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Habitat selection by Burrowing Owls *Athene cunicularia* in the Pampas of Argentina: a multiple-scale assessment

Alejandro V. Baladrón*, Juan P. Isacch, Matilde Cavalli & María S. Bó

Marine and Coastal Research Institute (IIMyC), CONICET - National University of Mar del Plata, Funes 3250 (B7602AYJ) Mar del Plata, ARGENTINA
*Corresponding author, e-mail: abaladro@mdp.edu.ar

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Abstract. Human-induced habitat changes have been typically linked to negative effects on native species, but an increasing number of studies show that many species are unaffected by these changes or even benefited from them. The Burrowing Owl *Athene cunicularia* is a raptor species that has deserved special attention in recent years due to its capacity to live in a variety of natural and modified habitats. In this study, we analyzed habitat characteristics that determine the habitat selection of the Burrowing Owl at the nest-patch, territory and landscape scales in the Pampas of Argentina. We performed broadcasting call surveys to evaluate presence-absence of owls at random points. In addition, we measured habitat variables in the field and used satellite imagery to obtain land-use information. We used Generalized Linear Models to explore the influence of habitat variables on the probability of occupancy by Burrowing Owls. Our results indicate that Burrowing Owls demonstrate good ability to live in a wide variety of habitat types and with different disturbance levels in the Pampas. At the nest-patch scale, which includes the nest-site and the surrounding patch around it, the presence of owls was positively associated with the horizontal visibility and was influenced by the land-cover type. At the territory scale, the occurrence of owls was positively associated with the presence of active (non-vegetated) dunes and negatively with croplands. At the landscape scale, the presence of owls was negatively associated with the disturbance level and positively with the amount of borders between habitats. A unique multi-scale model containing variables of the three spatial scales was more robust to explain variation in Burrowing Owl occupancy patterns than any single-scale model. This would reveal the hierarchical nature of habitat selection by Burrowing Owls in the Pampas, comparable to that observed in North American populations.

Key words: *Athene cunicularia*, nest-patch, territory, landscape, urban areas, agroecosystems, sand dunes, habitat selection, owl

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INTRODUCTION

Choosing a place to live is one of the most important decisions made by wildlife, because it is directly related to the access to resources that animals need to fulfill their ecological requirements (Wilbur et al. 1974, Wiens 1989, Boyce & McDonald 1999). It is assumed that animals use environmental cues to select the habitats where they maximize their chance to survive and breed successfully (Rosenzweig 1985, Danchin et al. 1998). Given that the balance between risks and rewards frequently changes according to the scale of measurement, habitat selection is an inherently scale-sensitive process (Mayor et al. 2009, McGarigal et al. 2016).

Human-induced environmental perturbations are important factors affecting habitat selection by animals, because they produce changes in the resources profile (Howard et al. 2001). Habitat reduction and fragmentation affect important resources which may be either impoverished (e.g., by decreasing food availability) or improved (e.g., by decreasing predation risk or competition), depending on the species, its position in the food web, and/or its behavioral plasticity (Chalfoun et al. 2002, Kight & Swaddle 2007). Although the increase of the perturbation has been typically linked to negative effects on native species (Howard et al. 2001, Verhulst et al. 2001), an increasing number of studies show that many species may be benefited by environmental changes, in particular those that exhibit high behavioral plasticity or ability to colonize novel habitats (Sih et al. 2011, Møller et al. 2014).

Since most raptors are top predators that occur in low numbers, use large areas for hunting, and have an intensive parental care (Newton 1979), their habitat requirements often involve important constraints for their distribution, density, and breeding success (Janes 1985). Habitat selection in raptors comprises several levels of spatial scales and is based on a hierarchical process (Tapia et al. 2007). Each scale produces different information on species' habitat selection. On the one hand, the local or "microhabitat" scale is important to know the vegetation characteristics such as height and cover of vegetation strata and suitable substrates for nest-site location. On the other hand, broad resolution or "macrohabitat" scales provide information on the configuration of land-uses and patchiness in the habitat matrix used as hunting areas (Janes 1985). However, the influence of habitat features at different spatial scales can change with raptors' body size, mobility and life-history traits, thus the terms microhabitat and macrohabitat are likely to be species-specific (Tapia et al. 2007). This multi-scale, hierarchical perspective has been demonstrated to be very useful for studying raptors' habitat selection as well as to be used as tools for prediction-based management strategies. This kind of analysis is especially applicable for large raptors (e.g. López-López et al. 2006, Muñoz & Real 2013, Di Vittorio & López-López 2014), but also may be useful for small raptors (e.g. Finn et al. 2002, Sergio et al. 2003, Piorecky & Prescott 2006).

The Burrowing Owl, *Athene cunicularia*, is a small raptor widely distributed throughout western North America, Florida, Central and South America (Poulin et al. 2011) that typically nests in cavities on the ground in short grass prairies or other sparse vegetation (Marks et al. 1994). Habitat requirements of this owl are quite broad because it is also found in modified habitats, such as rangelands, croplands, golf courses, cemeteries, airports, and vacant lots in urban areas (Poulin et al. 2011). The location of the nesting site is very important for Burrowing Owls, because usually they use the nesting burrow as refuge or resting place during the non-breeding period, and often reuse the same areas during successive breeding periods (Plumpton & Lutz 1993, Machicote et al. 2004). Thus, the habitat used by this raptor throughout the year is closely related to the selection of its nesting site, and hence to its reproductive performance (Conway et al. 2006, Berardelli et al. 2010).

The great majority of studies on the Burrowing Owl's habitat selection have been conducted in the northern range of its distribution. These indicate that it selects open habitats with dominance of short grass vegetation and bare ground for nesting (e.g. Green & Anthony 1989, Plumpton & Lutz 1993, Restani et al. 2001), but also show that the habitat matrix surrounding the nest-site would play a critical role in the selection of nesting areas, because it may influence the predation risk and the availability of food resources (e.g., Orth & Kennedy 2001, Berardelli et al. 2010, Crowe & Longshore 2013). Thus, processes involved in Burrowing Owl habitat selection would be determined by the simultaneous effect of several habitat features at multiples scales (Lantz et al. 2007, Thiele et al. 2013).

In North America, Burrowing Owls are characterized by their association with fossorial mammals (e.g. prairie dogs, *Cynomys* spp.), depending on abandoned colonies or burrows of these animals for nesting (Poulin et al. 2011, Alverson & Dinsmore 2014). Thus, the distribution, habitat characteristics, and population dynamics of northern Burrowing Owl populations are connected to those of these animals (Orth & Kennedy 2001, Conway et al. 2006). An exception is represented by Burrowing Owls that inhabit the Florida peninsula, which usually excavate their own burrows (Millsap & Bear 2000). In the southernmost range of the Burrowing Owl's geographical distribution, at the Pampas of Argentina, this species has been historically associated with the Plains Vizcacha *Lagostomus maximus*. This is a large rodent that constructs communal burrow systems comparable to those of colonial mammals in North America (Davidson et al. 2012). In the last century, vizcacha populations were decimated due to the fact that they were considered an agricultural pest, and still continue to decline, as a result of eradication programs (Branch et al. 2002, Machicote et al. 2004). However, southern Burrowing Owl populations seem to be unaffected by this situation, and far from showing population declines, they have expanded their habitat range (Codesido et al. 2012). Although they also use mammals' caves, the rule for the Burrowing Owl at southern latitudes seems to have been to dig their own burrows rather than occupy pre-excavated burrows of other animals (Hudson 1920, Marks et al. 1994). Another difference is that, unlike most northern populations that are migratory or disperse widely to some extent, southern populations are year-round residents (Humphrey et al. 1970, Belton 1984, Narosky & Di Giácomo 1993) and use the same burrow during both breeding and non-breeding seasons (Poulin et al. 2011, Cavalli et al. 2016).

The Burrowing Owl is considered a species of conservation concern in North America, due to the population declines that this species showed in parts of its range (Orth & Kennedy 2001, Poulin et al. 2005, Conway et al. 2006). Such population changes have been attributed to human-induced habitat modification, as poisoning, hunting, and the control of fossorial mammals whose abandoned caves this owl uses for nesting (Poulin et al. 2011). Other populations, however, have been less impacted and even increased their ranges in some areas of North America (Macías-Duarte & Conway 2015), frequently thriving and reaching their highest densities in modified habitats (Rosenberg & Haley 2004). A similar process of habitat degradation has occurred in the Pampas of Argentina (Bilenca & Miñarro 2004). The modification of great areas of native grasslands as a result of agricultural intensification and urban development has been detrimental for raptors in general, but no declines have been reported for the Burrowing Owl (Filloy & Bellocq 2007, Codesido et al. 2012). At these latitudes, Burrowing Owls have shown a considerable ability to exploit novel habitats to the point of being one of the commonest raptors in agricultural and residential areas (Bellocq 1997, Carrete & Tella 2011). The lack of dependency on pre-excavated burrows may be one of the keys to the expansion of the range of suitable areas for nest settlement.

In this study, we performed a multiple-scale assessment of the habitat characteristics selected by the Burrowing Owl at the southernmost end of its distribution in the Pampas of Argentina. Our aims were: i) to identify the environmental cues used by this owl for the selection of the nesting area, ii) to determine the importance of each scale in the process of habitat selection, and iii) to generate a predictive model to identify current and potential habitats for Burrowing Owls in the Pampas.

METHODS

Study area

The Pampas Region is included in the biome known as Rio de la Plata Grasslands, a prairie of grasslands that covers the temperate plains of South America, and represents one of the most extensive areas of grasslands of the Neotropics (Soriano et al. 1991). The landscape in the Pampas region is dominated by grasslands, although the original gramineous vegetation community has been highly modified by agriculture (Bilenca & Miñarro 2004). In particular, the study area is included in a subset of the region called Flooding Pampas. This subregion comprises a mosaic of different land-uses, including a diverse array of natural vegetation, such as native grasslands, marshes, coastal dunes, and native forests, and modified environments, such as grazing fields, croplands and urban zones (Pedrana et al. 2008, Zelaya et al. 2016). The dominance of one or another of these land-uses depends on soil conditions. Livestock production has been traditionally the main productive activity in the Flooding Pampas, and most of the land is devoted to grazing fields, whereas croplands are limited to best-quality upland soils. Native habitats are typically represented by patches of tall grasslands mainly located in areas where soils are flooded, brackish, or sandy (León et al. 1984). 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 periurban areas (small touristic villages with < 800 inhab. and scattered houses) and suburban areas of larger cities in a lesser extent (Pedrana et al. 2008, Zelaya et al. 2016).

Habitat classification

We performed a map of land-uses for the study area from the Landsat Thematic Mapper (TM) satellite imagery (path-row 224-86; available at http: www.cbers.inpe.br; date: November 2011), with a cell size of 30 m and UTM (WGS-84) projection. The original image was cropped to the size of the surveyed area (~3500 km^2), which is bounded by National Route 2 to the W, by the Atlantic Ocean to the E, by Mar del Plata city to the S, and by Villa Gesell city to the N (Fig. 1). This area was arbitrarily selected by being a representative portion of the Flooding Pampas which encompass the whole range of habitat types and land uses typical of the region used by Burrowing Owls.

A total of 250 field and map points were gathered to obtain land-use information (Campbell 2002). A part of these points were used to generate the necessary training sites to perform a supervised classification of the satellite image (Isacch et al. 2006). Nine land-use classes were defined: water, croplands, plowed fields, grazing fields, urban (which includes periurban and suburban areas), grasslands, forests (including groves, native woodlands, and exotic forests), vegetated dunes, and active (non-vegetated) dunes. We used the maximum likelihood algorithm, which is

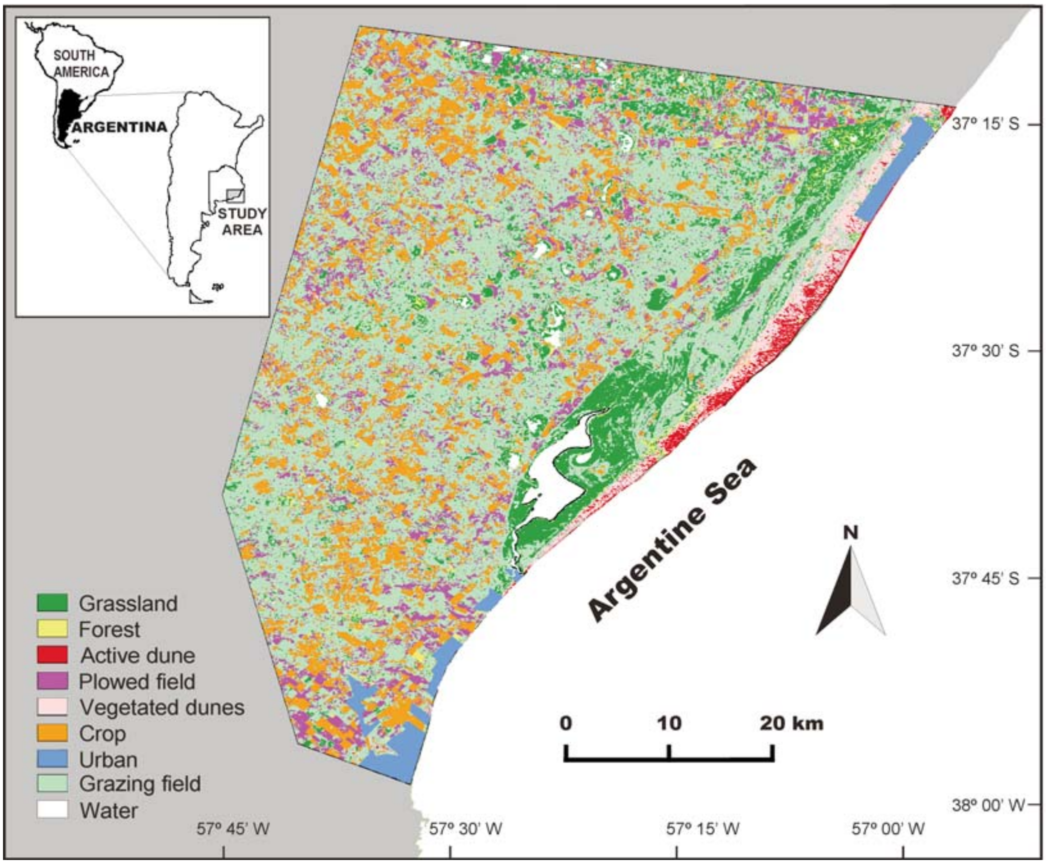

Fig. 1. Map of land-use for the study area at the southeastern portion of the Pampas of Argentina, performed through supervised classification of Landsat Thematic Mapper (TM) satellite image.

based on the probability density function associated with a particular training-site signature (Campbell 2002). According to this classification procedure, pixels are assigned to the most likely class based on a comparison of the posterior probability that it belongs to each of the signatures being considered (Isacch et al. 2006). Other set of points was reserved to assess the accuracy of classification, which was estimated using the Kappa index (Rosenfield & Fitzpatric-Lins 1986). All procedures were performed using ERDAS 8.4 (Leica Geosystems 2001).

According to our classification on the satellite image, the study area was dominated by agroecosystems (82.4% of total area), mainly by grazing fields (58.6%) and croplands/plowed fields to a lesser extent (23.7%). Natural areas occupied less than 15% of the total area surveyed, of which 10.4% corresponded to pampas grasslands and 4% to vegetated and active sand dunes. The least common land-cover types were urban areas (2.2% of total area) and woodlands (1.05%). The accuracy of the overall classification was 91.5%.

Owl's surveys

From October 2011 to May 2013, we determined the presence of Burrowing Owls by conducting call-broadcast surveys (Andersen 2007, Conway et al. 2008) in the study area. Based on preliminary surveys, the distribution of survey points was stratified according to three main land-cover types used by owls: 1) sand dunes, which are constrained to the dunes fringe along the seacoast and represent the natural habitat of the species; 2) urban areas, which are found at small coastal villages and in the periphery of cities; and 3) agroecosystems, which are the dominant environmental unit at the study area and include grazing fields, croplands, and plowed fields. A total of 90 points were randomly distributed in the study area: 14 points at sand dunes, 13 at urban areas, and 63 at agroecosystems. Each point identified coordinates at which we chose in the field the nearest plot suitable to conduct owl surveys and habitat analyses (Pedrana et al. 2008). We considered suitable those areas potentially used by the species, thus we excluded plots dominated by forests, wetlands, mature crops, native tall grasslands (> 1 m), or building and paved areas. The minimum distance between contiguous points was set at 2 km for agroecosystems and 1 km for urban areas and sand dunes, in order to cover the entire sampling area and preserve samples independency (Bibby et al. 2000). At each point, we broadcast Burrowing Owl's song and alarm calls, and registered the presence-absence of individuals (Andersen 2007, Conway et al. 2008). Because Burrowing Owls stay in the same nesting area throughout the year and develop most activities in the nest-patch, it was assumed that a nest was located in the immediacy of the survey point. We revisited all the sites where owls were detected once during the breeding period to locate their nest burrows. Nesting was confirmed for all cases during second visits through this methodology within 150 m from the survey point, thus indicating the reliability of positive records. One potential caveat in our study is that we did not perform a secondary inspection of negative records and thus we cannot estimate the occurrence of false absences. However, given that survey points were randomly distributed, the chance of false negative records was similarly scattered among land-cover types, so we think that this problem should not significantly impact our results.

Habitat selection

We evaluated the relationship between eight habitat variables and Burrowing Owl's occurrence using three concentric spatial scales of resolution, radiating out from the survey point (Table 1; Lantz et al. 2007). Given that habitat metrics and variables are usually correlated through spatial scales (Pedrana et al. 2008, Block et al. 2016), we used different variables at the three scales (see Table 1) in order to gather the most valuable information of each of them and avoid data redundancy (Orth & Kennedy 2001). To test correlation among explanatory variables, we built Spearman rank matrices in order to exclude the correlated variables (i.e. $r > 0.8$, Crawley 2007); no relationship between variables within or among scales was detected (data not shown).

We defined the local or "nest-patch" scale as 150-m from the survey point. At this scale, we registered the land-cover type (LCOV) where the nest-patch was included (agroecosystem, urban, sand dunes) and the structure of the vegetation (Table 1). The structure of the vegetation determines the horizontal visibility in the nest-patch and is one of the most important factors determining the presence of Burrowing Owls (MacCracken et al. 1985, Green & Anthony 1989, Plumpton & Lutz 1993). To estimate this, we randomly selected five plots within 150-m radius of the survey point to estimate the horizontal visibility in the nest-patch (Green & Anthony 1989). Percent cover of bare ground, short vegetation (< 15 cm), and tall vegetation (> 15 cm) were measured at each plot using a 1-m^2 quadrat frame. An index of horizontal visibility (HVIS) was then calculated by multiplying the percentages of bare ground and short vegetation cover of each plot and later averaging them.

We defined the intermediate or "territory" scale as 600-m from the survey point. Given that available information on the Burrowing Owl's home range is scarce for South America (Villarreal et al. 2005), we used as reference the average home range of the species based on radio-tracked individuals in North America. These studies indicate that most activities of this owl are restricted to within 600 m of the nest burrow (Haug & Oliphant 1990, Gervais et al. 2003, Rosenberg & Haley 2004). At this scale, we evaluated the land-use composition in the area (i.e. how much of the landscape consists of a particular class) by using the software Fragstats 4.2 (available from the Landscape Ecology lab of University of Massachusetts at: http://www.umass.edu/landeco/research/fragstats/fragstats.html) considering the following land-uses from the classified satellite image: croplands (CROP), grazing fields (FIELD), urban areas (URBAN), pampas grasslands (GRAS), forests (FOR), vegetated dunes (VDUN), and active dunes (ADUN) (Table 1). Because the proportions that describe habitat composition add up to 1 over all land-uses, such data are not independent (unit-sum constraint; Aebischer et al. 1993). To remove such linear dependency, data were transformed using the log-ratio transformation (Aebischer et al. 1993).

We defined the "landscape" scale as 1200-m from the survey point. From our personal observation in the study area, this is approximately the maximum distance that Burrowing Owls live and forage within. Moreover, this value is similar to that reported by Gervais et al. (2003) based on radio-tracked owls in California. We used the software Fragstats 4.2 to calculate the following variables: 1) the proportion of modified areas (MOD), which described the ratio between the area covered by modified land-uses (e.g. croplands, grazing fields, urban areas) and the total area (Pedrana et al. 2008) and may be used to evaluate the tolerance of species to habitat disturbance (McGarigal et al. 2012); 2) the amount of borders (BOR), which is an absolute measure of total border length of all patches, used to represent habitat configuration (McGarigal et al. 2012); and 3) the fractal dimension (FRAC), an index of patch shape complexity based in the perimeter-area relationship, which is suggestive of a common ecological process of anthropogenic influence affecting patches across a wide range of scales (McGarigal et al. 2012) (Table 1).

Statistical analyses

We used Generalized Linear Models (GLMs, Crawley 2007) to explore the influence of habitat variables on the probability of occupancy by Burrowing Owls. For each scale, we formulated different *a priori* hypotheses based on previous reports to build the candidate models explaining the variability in the presence of this species (Table 2). In all cases, the response variable was presence-absence, which followed a binomial distribution (1 = positive detection; 0 = negative detection). We used a model-selection approach to select the most explicative model/s (Franklin et al. 2001) using Akaike Criterion for small samples (AICc) (Burnham & Anderson 2002). Models with ΔAICc < 2 were considered the most parsimonious and hence more robust to explain the observed variability. Goodness-of-fit for each model was evaluated by examining plots of standardized residuals, and the dispersion factor was checked in every case (Crawley 2007).

Using the models with ΔAICc < 2 at nest-patch, territory, and landscape scales all together, we performed another model selection procedure from a multiscale perspective. A multiscale global model (GM) assumes that habitat occupancy by Burrowing Owls is explained by a combination of variables at several scales (Lantz et al. 2007, Thiele et al. 2013). Selected variables were included in the model-selection procedure to choose the most explicative model/s of habitat occupancy (Burnham & Anderson 2002). Again, we considered as more parsimonious those models with ΔAICc < 2, evaluated goodness-of-fit for each model by examining plots of standardized residuals, and checked the dispersion factor (Crawley 2007). In addition, we calculated the explained variability of each model as the ratio: (null deviance-residual deviance)/null deviance. For all analyses we used R software, Version 3.1.1 (R Development Core Team 2015).

RESULTS

The proportion of occupied sites in relation to total survey points varied among land-cover types: it was lowest in agroecosystems (21%; n = 63), intermediate in sand dunes (36%; n = 14), and highest in urban areas (46%; n = 13). At the nest-patch scale, two models showed ΔAICc < 2 (Table 3), which explained 10.6% of the total variability. The full model was the most parsimonious, thus supporting the hypothesis that vegetation structure and land-cover type were both important nest-patch features to determine the likelihood of occupancy by Burrowing Owls in the study area. It was followed by the univariate model that included HVIS, which highlights the importance of the horizontal visibility to improve the detection of predators. At the territory scale, two univariate models, one of them including the

Table 1. Description of habitat variables measured around survey points (occupied and non-occupied) at three spatial scales (nest-patch, territory and landscape) used to characterize the Burrowing Owl's habitat in the Pampas of Argentina.

Scale	Variable	Acronym	Description
Nest-patch	Land-cover	LCOV	Main land-cover type (agroecosystem, urban, sand dunes)
	Horizontal visibility	HVIS	Percent cover of bare ground and short vegetation (%)
Territory	Grazing fields	FIELD	Extent of areas used for cattle ranching (%)
	Urban areas	URBAN	Extent of urbanized areas (%)
	Vegetated sand-dunes	VDUN	Extent of psammophytic grasslands (%)
	Active sand-dunes	ADUN	Extent or bare sand (%)
	Grasslands	GRAS	Extent of tall grassland (%)
	Croplands	CROP	Extent of areas used for cropping (%)
	Forest	FOR	Extent of forests and tree covered areas (%)
Landscape	Modified habitats	MOD	Percent cover of modified areas (%)
	Borders	BOR	Total border length of all patch types (m)
	Fractal dimension	FRAC	Index of patch-shape complexity

Table 2. Set of candidate models to explain the presence-absence of the Burrowing Owl (BO) in the pampas of Argentina. Models were developed based on *a priori* hypotheses, supported by previous studies on the species. Acronyms for variables are listed in Table 1. Reference studies are indicated as superscript numbers: [1]Martínez 2013, [2]Cavalli et al. 2014, [3]Green & Anthony 1989, [4]Thiele et al. 2013, [5]Haug & Oliphant 1990, [6]Orth & Kennedy 2001, [7]Botelho & Arrowood 1998, [8]Millsap & Bear 2000, [9]MacCracken et al. 1985, [10]Stevens et al. 2011, [11]Gervais et al. 2003, [12]Thiele et al. 2013, [13]Bellocq 1997.

Scale	Hypothesis	References	Variables in the model
Nest-patch	Habitat occupancy of BO is explained by all nest-patch features	Full model	LCOV HVIS
	The presence of BO depends on the land-cover type where the nest-patch is located	In the study area, BO occupies nest-patches at agroecosystems, sand dunes and urban areas[1,2]	LCOV
	The presence of BO is explained by structure of vegetation in the nest-patch	High levels of horizontal visibility would improve the detection of predators[3,4]	HVIS
	No nest-patch variable explains the presence of BO	Null Model	1
Territory	Habitat occupancy of BO is explained by total land-use composition in the territory	Full model	CROP, FIELD, URBAN, GRAS, FOR, VDUN, ADUN
	The presence of BO is favored by some land-use types	Open agroecosystems provide adequate open lands for nesting and abundance of food resources on field margins[5,6]	FIELD
		Moderate levels of urbanization provide food and protection against predators[6,7,8]	URBAN
		Vegetated areas of the dunes fringe is the native habitat of BO in the study area[1]	VDUN
		Sandy substrates facilitate digging activity[9]	ADUN
		Tall grasslands are used by BO as hunting areas[10]	GRAS
	The presence of BO is discouraged by some land-use types	Use of pesticides and intensive agriculture have deleterious effect on BO reproduction[11]	CROP
		BO avoids treed or forested areas[12]	FOR
	No territory variable explains the presence of BO	Null Model	1
Landscape	Habitat occupancy of BO is explained by all landscape features	Full model	MOD BOR FRAC
	The presence of BO is explained by the percentage of modified areas	It has been suggested that BO may be benefited by moderate levels of modification[10]	MOD
	The presence of BO is explained by the amount of borders	BO makes an extensive use of borders, which provide perching sites and food[5,13]	BOR
	The presence of BO is explained by the complexity of patches	It has been suggested that complex, heterogeneous landscapes may benefit BO hunting activity[6]	FRAC
	No landscape variable explains the presence of BO	Null Model	1

percentage of active dunes (ADUN) and the other one including the percentage of croplands (CROP), were selected as the best to explain the observed variability (14% of total variability, Table 3). At the landscape scale, most of the variability (10.8%) was explained by the full model, which included the three landscape variables measured (Table 3).

We performed another model selection procedure from a multiscale approach using the models with $\Delta AICc < 2$ of nest-patch, territory, and landscape scales. Competing models of each scale (see Table 3), the multiscale global model (GM), and the null model (NM) were compared and selected using the AICc criterion. The only model with $\Delta AICc < 2$ was the GM, which supported the

Table 3. Summary of model-selection results for candidate models explaining the presence/absence of Burrowing Owls in the Pampas of Argentina. *k* (number of estimated parameters), AIC_c, ΔAIC_c and w_i values for all candidate models are presented. Acronyms for variables are listed in Table 1.

Scale	Variables	*k*	AIC_c	ΔAIC_c	w_i
Nest-patch	LCOV + HVIS	4	98.95	0	0.53
	HVIS	2	99.3	0.35	0.44
	null	1	105.81	6.85	0.02
	LCOV	3	106.15	7.2	0.01
Territory	ADUN	2	100.2	0	0.43
	CROP	2	101.02	0.81	0.29
	URB	2	103.71	3.51	0.08
	VDUN	2	103.85	3.65	0.07
	FIELD	2	104.73	4.52	0.05
	FOR	2	105.38	5.18	0.03
	null	1	105.81	5.6	0.03
	GRAS	2	106.12	5.91	0.02
	all	8	108.62	8.41	0.01
Landscape	MOD + BOR+ FRAC	4	101.06	0	0.6
	MOD	2	103.61	2.55	0.17
	FRAC	2	104.28	3.22	0.12
	BOR	2	105.73	4.67	0.06
	null	1	105.81	4.75	0.06

Table 4. Summary of multiscale model-selection results for candidate models explaining the presence/absence of Burrowing Owls in the Pampas of Argentina. AIC_c, ΔAIC_c and w_i values for all candidate models are presented. Acronyms for variables are listed in Table 1.

Scale	Variables	AIC_c	ΔAIC_c	w_i
Multiscale	all	89.94	0	0.97
Nest-patch	LCOV + HVIS	98.95	9.01	0.01
Nest-patch	HVIS	99.3	9.37	0.01
Territory	ADUN	100.2	10.27	0.01
Territory	CROP	101.02	11.08	0
Landscape	MOD + BOR+ FRAC	101.06	11.12	0
Null	null	105.81	15.87	0

hypothesis that the probability of occupancy by Burrowing Owls is explained by a combination of features at several scales (Table 4). This model explained 29% of the observed variability. Significant variables influencing the chance of occupancy by the Burrowing Owl (i.e. the 95% CI did not include zero) belonged to the three spatial scales analyzed (Table 5). The presence of this species was positively associated with the horizontal visibility in the patch (HVIS; Fig 2A), with the percentage of active dunes in the territory (ADUN; Fig 2B), and with the amount of borders in the landscape (BOR; Fig. 2C), and negatively associated with the fractal dimension (FRAC; Fig. 2D). Other non-significant variables influencing the occupancy by Burrowing Owls were LCOV, CROP and MOD (Table 5). The association with these variables suggests a tendency for the presence of owls to be positively associated with urban areas at the nest-patch scale, and negatively with the percentage of croplands in the territory and the extent of modified habitats in the landscape.

DISCUSSION

Animals take decisions based on cues at different scales to select their habitats (Mayor et al. 2009, McGarigal et al. 2016). This applies especially to birds which due to their ability to fly at high altitude and to move long distances may take advantage of having a wider picture of environmental features (Wiens 1989, Fuller 2012, Jedlikowski et al. 2016). In a context of habitat change, birds showing specialized requirements of habitat are considered to be more susceptible to land conversion than species with the ability to nest in a variety of habitat conditions (Coreau & Martin 2007).

Table 5. Variables estimates (β), Standard Error (SE), and 95% confidence interval (CI) limits for each explanatory variable in the global model for the presence/absence of the Burrowing Owl in the Pampas of Argentina. Acronyms for variables are listed in Table 1.

Scale	Habitat feature	β	SE	CI
Patch	LCOV (agroecosystem)	-4.570	3.612	-12.17; 2.13
	LCOV (sand dunes)	-2.403	2.159	-7.01; 1.6
	LCOV (urban)	0.020	1.209	-2.8; 2.31
	HVIS	2.068	1.034	0.02; 4.18
Territory	ADUN	0.683	0.276	0.19; 1.28
	CROP	-0.198	0.141	-0.48; 0.08
Landscape	MOD	2.182	3.467	-4.37, 9.36
	BOR	0.000	0.000	0.00004; 0.0002
	FRAC	-0.126	0.064	-026; -0.001

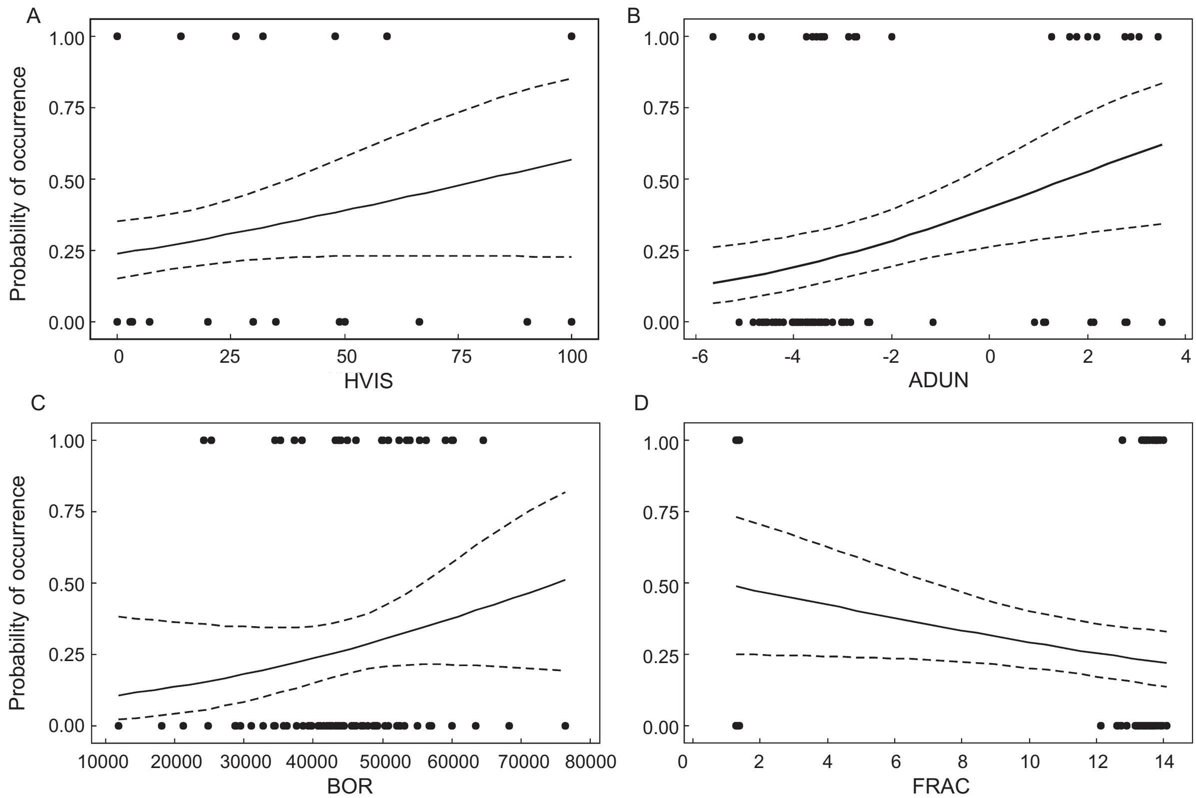

Fig. 2. Modeled probabilities of occurrence of Burrowing Owls for four habitat variables: A — horizontal visibility (HVIS), which represents the cover of bare ground and short vegetation in the patch (expressed as percentage); B — active dunes (ADUN), which represents the cover of bare sand in the territory (expressed as log-ratio transformed percentage); C — amount of borders (BOR), which represents the total border length of all patch types in the landscape (expressed in meters); D — fractal dimension (FRAC), which represents an index of patch-shape complexity in the landscape.

However, habitat generalists may be also vulnerable to habitat conversion. This is because human activities often induce changes on proximate stimuli that birds use for the choice of habitats (e.g. landscape structure, foraging opportunities, nest-sites availability, presence of other species; Cody 1985), and a misinterpretation of such cues may result in maladaptative responses of birds to habitat modifications (Schlaepfer et al. 2002, Van Buskirk 2012). Evaluating such cues from a multi-scale perspective can be a powerful tool to elucidate patterns of habitat occupancy but also to optimize conservation efforts and management actions (Coreau & Martin 2007).

In this study, we found that habitat selection by Burrowing Owls in the Flooding Pampas of Argentina was influenced by habitat features at several spatial scales. Our results show that a unique multi-scale model containing variables of the nest-patch, territory and landscape scales was more robust to explain variation in Burrowing Owl occupancy pattern than any single-scale model. These findings reveal that the habitat selection in the Burrowing Owl would be a hierarchical process, comparable to that observed in North American populations (Lantz et al. 2007, Thiele et al. 2013). In this context, the land-cover type where the nest-patch was inserted was an important feature to determine the presence of Burrowing Owls. Like their North American counterparts (Martin 1973, Rich 1986, Conway et al. 2006, Berardelli et al. 2010), the Burrowing Owl in the Pampas showed plasticity to live in a wide array of habitat conditions, including both modified areas, such as agroecosystems and urbanized zones, and near-pristine grassland remnants at vegetated sand dunes. Burrowing Owls showed the lowest occupancy level in agroecosystems (21% of survey points). Probably, this result does not reflect an avoidance of this habitat by owls, but that they are more spaced in comparison with other land-cover types. Given the dominance of agroecosystems in the study area, it is probably the habitat that holds more owls of all land-cover types, but nests are probably less clustered. In this land-cover Burrowing Owls were especially associated to grazing fields, which are considered more stable habitats than other types of agroecosystems, like croplands, where owls may be affected by agricultural activities such as fumigation or crop plowing (Rodríguez-Estrella 1997, Gervais et al. 2003, Conway et al. 2006). In contrast, the Burrowing Owl was more commonly found at urban areas even when this land-cover type is the least common in the study area (46% of survey points occupied by owls), probably because owl nests are clustered in this land-cover type (Martínez 2013). It has been reported that moderate levels of urbanization may benefit the settlement of Burrowing Owls, in relation to the provision of prey and protection from predators (Trulio 1997, Botelho & Arrowood 1998, Berardelli et al. 2010), but at high levels of urbanization these beneficial effects may be offset by negative effects, such as collisions with human-constructed objects, poisoning and electrocution (Millsap & Bear 2000, Orth & Kennedy 2001, Hager 2009). The scarce urban development of villages that characterize the study area may be especially attractive to this species, and may explain the density of owls in this land-cover. The native habitat of sand dunes configures an intermediate situation between agroecosystems and urban areas in terms of occupancy by Burrowing Owls (36% of survey points with positive records). It has been reported that some populations of Burrowing Owls in North America often occur at higher densities in modified areas than observed in natural habitats (Millsap & Bear 2000, Rosenberg & Haley 2004). A similar situation may be occurring in our study area, where native habitats of sand dunes have suffered an important reduction in recent years due the advance of urbanization and exotic forestation (Bilenca & Miñarro 2004) and the number of Burrowing Owls pairs has declined concomitantly (Authors' unpubl. data). Low density in natural areas may be also related to reduced carrying capacity in this habitat, which may force juveniles to disperse out of the parental territory in order to avoid competition (Pulliam 1988), as has been reported for northern populations (e.g. Berardelli et al. 2010). Although we did not evaluate survival or reproductive performance, previous research in the study area indicates that breeding success of Burrowing Owls is lowest in agroecosystems, thus indicating that this is a suboptimal habitat for the species (Martínez 2013, Cavalli et al. 2016). This result is comparable to that reported by Conway et al. (2006) in North America, who suggest a source-sink dynamic for Burrowing Owls in Washington, with low-quality agricultural areas working as population sinks.

At the local scale, we found that patches with good horizontal visibility (i.e. high proportion of bare ground and vegetation < 15 cm) were more susceptible of being occupied by Burrowing Owls, irrespective of the land-cover type where the nest-patch is inserted. The visibility of the area surrounding the nests would be important in relation to an enhanced foraging efficiency and anti-predatory responses, principally during breeding season (Green & Anthony 1989, Ronan 2002, Thiele et al. 2013), because both adults and fledglings spend most of their time near the nest during that period. This coincides with previous reports for North America which indicate that this owl occupies areas with shorter vegetation relative to unoccupied sites (MacCracken et al. 1985, Plumpton & Lutz 1993, but see Crowe & Longshore 2013).

At the intermediate scale, which includes the average home range of the species, we found that Burrowing Owls preferred territories with at least some fraction of their areas featuring sand dunes. It has been reported that sand content may be important for this species in relation to the energetic cost of digging the burrow and maintenance activities (MacCracken et al. 1985). In our study area, the sizes of owls' burrows vary depending on the soil composition at each land-cover type (Martínez 2013). Burrows located in areas of coarse sandy soils usually have large entrances and long tunnels (MacCracken et al. 1985), and their durability and drainage are improved too (Rodríguez-Estrella 1997). This result may be revealing a tendency of owls to nest in areas close to the seacoast, like sand dunes and small coastal villages. In addition, we found that the probability of occupancy of territories diminished as the area covered by croplands increased. Previous studies have suggested that Burrowing Owls may benefit from a mixture of habitat types in agricultural areas (Restani et al. 2008). In this sense, areas where croplands dominate may discourage the settlement of Burrowing Owls, because they are relatively homogeneous habitats and also because they are often located in fine-textured soils with high content of silt and clay, inappropriate for burrow construction (Stevens et al. 2011). In addition, agricultural practices associated to intensive cropping (e.g. fumigation or plowing; Bellocq 1997, Gervais et al. 2003) have been demonstrated to have negative effects on the survival and reproductive output of Burrowing Owls (Haug & Oliphant 1990, Rodríguez-Estrella 1997, Dechant et al. 2003 and citations therein).

At the broadest resolution scale analyzed, the presence of Burrowing Owls showed a negative relationship with indicators of habitat disturbance, such as the percentage of modified habitats and the fractal dimension in the landscape. This may evidence a compensatory effect of human activities on owl conservation at different scales. Thus, the apparently beneficial effects of cattle grazing (Uhmann et al. 2001, Mueller et al. 2011) or urbanization (Millsap & Bear 2000, Berardelli et al. 2010) in generating adequate conditions for nesting (e.g. open patches) or hunting (e.g. heterogeneous habitats) at the finer scale may be offset by the detrimental effect of the excessive disturbance in the landscape matrix (Lantz et al. 2007). Habitat fragmentation and degradation have been postulated as the main causes of Burrowing Owl declines in some areas of North America (Poulin et al. 2011). In addition, we found that owls occupied those sites with higher density of borders. These lineal habitats would provide improved hunting opportunities for owls, because the spontaneous vegetation promotes conditions for increased prey availability (Bellocq 1987), as well as perching sites adequate for nest vigilance and anti-predatory activities (Haug & Oliphant 1990, Orth & Kennedy 2001).

Previous works have shown that several characteristics of the Burrowing Owl, such as its behavioral plasticity (Martin 1973), nest-site philopatry (Poulin et al. 2011), and reduced home range in comparison to other raptors (Gervais et al. 2003), are all factors that would explain the ability of northern populations to live in a variety of habitat conditions. Although southern populations have been much less studied, recent studies have shown that generalist diet and opportunistic hunting mode (Cavalli et al. 2014) as well as tolerance to human presence (Carrete & Tella 2011, Cavalli et al. 2016), may explain the enhanced capacity of Burrowing Owls to live in a variety of natural and modified habitats in the Pampas. In this sense, the population dynamic of the species deserves detailed study, in order to assess the viability of populations at different environmental conditions and the movement of individuals among habitat types. These factors would be critical to evaluate the importance of native habitats as population sources and how future changes in land-use may affect the persistence of Burrowing Owls in the southern portion of its distribution range.

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REFERENCES

Aebischer N. J., Robertson P. A., Kenward R. E. 1993. Compositional analysis of habitat use from animal radiotracking data. Ecology 74: 1313–1325.

Alverson K. M., Dinsmore S. J. 2014. Factors affecting Burrowing Owl occupancy of prairie dog colonies. Condor 116: 242–250.

Andersen D. E. 2007. Survey techniques. In: Bird D. M., Bildstein K. L. (eds). Raptor research and management techniques. Hancock House, Washington, pp. 89–100.

Bellocq M. I. 1987. [Hunting habitat selection and differential predation of *Athene cunicularia* on rodents at agricultural ecosystems]. Rev. Chil. Hist. Nat. 60: 81–86.

Bellocq M. I. 1997. Ecology of the burrowing owl in agroecosystems of the central Argentina. In: Lincer J. R. (ed.). The Burrowing Owl, its biology and management: including the proceedings of the First International Burrowing Owl Symposium. J. Raptor Res. Report 9: 52–57.

Belton W. 1984. Birds of Rio Grande do Sul, Brazil. Part 1: Rheidae through Furnariidae. B. Am. Mus. Nat. Hist. 178: 369–636.

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

Bibby C. J., Burgess N. D., Hill D. A., Mustoe S. 2000. Birds census techniques. Academic Press, London.

Bilenca D., Miñarro F. 2004. [Identification of valuable grassland areas in Pampas and Campos of Argentina, Uruguay and South Brazil]. Fundación Vida Silvestre Argentina, Buenos Aires.

Block C., Pedrana J., Stellatelli O. A., Vega L. E., Isacch J. P. 2016. Habitat suitability models for the sand lizard *Liolaemus wiegmannii* based on landscape characteristics in temperate coastal dunes from Argentina. Austral Ecol. 41: 671–680.

Botelho E. S., Arrowood P. C. 1998. The effect of burrow site use on the reproductive success of a partially migratory population of western Burrowing Owls. J. Raptor Res. 32: 233–240.

Boyce M. S., McDonald L. L. 1999. Relating populations to habitats using resource selection functions. Trends Ecol. Evol. 14: 268–272.

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

Burnham K. P., Anderson D. R. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second Edition. Springer-Verlag, New York.

Campbell J. B. 2002. Introduction to remote sensing. Third Edition. The Guilford Press, New York.

Carrete M., Tella J. L. 2011. Inter-individual variability in fear of humans and relative brain size of the species are related to contemporary urban invasion in birds. PLoS One 6: e18859.

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

Chalfoun A. D., Thompson F. R., Ratnaswamy M. J. 2002. Nest predators and fragmentation: a review and meta-analysis. Conserv. Biol. 16: 306–318.

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

Cody M. L. (ed.) 1985. Habitat selection in birds. Academic Press, San Diego, California.

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

Conway C. J., Garcia V., Smith M. D., Hughes K. 2008. Factors affecting detection of Burrowing Owl nests during standardized surveys. J. Wildl. Manage. 72: 688–696.

Coreau A., Martin J. -L. 2007. Multi-scale study of bird species distribution and of their response to vegetation change: a Mediterranean example. Landsc. Ecol. 22: 747–764.

Crawley M. J. 2007. The R Book. John Wiley & Sons. Chichester.

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

Danchin E., Boulinier T., Massot M. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79: 2415– 2428.

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

Dechant J. A., Sondreal M. L., Johnson D. H., Igl L. D., Goldade C. M., Rabie P. A., Euliss B. R. 2003. Effects of management practices on grassland birds: Burrowing Owl. USGS Northern Prairie Wildlife Research Center, Jamestown, ND.

Di Vittorio M. D., López-López P. 2014. Spatial distribution and breeding performance of Golden Eagles *Aquila chrysaetos* in Sicily: implications for conservation. Acta Ornithol. 49: 33–45.

Filloy J., Bellocq M. I. 2007. [Raptorial bird responses to land use: a regional approach]. Hornero 22: 131–140.

Finn S. P., Marzluff J. M., Varland D. E. 2002. Effects of landscape and local habitat attributes on northern goshawk site occupancy in western Washington. Forest Sci. 48: 427– 436.

Franklin A. B., Shenk T. M., Anderson D. R., Burnham K. P. 2001. Statistical model selection: an alternative to null hypothesis testing. In: Shenk T. M., Franklin A. B. (eds). Modeling in natural resource management: development, interpretation, and application. Island Press, Washington, pp. 75–90.

Fuller R. J. 2012. Birds and habitat: relationships in changing landscapes. Cambridge University Press.

Gervais J. A., Rosenberg D. K., Anthony R. G. 2003. Space use and pesticide exposure risk of male Burrowing Owls in an agricultural landscape. J. Wildl. Manage. 67: 156–165.

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

Hager S. B. 2009. Human-related threats to urban raptors. J. Raptor Res. 43: 210–226.

Haug E. A., Oliphant L. W. 1990. Movements, activity patterns, and habitat use of burrowing owls in Saskatchewan. J. Wildl. Manage. 54: 27–35.

Howard M. N., Skagen S. K., Kennedy P. L. 2001. Does habitat fragmentation influence nest predation in the shortgrass prairie? Condor 103: 530–536.

Hudson W. H. 1920. Birds of La Plata. J. M. Dent and Sons. Toronto.

Humphrey P. S., Bridge D., Reynolds P. W., Peterson R. T. 1970. Birds of Isla Grande (Tierra del Fuego). Preliminary Smithsonian Manual, Museum of Natural History, University of Kansas, Lawrence, Kansas.

Isacch J. P., Costa C. S. B., Rodríguez-Gallego L., Conde D., Escapa M., Gagliardini D. A., Iribarne O. O. 2006. Distribution of saltmarsh plant communities associated with environmental factors along a latitudinal gradient on the south-west Atlantic coast. J. Biogeogr. 33: 888–900.

Janes S. W. 1985. Habitat selection in raptorial birds. In: Cody M. L. (ed.). Habitat selection in birds. Academic Press, San Diego, California, pp. 159–188.

Jedlikowski J. Chibowski P., Karasek T., Brambilla M. 2016. Multi-scale habitat selection in highly territorial bird species: Exploring the contribution of nest, territory and landscape levels to site choice in breeding rallids (Aves: Rallidae). Acta Oecol. 73: 10–20.

Kight C. R., Swaddle J. P. 2007. Associations of anthropogenic activity and disturbance with fitness metrics of eastern bluebirds (*Sialia sialis*). Biol. Conserv. 138: 189–197.

Lantz S. J., Conway C. J., Anderson S. H. 2007. Multiscale habitat selection by burrowing owls in black-tailed prairie dog colonies. J. Wildl. Manage. 71: 2664–2672.

Leica Geosystems. 2001. ERDAS Imagine 8.4 Interpretation Software. Leica Geosystems GIS & Mapping, LLC, Atlanta.

León R. J. C., Rusch G. M., Oesterheld M. 1984. [Pampas grasslands: agricultural impact]. Phytocoenologia 12: 201–218.

López-López P., García-Ripollés C., Aguilar J. M., García-López F., Verdejo J. 2006. Modelling breeding habitat preferences of Bonelli´s eagle (*Hieraaetus fasciatus*) in relation to topography, disturbance, climate and land use at different spatial scales. J. Ornithol. 147: 97–107.

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

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

Macías-Duarte A., Conway C. J. 2015. Distributional changes in the western Burrowing Owl (*Athene cunicularia hypugaea*) in North America from 1967 to 2008. J. Raptor Res. 49: 75–83.

Marks J. S., Canning R. J., Mikkola H. 1994. Family Strigidae (Typical Owls). In: del Hoyo J., Elliot A., Sargatal J. (eds). Handbook of the Birds of the World. Vol. 5: Barn-owls to Hummingbirds. Lynx Editions, Barcelona, pp. 76–242.

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

Martínez G. 2013. [Nest-site selection and nesting success of the Burrowing Owl: importance of microscale variables]. M.Sc. Thesis. University of Mar del Plata, Mar del Plata.

Mayor S. J., Schneider D. C., Schaefer J. A., Mahoney S. P. 2009. Habitat selection at multiple scales. Ecoscience 16: 238–247.
McGarigal K., Cushman S. A., Ene E. 2012. FRAGSTATS v4: Spatial Pattern Analysis Program for Categorical and Continuous Maps. Computer software program produced by the authors at the University of Massachusetts, Amherst, Massachusetts.
McGarigal K., Wan H. Y., Zeller K. A., Timm B. C., Cushman S. A. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecol. 31: 1–15.
Millsap B. A., Bear C. 2000. Density and reproduction of burrowing owls along an urban development gradient. J. Wildl. Manage. 64: 33–41.
Møller A. P., Jokimäki J., Skorka P., Tryjanowski P. 2014. Loss of migration and urbanization in birds: a case study of the blackbird (*Turdus merula*). Oecologia 175: 1019–1027.
Mueller M. S., Grigione M. M., Sarno R. J. 2011. Nonurban habitat use of Florida burrowing owls: Identifying areas of conservation importance. J. Raptor Res. 45: 143–149.
Muñoz A. R., Real R. 2013. Distribution of Bonelli's Eagle *Aquila fasciata* in southern Spain: scale may matter. Acta Ornithol. 48: 93–101.
Narosky T., Di Giacomo A. 1993. [Birds of Buenos Aires Province: distribution and status]. Asociación Ornitológica del Plata, Vázquez-Massini and L.O.L.A (Literature of Latin America). Buenos Aires, Argentina.
Newton I. 1979. Population ecology of raptors. Buteo Books, Vermillion.
Orth P. B., Kennedy P. L. 2001. Do land-use patterns influence nest-site selection by Burrowing owls (*Athene cunicularia hypugaea*) in northeastern Colorado? Can. J. Zool. 79: 1038–1045.
Pedrana J., Isacch, J. P., Bó M. S. 2008. Habitat relationships of diurnal raptors at local and landscape scales in southern temperate grasslands of Argentina. Emu 108: 301–310.
Piorecky M. D., Prescott D. R. 2006. Multiple spatial scale logistic and autologistic habitat selection models for northern pygmy owls, along the eastern slopes of Alberta's Rocky Mountains. Biol. Conserv. 129: 360–371.
Plumpton D. L., Lutz R. S. 1993. Nesting habitat use by burrowing owls in Colorado. J. Raptor Res. 27: 175–179.
Poulin R. G., Todd L. D., Dohms K. M., Brigham R. M., Wellicome T. I. 2005. Factors associated with nest- and roost-burrow selection by Burrowing Owls (*Athene cunicularia*) on the Canadian prairies. Can. J. Zool. 83: 1373–1380.
Poulin R., Todd L. D., Haug E. A., Millsap B. A., Martell M. S. 2011. Burrowing Owl (*Athene cunicularia*). The Birds of North America Online. Poole A. (ed.). Cornell Lab of Ornithology, Ithaca, New York.
Pulliam H. R. 1988. Sources, sinks, and population regulation. Am. Nat. 132: 652–661.
R Development Core Team 2015. R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, available at http://www.r-project.org
Restani M., Rau L. R., Flath D. L. 2001. Nesting ecology of Burrowing Owls occupying black-tailed prairie dog towns in southeastern Montana. J. Raptor Res. 35: 296–303.
Rich T. 1986. Habitat and nest-site selection by burrowing owls in the sagebrush steppe of Idaho. J. Wildl. Manage. 50: 548–555.
Rodríguez-Estrella R. 1997. Nesting sites and feeding habits of the Burrowing Owl in the biosphere reserve of Mapimi, Mexico. J. Raptor Res. 9: 99–106.
Ronan N. A. 2002. Habitat selection, reproductive success, and site fidelity of burrowing owls in a grassland ecosystem. M.Sc. Thesis. Department of Fisheries and Wildlife, Oregon State University, Corvallis.
Rosenberg D. K., Haley K. L. 2004. The ecology of Burrowing Owls in the agroecosystem of the Imperial Valley, California. Stud. Avian Biol. 27: 120–135.
Rosenfield G. H., Fitzpatric-Lins K. 1986. A coefficient of agreement as a measure of thematic classification accuracy. Photogramm. Eng. Rem. S. 52: 223–227.
Rosenzweig M. L. 1985. Some theoretical aspect of habitat selection. In: Cody M. L. (ed.). Habitat selection in birds. Academic Press, San Diego, California, pp. 517–540.
Schlaepfer M. A., Runge M. C., Sherman P. W. 2002. Ecological and evolutionary traps. Trends Ecol. Evol. 17: 474–480.
Sergio F., Pedrini P., Marchesi L. 2003. Spatio-temporal shifts in gradients of habitat quality for an opportunistic avian predator. Ecography 26: 243–255.
Sih A., Ferrari M. C., Harris D. J. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evol. Appl. 4: 367–387.
Soriano A., León R. J., Sala O. E., Lavado R. S., Deregibus V. A., Cauhépé M. A., Scaglia O. A., Velásquez C. A., Lemcoff J. H. 1991. Río de la Plata Grasslands. In: Coupland R. T. (ed.). Natural Grasslands. Elsevier, New York, pp. 367–407.
Stevens A. F. J., Bayne E. M., Wellicome T. I. 2011. Soil and climate are better than biotic land cover for predicting home-range habitat selection by endangered burrowing owls across the Canadian Prairies. Biol. Conserv. 144: 1526–1536.
Tapia L., Kennedy P. L., Mannan R. W. 2007. Habitat sampling. In: Bird D. M., Bildstein K. L. (eds). Raptor research and management techniques. Hancock House, Washington, pp. 153–170.
Thiele J. P., Bakker K. K., Dieter C. D. 2013. Multiscale nest site selection by Burrowing Owls in western South Dakota. Wilson J. Ornithol. 125: 763–774.
Trulio L. 1997. Burrowing Owl demography and habitat use at two urban sites in Santa Clara County, California. J. Raptor Res. 9: 84–89.
Uhmann T. V., Kenkel N. C., Baydack R. K. 2001. Development of a habitat suitability index model for burrowing owls in the eastern Canadian prairies. J. Raptor Res. 35: 378–384.
Van Buskirk J. 2012. Behavioural plasticity and environmental change. In: Candolin U., Wong B. B. (eds). Behavioural responses to a changing world: mechanisms and consequences. Oxford University Press, Oxford, pp. 145–158.
Verhulst S., Oosterbeek K., Ens B. J. 2001. Experimental evidence for effects of human disturbance on foraging and parental care in oystercatchers. Biol. Conserv. 101: 375–380.
Villarreal D., Machicote M., Branch L. C., Martínez J. J., Gopar A. 2005. Habitat patch size and local distribution of burrowing owls (*Athene cunicularia*) in Argentina. Ornitol. Neotrop. 16: 529–537.
Wiens J. A. 1989. Spatial scaling in ecology. Funct. Ecol. 3: 385–397.
Wilbur H. M., Tinkle D. W., Collins J. P. 1974. Environmental certainty, trophic level, and resource availability in life history evolution. Am. Nat. 108: 805–817.
Zelaya K., van Vliet J., Verburg P. H. 2016. Characterization and analysis of farm system changes in the Mar Chiquita basin, Argentina. Appl. Geogr. 68: 95–103.

STRESZCZENIE

[Czynniki wpływające na wybór siedliska przez pójdźki ziemne na terenie argentyńskiej pampy — analizy w trzech skalach przestrzennych]

Zmiany siedliskowe spowodowane działalnością człowieka zwykle wiążą się z negatywnym wpływem na gatunki rośli i zwierząt. Jednak

coraz większa liczba badań pokazuje, że wiele gatunków nie reaguje na te zmiany, lub są one wręcz dla nich korzystne. Pójdźka ziemna jest drapieżnym ptakiem, któremu w ostatnich latach poświęcono wiele uwagi ze względu na zdolność do życia w różnych siedliskach, zarówno naturalnych jak i zmienionych przez człowieka. Dotychczasowe badania prowadzono głównie w populacjach na północnym skraju zasięgu tego gatunku (w Ameryce Północnej), gdzie sowy te są silnie związane z norami kopanymi przez ssaki (np. nieświszczuki). Na południowym skraju zasięgu (argentyńskie pampy), pójdźki ziemne głównie same kopią nory, chociaż mogą też korzystać z nor wykopanych przez ssaki. Ponadto w odróżnieniu od większości populacji z północnego skraju zasięgu, w których pójdźki migrują, osobniki z południowych populacji są osiadłe i wykorzystują swoje nory zarówno w okresie lęgowym jak i pozalęgowym. W pracy przeanalizowano czynniki, które determinują wybór siedliska przez pójdźki ziemne z południowego skraju zasięgu. Analizy przeprowadzono w trzech skalach — gniazda, terytorium i krajobrazu.

Badania prowadzono w środowisku argentyńskiej pampy, na której można wyróżnić trzy główne rodzaje środowisk — agrocenozy, wydmy oraz tereny zurbanizowane. Informacje o sposobie zagospodarowania terenu uzyskano wykorzystując zarówno prace terenowe jak i zdjęcia satelitarne, definiując dziewięć rodzajów siedlisk: obszary wodne, tereny upraw, zaorane pola, tereny przeznaczone pod wypas, tereny zurbanizowane, tereny trawiaste, lasy, porośnięte wydmy oraz wydmy aktywne (nie porośnięte roślinnością) (Fig. 1). Badania prowadzono metodą punktową przy użyciu stymulacji głosowej. Obecność sów badano w 90 punktach — 14 zlokalizowanych na wydmach, 13 w środowiskach zurbanizowanych i 63 w agrocenozach. Minimalna odległość między punktami wynosiła 2 km na terenach agrocenoz i 1 km na terenach zurbanizowanych i wydmach. Dla każdego punktu określano zmienne środowiskowe w trzech skalach: miejsca gniazdowego — do 150 m od punktu stymulacji, terytorium — do 600 m, oraz krajobrazu — do 1200 m (Tab. 1). Ze względu na fakt, że cechy siedliska rozpatrywane w różnych skalach są ze sobą skorelowane, w każdej rozpatrywanej skali użyto innych zmiennych. Wybór tych zmiennych związany był z hipotezami opartymi o wyniki wcześniejszych badań nad pójdźką ziemną (Tab. 2).

Pójdźki ziemne najrzadziej występowały w agrocenozach, zaś najczęściej — w środowiskach zurbanizowanych. W skali miejsca gniazdowego wybór siedliska zależał od wszystkich rozpatrywanych predyktorów, czyli od typu środowiska (agrocenoza, tereny zurbanizowane, wydmy) oraz widoczności poziomej będącej funkcją tego, jaką część terenu w promieniu 150 m stanowi teren nieporośnięty lub porośnięty niską roślinnością (Tab. 3, 5, Fig. 2A). W skali terytorium, występowanie pójdźki było najlepiej tłumaczone przez dwa spośród siedmiu rozpatrywanych czynników: procentowy udział czynnych wydm (dodatnia zależność) oraz procentowy udział terenów uprawnych (ujemna zależność) (Tab. 3, Fig. 2B). W skali krajobrazowej wybór siedliska tłumaczyły wszystkie rozpatrywane czynniki: całkowita długość granic pomiędzy siedliskami (dodatnia zależność), udział środowisk zmienionych przez człowieka (ujemna zależność) oraz stopień skomplikowania kształtów płatów środowiskowych (ujemna zależność) (Tab. 3, 5, Fig. 2C, D). Model łączący wszystkie czynniki badane w różnych skalach przestrzennych był zdecydowanie lepiej dopasowany do uzyskanych danych niż każdy z modeli dla poszczególnych skal (Tab. 4). Wskazuje to na hierarchiczny charakter wyboru siedlisk przez pójdźki ziemne gniazdujące na terenie argentyńskiej pampy, porównywalny do tego obserwowanego w populacjach z Ameryki Północnej.