Microscale nest-site selection by the Burrowing Owl (*Athene cunicularia*) in the pampas of Argentina

Author(s): Guadalupe Martínez, Alejandro V. Baladrón, Matilde Cavalli, María S. BÓ, and Juan P. Isacch

Source: The Wilson Journal of Ornithology, 129(1):62-70.
Published By: The Wilson Ornithological Society
DOI: http://dx.doi.org/10.1676/1559-4491-129.1.62
URL: http://www.bioone.org/doi/full/10.1676/1559-4491-129.1.62

The Wilson Journal of Ornithology 129(1):62–70, 2017

MICROSCALE NEST-SITE SELECTION BY THE BURROWING OWL (*ATHENE CUNICULARIA*) IN THE PAMPAS OF ARGENTINA

GUADALUPE MARTÍNEZ,[1] ALEJANDRO V. BALADRÓN,[1,2] MATILDE CAVALLI,[1] MARÍA S. BÓ,[1] AND JUAN P. ISACCH[1]

ABSTRACT.—Habitat modifications have led many bird species to occupy areas with different characteristics, including human-altered landscapes. In this study, we analyzed how land use influences the nest-site selection at the microscale level by Burrowing Owls (*Athene cunicularia*) breeding in vegetated sand dunes, periurban areas, and agroecosystems in the Pampas of Argentina. We compared the characteristics of the nest site (percentage of open space) and the nest patch (distance to conspecific nests, tall vegetation and perches and number of perches) within and among the three land-cover types. In addition, we evaluated the breeding performance (nesting success and productivity) of owls nesting in these land-cover types. We found that nest microsite variables did not vary between owl-occupied and owl-unoccupied sites within nest patches, but they differed among land-cover types. Although nest patches differed in their availability of perches at each land-cover type, distance from the nest to the nearest perch did not vary between them. Distances to tall vegetation and to conspecific nests were highly variable and did not differ among land-cover types. Our results indicate that Burrowing Owls that inhabit the Pampas used a variety of land-cover types for nesting and showed little selectivity of nest sites and nest patches, thus reinforcing the idea that they are habitat generalists. *Received 8 June 2015. Accepted 13 April 2016.*

Key words: *Athene cunicularia*, modified habitat, natural habitat, nesting success, productivity.

INTRODUCTION

The choice of a nesting habitat is a key component of fitness for birds, since it influences their nesting success through factors such as predation, starvation, and competition (Boyce and McDonald 1999). Among raptors, the selection of a nesting site comprises several levels of spatial scales, and it is based on a hierarchical process (Tapia et al. 2007). On one hand, at the local spatial resolution or "microscale," it is important to recognize which are the vegetation and substrate characteristics necessary for nest placement. On the other hand, broad habitat resolution or "macroscale" provides information on the configuration of land uses and patchiness in the habitat matrix used as hunting areas (Janes 1985). The influence of each spatial scale can change with a raptor's body size, mobility, and life history traits (Tapia et al. 2007).

The Burrowing Owl (*Athene cunicularia*) is a raptor distributed across the Americas (Poulin et al. 2011). Burrowing Owls are typically associated with short grass prairies or other sparse vegetation (Coulombe 1971, Green and Anthony 1989, Plumpton and Lutz 1993). They nest in burrows in the ground and show high flexibility in occupying a variety of natural and modified habitats (Marks et al. 1999). In North America, Burrowing Owls are characterized by their association with fossorial mammals like prairie dogs (*Cynomys* spp.), ground squirrels (*Spermophilus* spp.), marmots (*Marmota* spp.), among others, depending on abandoned colonies or burrows of these animals for nesting (Poulin et al. 2005). Thus, the distribution, habitat characteristics, and population dynamics of northern populations of Burrowing Owls are connected to those of these animals (Orth and Kennedy 2001, Conway et al. 2006). On the opposite end of the distribution range of Burrowing Owls, at the pampas of Argentina, this species has been historically associated with the plains vizcacha (*Lagostomus maximus*). This large rodent constructs communal burrow systems comparable to those of colonial mammals in North America (Davidson et al. 2012). In the last century, populations of vizcacha were decimated because they are considered an agricultural pest; they continue to decline as a result of eradication programs (Branch et al. 2002). However, populations of southern Burrowing Owls seem to be unaffected by this situation, and far from showing population declines, they have actually expanded their habitat range (Codesido et al. 2012; AVB, unpubl. data). The key for the expansion of southern owls may be related to the

[1] Laboratorio de Vertebrados, Instituto de Investigaciones Marinas y Costeras (IIMyC), CONICET - Universidad Nacional de Mar del Plata, Funes 3350 - Mar del Plata (B7602AYJ), Argentina.
[2] Corresponding author, e-mail: abaladro@mdp.edu.ar

lack of dependency on colonies of vizcacha and the owls' ability to dig their own burrows.

Most studies on habitat characteristics of Burrowing Owls have been carried out in North America. These indicate that Burrowing Owls select open patches with dominance of short grass vegetation and bare ground for nesting, thus highlighting the critical role of the microscale variables in the selection process (e.g., Green and Anthony 1989, Plumpton and Lutz 1993, Restani et al. 2001, Thiele et al. 2013). However, other studies stressed the importance of the macroscale variables, such as the habitat matrix surrounding the nest-site (e.g., Orth and Kennedy 2001, Lantz et al. 2007, Berardelli et al. 2010) and the influence of climatic conditions at the landscape level (Stevens et al. 2011, Crowe and Longshore 2013). Although much less is known about the habitat preference of this species in South America (e.g., Coccia 1984; Bellocq 1987, 1997), more recent studies indicate that Burrowing Owls would show similar habitat characteristics to their northern counterparts (i.e., areas with high percentages of bare ground and short vegetation; Machicote et al. 2004, Villarreal et al. 2005). However, these studies have been carried out only in areas with colonies of vizcacha, and the characteristics of habitat for Burrowing Owls in other types of land-cover are practically unknown.

In this study, we assessed the microscale characteristics of areas used by Burrowing Owls for nesting in the Pampas region of Argentina. At this region, the native habitats of Burrowing Owls are the vegetated-sand dunes along the seacoast, but they are also common in agroecosystems (dominated by grazing fields), and periurban areas, such as touristic villages (Cavalli et al. 2014). These three land-cover types differ in structure and modification level, ranging from almost-pristine (vegetated sand dunes), moderately modified (agroecosystems), to highly modified land uses (periurban areas).

Firstly, we focused on the finest resolution scale, the microsite, to evaluate the importance of the position of the nest burrow within the nest-patch. Since Burrowing Owls do not depend on pre-excavated burrows for nesting in the study area, they may select practically any site within the nest-patch to locate the nest burrow. In this sense, we expect to find that Burrowing Owls dig their nests in those locations with higher proportion of bare ground and short vegetation within the nest-patch (MacCracken et al. 1985, Green and Anthony 1989, Machicote et al. 2004). Secondly, we evaluated if the main characteristics of the nest patch vary among land-cover types (vegetated sand dunes, agroecosystems, and periurban areas). At this scale, three factors are important for Burrowing Owls: access to perching sites, distance to conspecific nests, and distance to tall vegetation areas (Machicote et al. 2004, Scobie et al. 2014). These factors may have different effect according to the nesting habitat. For instance, perching sites improve an owl's ability to detect both predator and prey by increasing its horizontal visibility (Green and Anthony 1989). The proximity of conspecific nests may have a positive effect, because owls can listen to the alarm calls of others to detect predators (Coulombe 1971), or a negative impact because of increased competition (Berardelli et al. 2010). The proximity of tall vegetation may be important, because these areas are major hunting areas for Burrowing Owls (Poulin et al. 2005, Villarreal et al. 2005). Since predation pressure and food availability may change according to nesting habitat (Cavalli et al. 2014, Rebolo-Ifrán et al. 2015), we expect to find differences in nest-patch variables among the three land-cover types. Thirdly, we compared the breeding performance of Burrowing Owls among the three land-cover types. Previous studies performed in North America suggest a relationship between Burrowing Owls' reproductive success and land use. For instance, Berardelli et al. (2010) found that Burrowing Owls' reproductive success was higher in grasslands than in urban areas of New Mexico, whereas Conway et al. (2006) found higher success in urban than in agricultural areas of Washington. Based on these studies, we expect to find a similar tendency in our study area, with owls showing the highest reproductive success in vegetated sand dunes, intermediate in periurban areas, and lowest in agroecosystems.

METHODS

Study Area.—The study was carried out along the southeast coast of the Pampas Region (Buenos Aires Province, Argentina), from Mar Azul city (37° 15′ S, 56° 57′ W) to Mar del Plata city (38° 00′ N, 57° 34′ W; Fig. 1). The study area comprises a mosaic of different land-uses, which

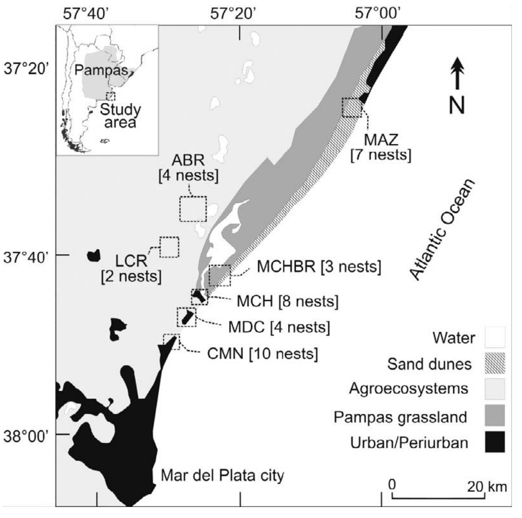

FIG. 1. Map of main land-uses for the study area at the southeastern portion of the Pampas of Argentina. Sampling locations are denoted by dashed-line squares. CMN: Camet Norte village, MDC: Mar de Cobo village, MCH: Mar Chiquita village, MAZ: Mar Azul village, MCHBR: Mar Chiquita Biosphere Reserve, ABR: Aguas Brillantes ranch, LCR: La Candelaria ranch. Number of nests at each sampling area is given in brackets.

includes a diverse array of natural vegetation, such as native grasslands, marshes, coastal dunes, and native forests, and modified environments, such as grazing fields, pasturelands, croplands, and periurban zones (Pedrana et al. 2008, Zelaya et al. 2016). Livestock production has been traditionally the main productive activity, and most of the land is devoted to grazing fields and pasturelands, whereas croplands are limited to best-quality upland soils. Along the coast of this region, native habitats are mostly limited to active bared-sand dunes, interdune valleys, and semifixed dunes with psammophytic grasslands. Urbanizations are mostly represented by small tourist villages and suburban areas of larger cities in a lesser extent (Pedrana et al. 2008, Zelaya et al. 2016).

Nest Detection.—Sampling was conducted from August 2010 to March 2011 in natural and modified habitats of the study area. We stratified our sampling according to the three main land-cover types used by owls for nesting: vegetated sand dunes, agroecosystems, and periurban areas (Cavalli et al. 2014; AVB, unpubl. data). Vegetated sand dunes were sampled at two locations: the Mar Chiquita Biosphere Reserve and the periphery of Mar Azul city (Fig. 1). These areas conserve almost pristine conditions and represent the least impacted habitat of the region. Periurban areas were sampled at three locations: Mar de Cobo, Camet Norte, and Mar Chiquita villages (Fig. 1). These are small tourist villages with scarce resident population density ($<$800 inhabitants) and scattered houses. Agroecosystems were sampled at two areas devoted to livestock production: Aguas Brillantes and La Candelaria ranches (Fig. 1). As for most parts of the study area, the landscape in these ranches is mostly represented by grazing fields (Zelaya et al. 2016). These are semi-natural shortgrass areas where native vegetation has been to some extent replaced by pastures such as tall fescue (*Festuca arudinacea*) and wheatgrass (*Thinopyrum ponticum*). The dominance of one or the other group of plants depends mainly on soil conditions. In all these areas, we searched for owl nests through ground searches, asking local people, and call-broadcasting surveys (Bibby et al. 1992). This variety of techniques allowed performing an exhaustive sampling of nests at each area and avoiding biases because of different configurations of each land-cover type, so we are confident that all owl nests were registered at each sampling area (Fuller and Mosher 1981).

Microscale Habitat Sampling.—The microsite level is the finest scale of habitat selection and involves the characteristics at the exact place where the nest is set. Since Burrowing Owls that inhabit the study area excavate their own burrows, all areas within the nest-patch are available for nest placement. To explore the selection at the microsite, we established a 2-m circle centered at the nest burrow and measured the characteristics of vegetation in four points according to the four cardinal points (MacCracken et al. 1985). At each point, we used a 1-m^2 quadrat to measure the percentage of open space (i.e., bare ground and vegetation cover $<$15 cm), which is an indicator of horizontal visibility (Green and Anthony 1989). Then, we established a second 10-m circle centered at the nest burrow and performed the same procedure (MacCracken et al. 1985). This was used to describe unused sites (i.e., owl-unoccupied sites) within the patch at a microsite level.

In addition, we recorded several variables related to nest-patch configuration. Firstly, we assessed the availability of perches in the patch, which are considered an important attribute of Burrowing Owls' nesting areas (Bellocq 1987, Rodríguez-Estrella and Ortega-Rubio 1993, Scobie et al. 2014). We considered a perch any structure (natural or artificial) on which we observed owls frequently, and all other structures of similar characteristics in the nest-patch. The sort of perches varied among land-cover types. In agroecosystems, these were represented mainly by fence posts, with shrubs and trees to a lesser extent. In vegetated sand dunes, owls used preferentially the top of high dunes as perching sites, and occasionally shrubs when available. The most diverse perches were offered in periurban areas, where owls used utility poles, fence posts, buildings, and trees as perching sites. At each nest, we measured the distance from the nest-site to the nearest perch and the number of perches in the patch within a 50-m radius from the nest burrow. The use of perches by owls beyond this distance was quite rare according to our preliminary observations. Two other variables related to nest-patch configuration were also measured: the distance from the nest-site to the nearest tall grass patch and the distance to the nearest conspecific nest (Rodríguez-Estrella and Ortega-Rubio 1993, Lantz et al. 2007, Stevens et al. 2011). When no conspecific nests were found within a 300-m radius from the nest burrow, we categorized the nest as $>$300 m, and excluded it from later analyses.

Breeding Success.—We visited all the occupied nests every 1–10 days prior to finding eggs in the nest (late Aug–early Oct). We used a night vision security camera connected to a computer to determine the date when incubation stage began (García and Conway 2009). From the moment the chicks were seen outside the burrow (when they were ~10 days old) until they fledged, we weekly visited each individual nest to count the number of chicks/fledglings. During these visits, two observers scanned the nest during 20–30 min from a vehicle or a blind location at a distance of 50–200 m, using either binoculars or spotting scopes (Rosenberg and Haley 2004). Multiple visits to nest sites throughout the breeding season (i.e., from early Oct–early Mar) allowed accurate determination of the maximum number of chicks fledged per nest (Restani et al. 2001, Gorman et al. 2003).

Since all nests were identified prior to the beginning of the incubation period and all nest fates were known, we estimated the owls' breeding performance by calculating apparent nesting success and productivity for each land cover type (Martin and Geupel 1993, Steenhof and Newton 2007, Brown et al. 2013). The nesting success was calculated as the number of nesting pairs that raise at least one chick to the fledgling stage at each land-cover type, and the productivity as the mean number of fledglings per nesting attempt and the mean number of fledglings per successful nest, counted on multiple visits to each nest (Conway et al. 2006, Berardelli et al. 2010).

Statistical Analyses.—To evaluate nest site selection, we compared the variables measured within and among land-cover types. We used Mann-Whitney *U*-tests to evaluate differences in percent open space between owl-occupied and owl-unoccupied sites within each land-cover type, and used Kruskall-Wallis tests to evaluate percent open space between owl nest sites in the different land-cover types (Zar 2010). Differences in productivity values between land-cover types were tested using Mann-Whitney *U*-tests and differences in nest success were compared using *Z*-test of equality of proportions with continuity correction (Zar 2010).

RESULTS

We monitored 38 nests of Burrowing Owls, 10 at vegetated sand dunes, 6 at agroecosystems, and 22 at periurban areas. At the microsite level, we did not find differences in the percentage of open space between owl-occupied and owl-unoccupied sites within each land-cover type (agroecosystems: $U_{1,6} = 15$, $P = 0.63$; vegetated sand-dunes: $U_{1,10} = 48$, $P = 0.88$; periurban areas: $U_{1,22} = 196.5$, $P = 0.29$; Fig. 2A). However, we found that percent open space was significantly lower for vegetated sand-dunes ($H_{2,38} = 10.98$, $P = 0.001$; Fig. 2A) when owl-occupied sites were compared among land-cover types.

Nest-patch configuration showed few differences among the three land cover types. Nesting patches showed significantly more perches at agroecosystems (median = 30 perches) than at periurban areas (median = 4 perches) and vegetated sand-dunes (median = 3.5 perches)

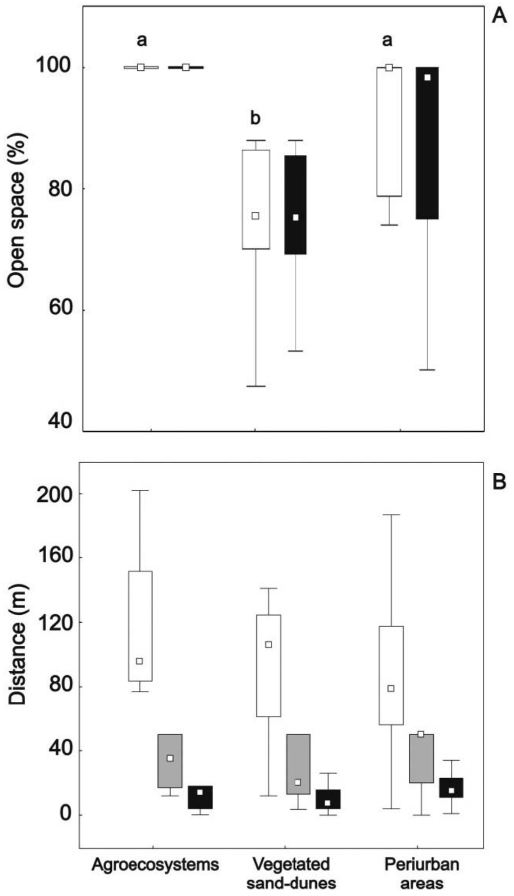

FIG. 2. (A) Percentage of open space in owl-occupied (white boxes) and owl-unoccupied sites (black boxes) within the nesting patches of Burrowing Owls in three land-cover types at the Pampas of Argentina. Differences in characteristics of owl-occupied sites among land-cover types are denoted by lowercase letters. (B) Distances from the nest-site to the nearest conspecific nest (white boxes), to the nearest tallgrass patch (gray boxes), and to the nearest perch (black boxes) in the three land-cover types used by Burrowing Owls for nesting in the Pampas of Argentina. Points inside the boxes indicate medians; boxes represent 25th–75th percentiles; whiskers represent the non-outlier range.

($H_{2,38} = 11.32$, $P = 0.035$). Although the number of perches varied, distance to the nearest perch was similar among land-cover types ($H_{2,38} = 1.98$, $P = 0.37$; Fig. 2B). Most mating pairs located their nests in sites with at least one perch within 20 m from the burrow (>75% of all nests). The distance to the nearest tall vegetation patch and to the nearest conspecific nest also did not differ among land-cover types ($H_{2,38} = 2.02$, $P = 0.36$ and $H_{2,30} = 1.32$, $P = 0.52$ respectively; Fig. 2B). We found that, irrespective of land-cover type, the majority of mating pairs preferred nesting farther than 20 m from tall vegetation patches and closer than 150 m from the nearest conspecific nest (>70% of all nests).

All nests sampled at agroecosystems were unsuccessful because of nest desertion. Thus, both productivity and nesting success were null in this land-cover type. Vegetated sand dunes and periurban areas showed similar values of nesting success (Z = 0.029, $P = 0.87$), with 50% of successful nests at vegetated sand-dunes and 55% of successful nests at periurban areas. Productivity was also similar between both land-cover types. The mean number of fledglings per nesting attempt was 1.30 ± 0.54 in vegetated sand-dunes and 1.50 ± 0.33 in periurban areas ($U_{10,22} = 104$, $P = 0.83$). The mean number of fledglings per successful nest was 2.6 ± 0.68 in vegetated sand-dunes and 2.75 ± 0.28 in periurban areas ($U_{5,12} = 29$, $P = 0.96$).

DISCUSSION

Burrowing Owls bred in areas with a variety of land uses in the Pampas of Argentina, including natural (vegetated sand-dunes) and modified (periurban areas and agroecosystems) habitats. At these three land-cover types, owls nested in sites with good horizontal visibility—i.e., high proportion of bare ground and short grass. The importance of these nest-site features have been previously reported for Burrowing Owls nesting in North and South America (e.g., MacCracken et al. 1985, Machicote et al. 2004). Our comparison at the microsite level shows that owls located their nest burrows in sites of similar characteristics than surrounding area within the nest-patch. Thus, contrary to expected, our results indicate that Burrowing Owls show little selectivity at the microsite level. This may be because the selection process occurs at broader scales as well as because owls select patches of homogeneous vegetation in terms of cover and height (Green and Anthony 1989).

Burrowing Owls' nest-patches shared some common characteristics irrespective of the land-cover type. This similarity is probably because of the variability in patch features within land-cover types, but also reveals the ability of Burrowing Owls to nest in different habitat contexts (Conway et al. 2006, Berardelli et al. 2010). In this sense, the presence of a nearby perch, the proximity of tall vegetation, and the distance to conspecific were consistent features through land-cover types. All these factors seem to be important to determine the suitability of the patch for nesting Burrowing Owls (Poulin et al. 2005, Berardelli et al. 2010, Scobie et al. 2014).

For instance, patch characteristics are important for Burrowing Owls in terms of predator detection and access to food resources. The presence of perches near the nest provide improved vigilance behavior, since elevated positions increase an owl's field of vision and may help it to detect predators earlier (Widén 1994, Andersson et al. 2009, Scobie et al. 2014). In addition, perches may be used during foraging, especially for searching prey through sit-and-wait hunting mode (Bellocq 1987). We found that although the type and number of perches available differed among land-cover types, the distance from the owl nest site to the nearest perch did not vary among them. This supports the idea that owls consider the presence (but not the amount) of vantage points in the patch as a key resource when selecting their nest sites (Rodríguez-Estrella and Ortega-Rubio 1993, Scobie et al. 2014).

The distance to tall vegetation areas may also be linked to predator detection, since it determines the horizontal visibility from the nest-site (Poulin et al. 2005). However, these may also be important hunting areas for Burrowing Owls, especially for capturing rodents (Bellocq 1997, Poulin et al. 2005, Villarreal et al. 2005). This supposes a tradeoff between minimizing predation risk and gaining access to important food resources. However, in our study area, Burrowing Owls rely on ground insects (mainly beetles) as their main food resource during the breeding season (Cavalli et al. 2014). This type of prey is often captured in open areas around the nest within the nest-patch (Green and Anthony 1989). Thus, it is likely that the distance to tall vegetation is not a critical factor in relation to food resources in the study area.

Despite the fact that in the Pampas the nesting habitat of Burrowing Owls is not constrained to colonies or burrows of other animals, we found that mating pairs tend to settle near the territory of other owls. This clumped distribution of Burrowing Owls' nests has been linked to cooperative vigilance for colonial populations in North America (Coulombe 1971) and may explain the distribution of nests in our study area. Burrowing Owls exhibit a conspicuous parental care behavior that includes vocalizations, threatening postures, and other aggressive displays to deter intruders (Green and Anthony 1989, Cavalli et al. 2016). Thus, mating pairs may benefit by using alarm call and displays of other owls for early detection of predators (Green and Anthony 1989). Again, a trade-off may occur if the beneficial effects of nesting in close proximity are offset by an increase in competition in areas where food resources are limited (Berardelli et al. 2010).

Many studies have reported on the breeding performance of Burrowing Owls in different habitats in North America (e.g., Thomsen 1971, Martin 1973, Haug 1985, Rodríguez-Estrella and Ortega-Rubio 1993, Millsap and Bear 2000, Holmes et al. 2003, Catlin et al. 2005, Conway et al. 2006, Berardelli et al. 2010, Barclay et al. 2011, Crowe and Longshore 2013). In South America, information on reproductive parameters of Burrowing Owls is quite limited (e.g., Coccia 1984, Bellocq 1997). In our study, we compared the breeding performance of Burrowing Owls nesting in three habitats of the Pampas, showing that its reproductive parameters varied with land cover in the study area. Even when the tendencies we found (i.e., similar breeding performance in vegetated sand-dunes and periurban areas and null in agroecosystems) do not support our prediction based in previous studies (Conway et al. 2006, Berardelli et al. 2010), the values of breeding success and productivity registered are comparable to those reported for northern populations in similar habitat conditions. It is worthy to note that comparisons of breeding performances of Burrowing Owls among different studies are very difficult because of methodology differences, especially for productivity calculation (Gorman et al. 2003), thus these comparisons should be considered with caution.

We found that breeding success of Burrowing Owls in vegetated sand dunes (50%) was fairly below values reported for other grassland habitats of the species at its northern range (e.g., 92%, Restani et al. 2001; 81%, Berardelli et al. 2010). The productivity measured as the mean number of fledglings per nest attempt and per successful nest in this land-cover type (1.3 and 2.6 respectively) was also lower than those reported for the owls nesting in natural areas of North America (2.5–2.6 fledglings/attempt and 3.1 fledglings/successful nest; Restani et al. 2001, Berardelli et al. 2010). For periurban areas, the breeding success of Burrowing Owls (55%) fell within the range reported for airports, parklands, and other urbanized areas of North America. In this type of land use, the success of owls is subject to the extension of the urbanized area and the level of development (Millsap and Bear 2000) and may show a wide variability among locations (e.g., 88%, Thomsen 1971; 41%, Conway et al. 2006; 51%, Trulio and Chromczak 2007; 67.5%, Berardelli et al. 2010). The mean number of fledglings per nest attempt and per successful nest (1.5 and 2.75 respectively) were similar to those reported by Conway et al. (2006) in Washington (1.5 fledglings/attempt and 3.1 fledglings/successful nest) but lower than reported by Berardelli et al. (2010) in New Mexico (2.6 fledglings/attempt and 3.9 fledglings/successful nest). The worst breeding performance for Burrowing Owls was found in agroecosystems, where breeding success was zero. Even when this result may be influenced by the low sample size (only six nests were monitored), other authors also reported low success for Burrowing Owls nesting in agroecosystems of central Argentina (e.g., 10%, Bellocq 1997; 35%, Machicote et al. 2004). In addition, it has been reported that success of northern populations rarely exceeds 50% (Haug 1985, Holmes et al. 2003, Conway et al. 2006), although occasionally it may reach up to 70% (Catlin et al. 2005).

In the Pampas of Argentina, the Burrowing Owl seems to be a species that is better able to cope with challenges that come with habitat modification. Like in northern populations, our results show that the Burrowing Owl behaves as a habitat generalist species in the Pampas (Codesido et al. 2012) and relies on a few environmental cues to select nesting areas (Crowe and Longshore 2013). However, our results also show that breeding performance of this owl may vary in different landscape contexts. Future studies should examine if its ability to nest in a variety of habitat conditions may result in optimal, beneficial, or even maladaptative responses to human-induced modifications (Van Buskirk 2012).

ACKNOWLEDGMENTS

We thank M. Pretelli, O. Stellatelli, N. Chiaradia, and E. Madrid for field assistance. This study was funded by the Universidad Nacional de Mar del Plata (EXA 15-E317). We acknowledge funding provided by Comisión de Investigaciones Científicas de la Provincia de Buenos Aires (student scholarship to GM), Western Bird Banding Association (grant to MC), and The International Osprey Foundation (grant to AVB).

LITERATURE CITED

Andersson, M., J. Wallander, and D. Isaksson. 2009. Predator perches: a visual search perspective. Functional Ecology 23:373–379.

Barclay, J. H., N. M. Korfanta, and M. J. Kauffman. 2011. Long-term population dynamics of a managed Burrowing Owl colony. Journal of Wildlife Management 75:1295–1306.

Bellocq, M. I. 1987. Habitat selection and differential predation by *Athene cunicularia* on rodents of agrarian ecosystems. Revista Chilena de Historia Natural 60:81–86.

Bellocq, M. I. 1997. Ecology of the Burrowing Owl in agrosystems of central Argentina. Raptor Research Reports 9:52–57.

Berardelli, D., M. J. Desmond, and L. Murray. 2010. Reproductive success of Burrowing Owls in urban and grassland habitats in southern New Mexico. Wilson Journal of Ornithology 122:51–59.

Bibby, C. J., N. D. Burgess, and D. A. Hill. 1992. Bird census techniques. Academic Press, San Diego, California, USA.

Boyce, M. S. and L. L. McDonald. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology and Evolution 14:268–272.

Branch, L., D. Villarreal, and M. Machicote. 2002. Conservation challenges of ecosystem engineers: case studies from grasslands and shrublands of North and South America. Open Country 4:37–48.

Brown, J. L., K. Steenhof, M. N. Kochert, and L. Bond. 2013. Estimating raptor nesting success: old and new approaches. Journal of Wildlife Management 77:1067–1074.

Catlin, D. H., D. K. Rosenberg, and K. L. Haley. 2005. The effects of nesting success and mate fidelity on breeding dispersal in Burrowing Owls. Canadian Journal of Zoology 83:1574–1580.

Cavalli, M., A. V. Baladrón, J. P. Isacch, G. Martínez, and M. S. Bó. 2014. Prey selection and food habits of breeding Burrowing Owls (*Athene cunicularia*) in natural and modified habitats of Argentine pampas. Emu 114:184–188.

Cavalli, M., J. P. Isacch, A. V. Baladrón, L. M. Biondi, and M. S. Bó. 2016. Differing nest-defence behaviour in urban and rural populations of breeding Burrowing Owls. Emu 116:428–434.

Coccia, M. 1984. Observaciones ecológicas sobre *Athene cunicularia partridgei*, Olrog, 1976, en pastizales inundables de la albufera de Mar Chiquita (provincia de Buenos Aires). Thesis. Universidad Nacional de Mar del Plata, Mar del Plata, Argentina.

Codesido, M., C. González-Fischer, and D. Bilenca. 2012. Agricultural land-use, avian nesting and rarity in the Pampas of central Argentina. Emu 112:46–54.

Conway, C. J., V. Garcia, M. D. Smith, L. A. Ellis, and J. L. Whitney. 2006. Comparative demography of Burrowing Owls in agricultural and urban landscapes in southeastern Washington. Journal of Field Ornithology 77:280–290.

Coulombe, H. N. 1971. Behavior and population ecology of the Burrowing Owl, *Speotyto cunicularia*, in the Imperial Valley of California. Condor 73:162–176.

Crowe, D. E. and K. M. Longhsore. 2013. Nest site characteristics and nesting success of the western Burrowing Owl in the eastern Mojave Desert. Journal of Arid Environments 94:113–120.

Davidson, A. D., J. K. Detling, and J. H. Brown. 2012. Ecological roles and conservation challenges of social, burrowing, herbivorous mammals in the world's grasslands. Frontiers in Ecology and the Environment 10:477–486.

Fuller, M. R. and J. A. Mosher. 1981. Methods of detecting and counting raptors: a review. Studies in Avian Biology 6:235–246

García, V. and C. J. Conway. 2009. Use of video probe does not affect Burrowing Owl reproductive parameters or return rates. Journal of Wildlife Management 73:154–157.

Gorman, L. R., D. K. Rosenberg, N. A. Ronan, K. L. Haley, J. A. Gervais, and V. Franke. 2003. Estimation of reproductive rates of Burrowing Owls. Journal of Wildlife Management 67:493–500.

Green, G. A. and R. G. Anthony. 1989. Nesting success and habitat relationships of Burrowing Owls in the Columbia Basin, Oregon. Condor 91:347–354.

Haug, E. A. 1985. Observations on the breeding ecology of Burrowing Owls in Saskatchewan. Thesis. University of Saskatchewan, Saskatoon, Canada.

Holmes, A. L., G. A. Green, R. L. Morgan, and K. B. Livezey. 2003. Burrowing Owl nest success and burrow longevity in north central Oregon. Western North American Naturalist 63:244–250.

Janes, S. W. 1985. Habitat selection in raptorial birds. Pages 159–188 *in* Habitat selection in birds (M. L. Cody, Editor). Academic Press Inc., Orlando, Florida, USA.

Lantz, S. J., C. J. Conway, and S. H. Anderson. 2007. Multiscale habitat selection by Burrowing Owls in black-tailed prairie dog colonies. Journal of Wildlife Management 71:2664–2672.

MacCracken, J. G., D. W. Uresk, and R. M. Hansen. 1985. Vegetation and soils of Burrowing Owl nest sites in Conata Basin, South Dakota. Condor 87:152–154.

Machicote, M., L. C. Branch, and D. Villarreal. 2004. Burrowing Owls and burrowing mammals: are ecosystem engineers interchangeable as facilitators? Oikos 106:527–535.

Marks, J. S., R. J. Cannings, and H. Mikkola. 1999. Family Strigidae (typical owls). Pages 76–243 *in* Handbook of the birds of the world. Volume 5. Barn-owls to hummingbirds (J. del Hoyo, A. Elliott, and J. Sargatal, Editors). Lynx Edicions, Barcelona, Spain.

Martin D. C. 1973. Selected aspects of Burrowing Owl ecology and behavior. Condor 75:446–456.

Martin, T. E. and G. R. Geupel. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. Journal of Field Ornithology 64:507–519.

Millsap, B. A. and C. Bear. 2000. Density and reproduction of Burrowing Owls along an urban development gradient. Journal of Wildlife Management 64:33–41.

Orth, P. B. and P. L. Kennedy. 2001. Do land-use patterns influence nest-site selection by Burrowing Owls (*Athene cunicularia hypugaea*) in northeastern Colorado? Canadian Journal of Zoology 79:1038–1045.

Pedrana, J., J. P. Isacch, and M. S. Bó. 2008. Habitat relationships of diurnal raptors at local and landscape scales in southern temperate grasslands of Argentina. Emu 108:301–310.

Plumpton, D. L. and R. S. Lutz. 1993. Nesting habitat use by Burrowing Owls in Colorado. Journal of Raptor Research 27:175–179.

Poulin, R. G., L. D. Todd, K. M. Dohms, R. M. Brigham, and T. I. Wellicome. 2005. Factors associated with nest- and roost-burrow selection by Burrowing Owls (*Athene cunicularia*) on the Canadian prairies. Canadian Journal of Zoology 83:1373–1380.

Poulin, R. G., L. D. Todd, E. A. Haug, B. A. Millsap, and M. S. Martell. 2011. Burrowing Owl (*Athene cunicularia*). The birds of North America. Number 61.

Rebolo-Ifrán, N., M. Carrete, A. Sanz-Aguilar, S. Rodríguez-Martínez, S. Cabezas, T. A. Marchant, G. R. Bortolotti, and J. L. Tella. 2015. Links between fear of humans, stress and survival support a non-random distribution of birds among urban and rural habitats. Scientific Reports 5:13723.

Restani, M., L. R. Rau, and D. L. Flath. 2001. Nesting ecology of Burrowing Owls occupying black-tailed prairie dog towns in southeastern Montana. Journal of Raptor Research 35:296–303.

Rodríguez-Estrella, R. and A. Ortega-Rubio. 1993. Nest site characteristics and reproductive success of Burrowing Owls (Strigiformes: Strigidae) in Durango, Mexico. Revista de Biología Tropical 41:143–148.

Rosenberg, D. K. and K. L. Haley. 2004. The ecology of Burrowing Owls in the agroecosystem of the Imperial Valley, California. Studies in Avian Biology 27:120–135.

Scobie, C., E. Bayne, and T. Wellicome. 2014. Influence of anthropogenic features and traffic disturbance on Burrowing Owl diurnal roosting behavior. Endangered Species Research 24:73–83.

Steenhof, K. and I. Newton. 2007. Assessing nesting success and productivity. Pages 181–192 *in* Raptor research and management techniques (D. M. Bird and K. L. Bildstein, Editors). Hancock House Publishers, Blaine, Washington, USA.

Stevens, A. F. J., E. M. Bayne, and T. I. Wellicome. 2011. Soil and climate are better than biotic land cover for predicting home-range habitat selection by endangered Burrowing Owls across the Canadian prairies. Biological Conservation 144:1526–1536.

Tapia, L., P. L. Kennedy, and R. W. Mannan. 2007. Habitat sampling. Pages 153–170 *in* Raptor research and management techniques (D. M. Bird and K. L. Bildstein, Editors). Hancock House Publishers, Blaine, Washington, USA.

Thiele, J. P., K. K. Bakker, and C. D. Dieter. 2013. Multiscale nest site selection by Burrowing Owls in western South Dakota. Wilson Journal of Ornithology 125:763–774.

Thomsen, L. 1971. Behavior and ecology of Burrowing Owls on the Oakland Municipal Airport. Condor 73:177–192.

Trulio, L. A. and D. A. Chromczak. 2007. Burrowing Owl nesting success at urban and parkland sites in northern California. Bird Populations Monographs 1:115–122.

Van Buskirk, J. 2012. Behavioural plasticity and environmental change. Pages 145–158 *in* Behavioural responses to a changing world: mechanisms and consequences (U. Candolin and B. B. M. Wong, Editors). Oxford University Press, Oxford, United Kingdom.

Villarreal, D., M. Machicote, L. C. Branch, J. J. Martinez, and A. Gopar. 2005. Habitat patch size and local distribution of Burrowing Owls (*Athene cunicularia*) in Argentina. Ornitología Neotropical 16:529–537.

Widén, P. 1994. Habitat quality for raptors: a field experiment. Journal of Avian Biology 25:219–223.

Zar, J. H. 2010. Biostatistical analysis. Fifth Edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zelaya, K., J. van Vliet, and P. H. Verburg. 2016. Characterization and analysis of farm system changes in the Mar Chiquita basin, Argentina. Applied Geography 68:95–103.