizona (Macías-Duarte 2011), California (Rosenberg and Haley 2004), and Washington (Conway et al. 2006).

The Burrowing Owls' responses to the removal of tall, dense vegetation were immediate in several situations: harvest of crops such as corn and sorghum, grassland fires, and burning of sugarcane. Their response to these land-use activities was similar to the Little Owls' foraging in recently harvested patches of dense vegetables in market gardens near Barcelona, Spain (Framis et al. 2011). These uses are

presumably linked to abundance of prey in dense, unharvested fields, and the increased availability of prey with the reduced height of the vegetation after harvesting. Burrowing Owls also used open spaces adjacent to dense patches of vegetation, as they do in the breeding season (Scobie 2015). These open areas may have provided visibility, to allow Burrowing Owls to detect predators such as Barn Owls (*Tyto alba*) and Short-eared Owls (*Asio flammeus*) that occurred in the study sites (H. Valdez-Gómez unpubl. data) and were implicated in Burrowing Owl mortalities (Green and Anthony 1989, Holroyd et al. 2003).

Roosts. Roosts play a critical role in the ecology of owls, particularly small owls such as Burrowing Owls, because roost characteristics and locations affect survival through reduced exposure to predation and inclement weather (Haug et al. 1993, Poulin et al. 2005, Scobie et al. 2014). The evenly spaced linear plowed furrows at Irapuato created abundant cavities that were highly visible due to the contrast between white limestone rocks and dark shadows beneath. Consequently, the distance between roosting Burrowing Owls was much less at Irapuato than at Zapopan. In both localities roost entrances were narrow with little variability. The internal diameter of natural winter roosts (range 0.15–0.25 m) in Texas (Williford et al. 2007) and summer nest sites ($\bar{x} = 0.15$ m) in Saskatchewan (Poulin et al. 2005) were similar to natural roosts at Zapopan. Our findings agreed with these studies and another in Idaho (Rich 1986), that the orientation of the roost entrances was random. Roost tunnels in our study areas were shorter than the average of 87 cm reported during the breeding season in Colorado (Plumpton and Lutz 1993), 150 cm in Oklahoma (Butts 1971), and 300 cm in Wyoming (Lantz et al. 2007).

Burrowing Owls roosted in tall bunchgrass in Saskatchewan during the post-reproductive period (Todd 2001), and in south Texas and Mexico in winter (Holroyd et al. 2010). One third of wintering Burrowing Owls in southeastern Texas used concrete roosts (Williford et al. 2007). The ease with which Burrowing Owls colonize artificial cavities (Trulio 1995, Williford et al. 2009) leads us to conclude that Burrowing Owls have flexible requirements for roost sites in winter. If suitable roost sites are densely spaced, Burrowing Owls can roost in close proximity to each other, as they did at Irapuato.

At Zapopan, nine of 12 Burrowing Owls changed roosts up to four times during the winter. This did not happen at Irapuato, although we had a similar frequency of visits. One possible reason was the use of the Zapopan quarry and arroyos by feral dogs (*Canis lupus familiaris*), which had dens near the Burrowing Owls' roosts. The Irapuato study site was surrounded by a chain-link fence that discouraged access by mammals.

The average distances between roosts and foraging areas were similar between sites and years, averaging about 600 m. Only four of 17 Burrowing Owls flew >1 km between roosts and foraging areas, but one of these flew up to 3.4 km over urban parts of Zapopan. Undoubtedly, the benefits conferred by suitable roost sites are offset by the distance the Burrowing Owls must travel to access foraging areas. Other roosts were located practically on the edge of crops and grasslands (minimum distance between roost site and foraging site was 32 m), reducing the risk of exposure to predators when flying between roosts and foraging areas at dusk and dawn (Hakkarainen et al. 2001, Macleod et al. 2008).

In this study, we found wintering Burrowing Owls occupied a variety of habitats, using primarily grassland and cropland for foraging. Marsh et al. (2014) cautioned that simple habitat use within foraging ranges may not reflect the actual value of a habitat to a foraging Burrowing Owl. However, in their study in the breeding season, Burrowing Owls were transiting across several environments on each foraging bout from a central nest site. Marsh et al. (2014) were able to determine in which habitat the Burrowing Owls actually caught prey. In our winter study, the Burrowing Owls did not move from habitat to habitat within each night. Rather they were relatively sedentary in one habitat each night. Thus, the telemetry fixes described in this study reflected the relative amount of nocturnal time in each habitat. The lack of movement likely reflected the ease of meeting the food demands of a single, non-nesting Burrowing Owl rather than those of breeding Burrowing Owls that are feeding nestlings, as in the Marsh et al. (2014) study.

Burrowing Owls demonstrated adaptability to anthropogenic changes to their natural habitats in central Mexico and may have been attracted by the croplands in both study areas. However, at Zapopan, Burrowing Owls avoided intense developments and spent less time around urban areas, farm buildings, and military facilities, suggesting that certain developments were more suitable than others for owls.

The high density of owls using human-made roosts at Irapuato may indicate that natural roosts were limited in the area, and that Burrowing Owls exhibited a semi-colonial tendency in the winter. The variation in habitat and roost site selection indicated that human land uses in Mexico were varied enough to accommodate Burrowing Owls' winter habitat needs. Woodin et al. (2008) likewise concluded that agriculture in south Texas facilitated the presence of wintering Burrowing Owls, more so than the dense shrubland in that region a century ago.

In conclusion, this study demonstrated that Burrowing Owls have relatively small winter foraging ranges in central Mexico where they use a variety of habitats for foraging and roosting. All Burrowing Owls in this study used anthropogenic landscapes and appeared to be highly adaptable to agricultural habitats in the winter.

ACKNOWLEDGMENTS

Funding for this project was provided by the Canadian Wildlife Service of Environment Canada, U.S. National Fish and Wildlife Foundation, Saskatchewan Wetland Conservation Corporation, World Wildlife Fund Canada, and Beaverhill Bird Observatory. We thank R. Peacock, V. Peacock, T. Navarro, and J. L. Vargas (a high school teacher) and his students at Valencianita for their enthusiastic involvement in this project. Finally we thank anonymous referees and James Dwyer for comments on earlier drafts of this report. This research was conducted under Master Bird Banding Permit 10157 from the Canadian Wildlife Service, Environment Canada, and permits Oficio Núm/INE/DGVS/0290 and 7843 from Dirección General de Vida Silvestre, Secretaría de Medio Ambiente y Recursos Naturales, Mexico.

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Received 2 December 2016; accepted 22 December 2017
Associate Editor: James F. Dwyer