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Short Communication

Prey selection and food habits of breeding Burrowing Owls (*Athene cunicularia*) in natural and modified habitats of Argentine pampas

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Abstract. Understanding the way animals respond to novel habitats and fluctuations in food resources can provide insights into the ability of species to settle in modified habitats. We studied the patterns of arthropod selection by Burrowing Owls in natural and modified habitats. We assessed the diet of this owl by means of pellet analysis and, simultaneously, we estimated relative abundance of arthropods in the field by trapping. A similar pattern of prey selection and avoidance was found among habitats, with coleopterans the main prey consumed. Food-niche breadth was low at all habitats, reflecting the dominance of a few prey items in the diet of the Burrowing Owl. Its wide trophic spectrum as well as its ability to take advantage of dominant resources suggests that, from a feeding perspective, the Burrowing Owl can readily colonise and adapt to newly human-modified habitats.

Additional keywords: bird, grassland, insects, South America, urban.

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Introduction

In novel habitats, species may need to modify behaviours to allow them to survive and adapt to the new conditions. One of the most important challenges that a species faces in a new habitat is finding food. Its success or failure in a novel environment will depend on the flexibility of its diet and the strategies used to obtain food (Tuomainen and Candolin 2011). Both dietary breadth and hunting behaviour define the feeding strategy of a predator (Jaksić and Marone 2006). Predators can be classified as generalists, if they consume a wide range of prey, or specialists, if they consume a narrow range (Schoener 1971). In addition, they may be considered to be opportunistic or selective depending on the proportions of prey consumed in relation to the relative abundance of those prey items in the foraging patch (Jaksić and Marone 2006).

Species that can occupy a wide niche range are more likely to succeed at colonising novel environments than species that are highly specialised (Tuomainen and Candolin 2011). Thus, flexible responses to novel foods, predators and competitors might be good indicators of an animal's ability to invade human-modified sites (Sih *et al*. 2011).

Because owls are top-order predators, they provide an excellent opportunity to assess how native species respond to modifications in habitat and the availability of food (Newton 1979). Owls often have specialised requirements in terms of foraging habitat, nesting sites and the abundance or diversity of food resources and, as such, are likely to be highly sensitive to changes in their native habitats (Jaksić and Marti 1981). The Burrowing Owl (*Athene cunicularia*) is widely distributed in the Americas and shows different responses to habitat modification (Berardelli *et al*. 2010). In the pampas of Argentina, native grassland habitats have been widely modified as the result of agricultural intensification (Bilenca and Miñarro 2004). Although some species of raptor have declined as a consequence of these changes (e.g. Pedrana *et al*. 2008; Carrete *et al*. 2009), the Burrowing Owl may colonise new habitats, such as agroecosystems and urbanised areas (Pedrana *et al*. 2008; Sánchez *et al*. 2008; Carrete and Tella 2010, 2011).

Throughout its geographical range, the Burrowing Owl has a generalist diet (York *et al*. 2002; Sánchez *et al*. 2008; Andrade *et al*. 2010) and although it is considered to be an opportunistic predator (Bellocq and Kravetz 1983; York *et al*. 2002) few studies have effectively sampled the availability of prey to support this categorisation (Bellocq 1987; Plumpton and Lutz 1993; Andrade *et al*. 2010). In addition, there are no data on whether the Burrowing Owl's diet and prey selectivity change in new habitats. This information could contribute to an explanation of the expansion of this species into modified habitats.

The aim of this study was to assess the consequences of habitat modification on prey selectivity of the Burrowing Owl by studying the diet of the Owl and abundance of its prey in natural and modified habitats.

Materials and Methods

Study area

The study was conducted along the south-eastern coast of Buenos Aires Province, Argentina, from Villa Gesell city in the north (37°15′S, 56°57′W) to Camet Norte village (37°49′S, 57°30′W). This area is in the south-eastern Pampas Region, where Burrowing Owls inhabit a heterogeneous matrix of native habitats (grasslands, vegetated sand-dunes) and modified habitats (agroecosystems, urban areas) (Pedrana *et al*. 2008; Sánchez *et al*. 2008).

Dietary analysis

The diet of the Burrowing Owl was determined by analysis of regurgitated pellets. Between September 2010 and January 2011, we collected pellets every 2 weeks from nests in three habitats: a natural habitat – vegetated sand-dunes – and two modified habitats – an agroecosystem and an urban area. Data were grouped in two seasons according to the breeding phenology of the Burrowing Owl: S1 (September–October), during which courtship behaviour begins and laying occurs, and S2 (November–January) comprising the incubation and nestling periods (Haug *et al*. 1993, M. Cavalli, unpubl. data). The sampling unit was the nest from which pellets were collected, with 4–10 nests per habitat in each season. Each pellet was dissected using standard techniques (Marti *et al*. 2007). We identified prey to the finest taxonomic level possible. For the statistical analysis, prey were classified to order. To control for differences in sampling effort among nests, the minimum number of pellets required to determine diet adequately was calculated by plotting the number of new prey categories per pellet against the cumulative number of pooled pellets (Marti *et al*. 2007). Cumulative prey curves for number of pellets reached an asymptote, indicating that sample sizes were sufficient to describe diet and for comparisons (data not presented). We expressed dietary composition as the relative frequency (F_D) of each prey type (the number of individuals of each prey category divided by the total number of prey consumed at each nest in each season).

We used generalised linear mixed models (GLMM) to test the effect of habitat and season (explanatory variables) on relative frequency of each prey type (F_D, the response variable) of major prey categories and of the items eaten most often. We used GLMMs with a binomial error distribution and logit link function (Crawley 2007). Nests identity was included as a random term to account for non-independence of data.

We calculated Levins' standarised food-niche breadth index (B') for each nest (Colwell and Futuyma 1971). We used linear mixed models (LMM) with Gaussian error distribution and identity link function to test the effect of habitat and season on values of B', considering nest as a random term. Data were checked for normality and homoscedasticity before performing the LMM (Crawley 2007).

Model fittings were visually assessed by inspecting plots of standardised deviance residuals for each model. We assessed goodness of fit for all models and estimated the variance initiation factor ($\hat{c}$) as residual deviance divided by degrees of freedom (Crawley 2007). We fitted GLMMs using the glmmPQL function of the MASS package and fitted LMMs using the nlme package with R version 2.15.0 (R Development Core Team 2013).

Abundance of prey

We concentrated our sampling effort on ground arthropods because previous studies had shown that these are the dominant prey of Burrowing Owls during the reproductive period (Sánchez *et al*. 2008). The relative abundance of ground arthropods was estimated using pitfall traps. This method, however, is likely to underestimate relative abundance of flying insects (Cooper and Whitmore 1990). Pitfall- trapping was done at the same time as the dietary sampling and in the same areas as sampled nests. We set 15 pitfall traps in three transects of five traps in each habitat, with each trap in a transect 10 m apart. The contents of traps were collected monthly between September 2010 and January 2011. Relative abundance of prey (F_P) was calculated as the number of individuals of each category divided by the total number of individuals per trap. Prey were classified into order for statistical analysis. Differences in the relative abundance of prey among habitats and seasons were tested using GLMM (binomial error distribution and logit link function), including trap identity as a random term.

Analysis of prey selectivity

To evaluate prey selection we compared the relative frequency of each prey consumed with its relative abundance in the field during each season. We calculated Bonferroni intervals for the observed proportion of prey eaten (Neu *et al*. 1974) to analyse seasonal dietary selectivity. In addition, we used the Ivlev's prey-selectivity index (E; Ivlev 1961) in order to estimate prey selectivity for arthropod taxa in the diet. Values of Ivlev's index range from –1 (complete avoidance) to +1 (exclusive selection) (Marti *et al*. 2007).

Results

A total of 178 Burrowing Owl pellets were collected from 28 nests in the study area (66 pellets from 9 nests in vegetated sand-dunes, 52 in 7 nests in the agroecosystem and 60 from 12 nests in the urban area). Arthropods were the most abundant type of prey in the diet, comprising 86% of total numbers of prey in the vegetated

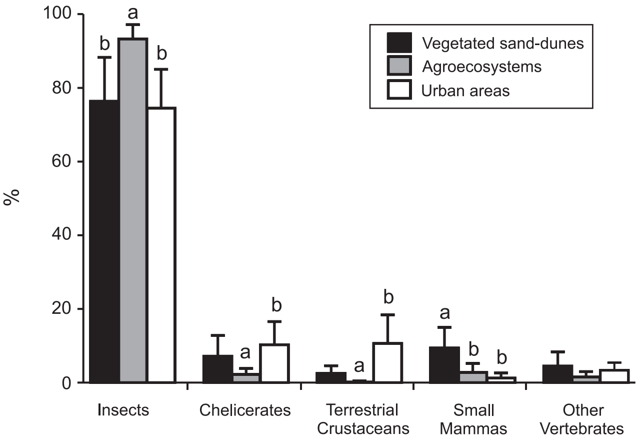

Fig. 1. Mean proportion (%) of main types of prey in the diet of the Burrowing Owl in three habitats of the Pampas Region of Argentina. Whiskers indicate standard error. Different lower-case letters indicate significant differences between habitats for each type of prey.

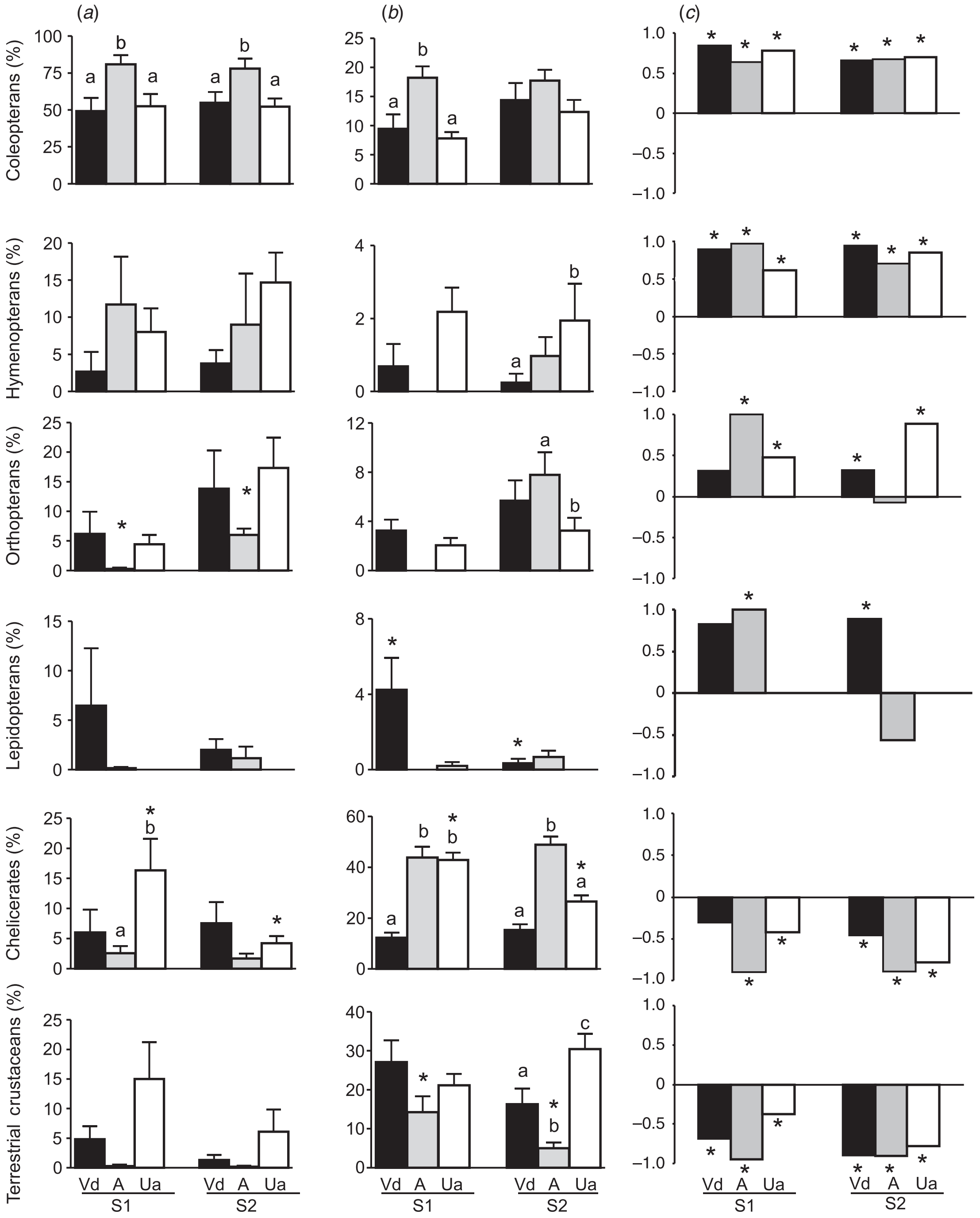

Fig. 2. (*a*) Mean relative frequencies (%) of main items eaten by Burrowing Owls in each habitat; (*b*) mean relative abundance of main items (%) estimated by field trapping in each habitat; and (*c*) Ivlev's prey-selectivity index (*E*) in each habitat, with positive values indicating prey selection and negative values indicating prey avoidance. Habitats: Vd, vegetated sand-dunes; A, agroecosystem; Ua, urban area. Seasons: S1, courtship and laying (September–October); S2, incubation and nestling periods (November–January). In Figs 2*a* and 2*b*, lower-case letters indicate significant differences between habitats in each season and asterisks indicate significant differences between seasons in each habitat; whiskers indicate standard errors. In Fig. 2*c*, asterisks indicate statistically significance in prey selection or avoidance.

sand-dunes, 95% in the agroecosystem and 95% in the urban area. Vertebrates, mainly small mammals, comprised only 4% of items consumed in the agroecosystem and urban area and 14% in the vegetated dunes (Fig. 1). There was no difference between seasons in the proportions of these main prey categories in the diet ($P > 0.06$).

Within arthropods, insects were the most frequently consumed group, but the proportions taken differed between habitats (Fig. 1). Among insects, coleopterans were the main prey in the diet in all habitats (Fig. 2*a*). Overall, the proportion of Coleoptera in the diet was higher in the agroecosystem than in the vegetated sand-dunes ($t=-3.39$, d.f. = 23, $P=0.002$) and the urban area ($t=-3.43$, d.f. = 24, $P=0.002$). Consumption of coleopterans was higher in the agroecosystem than in the urban area or the vegetated dunes in both seasons (Fig. 2*a*). However, no differences in Coleoptera consumption were detected between seasons within the same habitat (Fig. 2*a*). Relative abundance of Coleoptera was higher in the agroecosystem than in the vegetated dunes or urban area in S1 (Fig. 2*b*). Selection for coleopterans was evident throughout the sampling period in the three habitats (Fig. 2*c*).

The abundance of hymenopterans was low in all habitats, but was higher in the urban area than in the vegetated dunes in S2 (Fig. 2*b*). Consumption of Hymenoptera did not differ between habitats (Fig. 2*a*) and Hymenoptera were selected in both seasons in all habitats (Fig. 2*c*). Orthopterans were represented in the diet and in the field in both seasons, with maximum values in S2 (Fig. 2*a*, *b*). Orthoptera were selected in both seasons in the urban area, in S1 in the agroecosystem and in S2 in the vegetated dunes (Fig. 2*c*). Lepidopterans formed only a small proportion of the diet and in the habitats (Fig. 2*a*, *b*); a preference for Lepidoptera was detected only in the agroecosystems in S1 and in the vegetated sand-dunes in S2 (Fig. 2*c*). Other groups of arthropods found less frequently in the diet of the Burrowing Owl were chelicerates (order Araneae) and terrestrial crustaceans (family Armadillidiidae), both comprising <10% of total prey (Fig. 1). Relative abundances of these two groups of arthropods were higher in the field than in the diet of the Burrowing Owl in most cases (Fig. 2*a*, *b*) indicating avoidance of these prey types throughout the sampling period (Fig. 2*c*).

Standardised food-niche breadth indices values did not vary between the two seasons ($P>0.05$). Indices were lower in the agroecosystem ($B'=0.12\pm0.04$) than in the vegetated sand-dunes ($B'=0.28\pm0.06$; $t=3.77$, d.f. = 32, $P=0.0007$) and the urban area ($B'=0.28\pm0.06$; $t=3.14$, d.f. = 32, $P=0.003$).

Discussion

The diet of the Burrowing Owl in the south-eastern pampas of South America was mainly composed of insects and small mammals; these items are known to be important for this species in both the northern and southern hemispheres (Marti 1973; Jaksić and Marti 1981; Bellocq and Kravetz 1983; York *et al.* 2002). Insects were the most frequently consumed prey type throughout the study period and in all three habitats, accounting for >74% of total prey consumed. Burrowing Owls selectively preyed on coleopterans in all habitats. This group is represented mainly by ground insects (Morrone and Coscarón 1998), so they can be captured with low effort. It has also been observed that the Burrowing Owl adopts a passive sit-and-wait strategy to capture this type of prey (Haug *et al.* 1993), which allows adults to feed while watching the nest, which is critical during the nestling stage (Newton 1979). Hence, consumption of coleopterans may be energetically favourable because of the low capture effort required and their availability near burrows. On the other hand, the consumption of orthopterans was mostly opportunistic even though Burrowing Owls in urban areas selected this type of prey during both seasons. Fewer Orthoptera were eaten than Coleoptera, consistent with the general pattern found in other studies in South America (e.g. Sánchez *et al.* 2008; Andrade *et al.* 2010). This contrasts with prey composition in North America, where orthopterans were the main item eaten during spring–summer in some studies (Green *et al.* 1993; York *et al.* 2002). Selection for certain prey types, such as coleopterans and orthopterans, may be explained by the formation of a search image for the most abundant item (Jaksić and Marone 2006). Consequently, prey types that are abundant in the field may be over-represented in the diet and an opportunistic species, like the Burrowing Owl, can exhibit preferences for certain prey types.

Although we found that relative frequencies of lepidopterans and hymenopterans in the diet of the Burrowing Owls were higher than would be predicted by relative abundance in the habitat, this result should be interpreted with caution. Field relative abundance of these groups may have been underestimated in our sampling. Moreover, the documented avoidance of chelicerates and terrestrial crustaceans by the Burrowing Owl may more reflect the cryptic habits of these organisms (Shear 1986; Smigel and Gibbs 2008).

The standardised food-niche breadth was lower (range 0.12–0.28) than expected for a generalist predator (Bó *et al.* 2007). However, the values recorded in our study were within the ranges of values calculated for this species in other sites in South America (e.g. 0.11–0.30 in north-western Paraguay, Andrade *et al.* 2004; 0.08–0.19 in central-eastern Argentina, Sánchez *et al.* 2008; 0.13–0.37 in central Argentinean Patagonia, Andrade *et al.* 2010). Even though our estimate of food-niche breadth was low (Marti *et al.* 2007; as above), we found that the Burrowing Owl consumed a wide range of prey, indicating a generalist diet. One possible explanation for the discrepancy between the rather low food-niche breadth index and the wide range of prey eaten is that opportunistic predators can face leptokurtic prey-abundance profiles, and so show restricted food-niche breadths (Jaksić and Marone 2006).

The relative similarity in the abundance of most insects in the three habitats studied combined with the Owl's diet suggests that this species would not need specific strategies to obtain food in human-modified habitats. The Burrowing Owl breeds in natural as well as in human-modified habitats, where insects are the main prey. Thus, its wide trophic spectrum as well as its ability to take advantage of dominant resources suggests that, from a feeding perspective, the Burrowing Owl has no limitations to colonising and adapting to new human-modified habitats.

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