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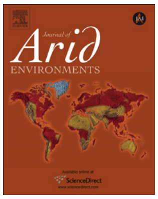

Spatial and temporal variations in the feeding ecology of ferruginous pygmy-owls (*Glaucidium brasilianum*) in semiarid forests of central Argentina

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ABSTRACT

Forested landscapes vary greatly in habitat structure and complexity due to natural and anthropogenic disturbances that may alter forest attributes. Habitat structure along with temporal factors may directly affect interactions between species, particularly those between predators and their prey. Our study assesses the effects of habitat structure in prey intake of a small avian predator, the ferruginous pygmy-owl (*Glaucidium brasilianum*) in semiarid forests of caldén (*Prosopis caldenia*) in central Argentina. Overall, the main prey of owls was small mammals, followed in importance by birds, insects and reptiles. The mean abundance of mammals in the diet was affected by season and year, while the abundance of birds in the diet was greater during spring-summer than during autumn-winter. As for insect prey, abundance of birds in the diet was also greater in open than in closed forests. Habitat type seems to plays an important role in the use of food resources by the ferruginous pygmy-owl in caldén forests. Due to the recurrence, spatial extent and remarkable effects of natural disturbances on habitat structure in these environments, our results suggest that habitat type and structure should be taken into account in diet studies of forest specialist avian predators in these habitats.

1. Introduction

Forested habitats are among the most variable habitats in terms of structure and complexity. Despite the appearance of a homogeneous landscape, small variations in soil (moisture, temperature and nutrient availability) and microclimate features (air humidity and temperature, light exposure) may result in a patchy distribution of forest types that differ in plant species composition and vertical structure (Kumar et al., 2011; Raynor, 1971; Tateno and Takeda, 2003). Human-induced and natural disturbances also play an important role in shaping habitat heterogeneity and structure in these environments. Disturbances can increase habitat complexity by reducing both canopy cover and competition for light and by enhancing sprouting of trees and brushes that in some cases may result in more densely covered forest types (Sarasola et al., 2005; Weishampel et al., 2007).

Habitat structure and spatial heterogeneity in forested habitats are also important environmental determinants of the distribution of animal species. In the particular case of predators and their prey, habitat complexity may affect the way in which they interact, determining the structure of ecological communities (August, 1983; Holt, 1984; Murdoch and Oaten, 1975). For specialized predators, for example, habitat complexity can influence the spatial distribution of the preferred prey; this may, in turn, determine a numerical response of predators (Solomon, 1949) through changes in their densities. By contrast, predators feeding on a wide spectrum of prey species can cope with changes in prey abundance by shifting the diet to prey upon alternative species (i.e. functional response; *sensu* Solomon, 1949).

Here we examined the feeding ecology of a small avian predator, the ferruginous pygmy-owl (*Glaucidium brasilianum*), in semiarid forests of caldén (*Prosopis caldenia*) in central Argentina in relation to variation in time and habitat type. This small owl (ca. 88°g) ranges from southern Texas and south Arizona through central and South America to Bolivia and Argentina (König and Weick, 2008; Proudfoot and Johnson, 2000). This cavity-nesting, diurnally active owl inhabits a variety of landscapes, from tropical and

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subtropical dry forest to semiarid, open-forest in the southern limits of its range (Holt et al., 1999; König and Weick, 2008; Proudfoot and Johnson, 2000). Several studies on its diet and foraging ecology indicate that ferruginous pygmy-owl is a generalist predator that preys on a wide spectrum of prey including mammals, birds, reptiles, amphibians, and invertebrates, although rodents and birds appear to be their main prey (Carrera et al., 2008; De la Peña and Salvador, 2010; Di Giacomo, 2005; Holt et al., 1999; Motta-Junior, 2007; Proudfoot and Johnson, 2000). This variability in its food habits may allow the ferruginous pygmy-owl to adapt to local changes in prey availability and abundance.

Ferruginous pygmy-owl may occur in high densities in semiarid forest of central Argentina and this occurrence pattern seems to be independent of vertical plant structure and habitat features at micro and macro scales (Campioni et al., 2013). However, habitat structure could have effects on field resources availability or on the way they are exploited by owls. Multi-scale resource selection studies have shown that resource availability affects owls' habitat selection and reproductive performance in desert environments (Flesch and Steidl, 2010). There is, however, little information on the ecology of forest-specialist owls for much of southern South America (Trejo et al., 2006) including semiarid forest of the Espinal region. While the food habits of the ferruginous pygmy-owl have been described locally for some habitat types across its range, no studies have yet analyzed the effects of spatial and temporal variability on the feeding ecology of this owl in a particular habitat. Our aims were hence to analyze ferruginous pygmy owl feeding ecology in semiarid caldén forest of the Espinal region. We hypothesize that, along with seasonality, habitat structure has important effects on prey type intake and on the occurrence of different prey types in the diet of this small, forest-specialist avian predator.

2. Materials and methods

2.1. Study area

The study was conducted in the Parque Luro Reserve (36° 55′ S, 64° 16'W), La Pampa province, central Argentina. The reserve (7604 ha) was declared as protected area in middle 1970's (Amieva, 1993) and it consists of a continuous xerophytic forests of caldén (*P. caldenia*), the characteristic landscape of the Espinal biome in this region of Argentina (Cabrera, 1994). However, forest areas in the reserve differ structurally due to soil features as well as the effects of past human (roads and forest clearing for tourist activities) and natural (wildfires) disturbances (Sarasola et al., 2005). However, such antrophogenic perturbations are not longer occurring and forest clearing or cutting, as well as cattle rising activities, have been banned from the area since it was established as a protected area by the Government of La Pampa province.

Broad, open areas of natural grassland are also common in some parts of the reserve, particularly in the tourist area of the reserve (400 ha). Nevertheless, our study was restricted to the non-tourist zone which is entirely dominated by a continuous of caldén forests without grassland areas. These semiarid forests are characterized by hot summers and cold winters with low humidity and low annual rainfall, typically concentrated in spring and summer (350 and 450 mm yr−1; Fernández and Busso, 1999). Habitats surrounding the reserve consist of agricultural areas planted with crops and perennial and annual pastures.

2.2. Sample collection and analysis

Pellets and prey remains were collected during 2001–2003 in twelve of the 50 nest-boxes set through the reserve as part of a long-term study on the breeding ecology of American kestrels (*Falco sparverius*) (Liébana et al., 2009; Sarasola et al., 2003). These nest boxes were usually occupied by pygmy-owls during the breeding seasons but also during winter when owls occupied nest boxes presumably for roosting. Year-round nest box occupancy allowed us to assign pellets and prey remains to geographic area, habitat type, and time of year. Because the ferruginous pygmy-owl is considered to be monogamous and territorial (Proudfoot and Johnson, 2000), the use of nest boxes by pygmy owls also allowed us to allocate diet samples to each site and to a discrete number of owls both throughout the study area and at each of the sampling sites. Mean distance between nest boxes used by owls was 5480 m ($n = 12$; minimum distance = 1215 m; maximum distance = 11,543 m). All the nest boxes from which we obtained pellet samples were set inside the forest and at a distance ranging between 50 and 80 m from the nearest road.

Pellets were hydrated and broken apart by hand and remains of prey items were separated for identification. Smalls mammals were identified to species on the basis of skulls, dentition, hairs and claws using keys (Chehebar and Martin, 1989; Pearson, 1995) and reference collections located at the Universidad Nacional de La Pampa (UNLPam). Insects were identified to family level by mandibles, heads, elytras, and other parts using reference collections also located at the UNLPam. To estimate the minimum number of individual prey items in each sample, we counted skulls of mammals and birds; we used whole heads, feet, elytras and mandibles for insects. When only hairs, bones, or feathers were found, these were counted as one individual and classified as unidentified.

For each sample of pellets and prey remains belonging to the same nest-box, we calculated the standardized food niche breadth (Bsta) following Colwell and Futuyma (1971). For the index calculation, vertebrate prey were categorized as species, genus, or order (in the case of unidentified birds), and invertebrate prey were categorized to family (Marti et al., 1993). We also calculated the geometric mean mass of vertebrate prey (MWVP) consumed in a diet sample by multiplying the log-transformed mean mass of each prey type by the number of that prey in the sample, summing these products, dividing by the total number of prey, and back-transforming this value. This procedure partially compensated for the skewed distribution of prey sizes and the potential to over- or under-estimate mean prey mass (Marti et al., 1993).

We calculated total prey biomass in the diet by multiplying the mean mass of each prey type by the number of that prey recorded. To compute prey biomass, we obtained the mean body mass of small mammal species and arthropods from Sarasola et al. (2003, 2007). Santillán (unpubl. data) provided data for the body mass of birds and amphibians, respectively. Unidentified prey items were not considered in the prey biomass calculation.

2.3. Habitat classification

We classified the habitat type surrounding each nest box where samples were collected (radius 200 m from the nest box). Classifications followed habitat categorizations for the reserve made by Gonzalez-Roglich et al. (2012) and vegetal physiognomic units identified in this habitat by Sarasola et al. (2005). We categorized forest types around sampling sites as open or closed forest. Differences between these two forest types are due mainly to foliage coverage at the ground (<0.5 m high) and shrub layer (0.75–3 m). The plant structure and physiognomy of the open forests resembles the typical physiognomy of caldén forest, with well developed ground (<0.5 m), subcanopy (3.25–6 m) and canopy (>6 m) strata but with an almost absent shrub layer. The closed forest, on the contrary, has similar vertical structural features as open forest with a less developed ground strata (grasses) and the inclusion of a well developed, dense and conspicuous shrub stratum that can reach in certain zones up to 50% of foliage cover at that height (Sarasola et al., 2005) (Table 1).

2.4. Statistical analysis

We evaluated spatial and temporal variation of prey consumed by pygmy-owls in Parque Luro Reserve by building generalized linear models (GLMs; McCullagh and Nelder, 1989) using the software R (R Development Core Team, 2009). The responses variables were the number of individuals consumed in each of the four defined prey categories: mammals (rodents and small marsupials), birds, reptiles-amphibians, and invertebrates. We considered pellets and prey remains from each nest box collected during each season as a sample and incorporated the independent variables in the models. The independent variables considered were habitat type, season and year. Habitat type was included in the models as a two-level factor (open or closed forest). Season was also included in the models as a two-level factor: autumn-winter (for samples collected between March to August), and spring-summer, (for samples collected from September to February). Finally, we included year of sample collection as a categorical variable with the aim of evaluating inter-annual variation in the diet of ferruginous pygmy-owls.

All models were built using a Poisson error distribution and a log link function. The significance of habitat, season, and year as explanatory variables of consumption of each prey category was tested using information theory. We built eight models (all possible variable combinations of main effects without interactions) for each prey category species and used the Akaike Information Criterion (AIC, Burnham and Anderson, 2002), which takes into account both the information explained by the model and its complexity in terms of number of estimated parameters, generating a rank from the best to the least likely model. Within a prey category, each model was considered as a hypothesis explaining the consumption of that prey. For this set of models, we first calculated the second-order AIC (AICc), which is similar to AIC but corrected for small sample size, the ΔAICc (the differences in AICc with respect to the AICc of the best candidate model), and AICc weight (w). The best hypothesis was weighed against the others using AICc weight, which gives an estimation of the likelihood of the hypothesis given the data (Wagenmakers and Farrell, 2004). Correlations between independent variables were tested, showing non-significant correlations ($p > 0.20$). Unless indicated mean ± S.D. are given.

3. Results

In total, 651 items were identified from 291 pellets and 137 prey remains collected during the study period. The main prey group in the diet of pygmy-owls was invertebrates (mostly insects, 46.7%) followed by small mammals (40.7%), birds (11.2%) and reptiles-amphibians (less than 2% for both prey groups). In terms of biomass, however, small mammals were the main prey group (79.3%) followed by birds (16.7%), insects (2.1%) and reptiles-amphibians (less than 2%) (Appendix 1, electronic version only).

Table 1
Differences in vertical plant structure between open and closed caldén forest types at the Parque Luro Reserve according to Sarasola et al. (2005). Values are expressed as mean percentage (±SD) with *t*-student test results for mean foliage coverage comparisons between forest types. Estimations on horizontal foliage coverage are based on 40 points sampled at each of ten 25 m radius circular plots randomly selected for each forest type ($N = 400$ for each forest type). See Sarasola et al. (2005) for further details on sampling methods.

Strata	Open forest	Closed forest	*t*-Value	*P*
Ground	72.0 (11.0)	52.5 (10.6)	3.77	<0.01
Shrub	5.2 (6.7)	22.7 (9.26)	4.97	<0.01
Sub-canopy	17.3 (12.6)	13.7 (6.5)	0.59	0.55
Canopy	5.7 (9.1)	2.17 (4.01)	0.97	0.34

We found statistical differences in the occurrence of each of the prey groups in the diet of pygmy owls when comparing different habitats, seasons and years. However, such differences were not always due to the same factors (i.e., habitat characteristics, season and year) or by factors affecting prey frequency in the same way. Abundance of mammals in the diet of owls, for example, varied both by season and year (Fig. 1). The model including these two temporal variables was more than five times better supported (AICc weight ratio = 0.84/0.16) than the competing model containing only season as explanatory variable (Table 2). Mammals were more abundant in the diet of owls during spring-summer (33.33 ± 16.92 individuals) than during autumn-winter (17.33 ± 8.81 individuals).

Abundance of birds in the diet was affected by habitat characteristics but also by temporal variables (Fig. 2). Abundance of birds in the diet was higher during spring-summer (11.33 ± 1.52) than during autumn-winter seasons (4.22 ± 4.81) and for open (9.40 ± 5.54) than for closed (3.57 ± 3.69) forest types. It was also greater in 2003 than in other years. The model containing all these variables was more than three times better supported (0.76/0.24) than the competing models (Table 2).

Habitat type also determined the mean number of invertebrate prey in the diet of pygmy-owls (Table 2). This prey type was more frequent in average (±S.E.) in samples obtained in open (35.4 ± 13.4) than in closed forest (14.4 ± 6.2). Reptiles and amphibians comprised only a small fraction of the prey spectrum in the owl's diet and their abundance in the diet of owls was not affected by either temporal or habitat variables.

Neither the MWVP nor the BSTA calculated for each of the samples were determined by the occurrence of a particular prey type, habitat features or temporal variables ($P > 0.20$ in all cases).

4. Discussion

The ferruginous pygmy-owl is considered to be a generalist predator. However, our study suggest that although ferruginous pygmy-owls do prey on a variety of prey from different taxa, the occurrence of prey types in their diet is also influenced by habitat and temporal factors.

Predation by ferruginous pygmy-owls upon small mammals, for example, was determined by temporal variables: these prey

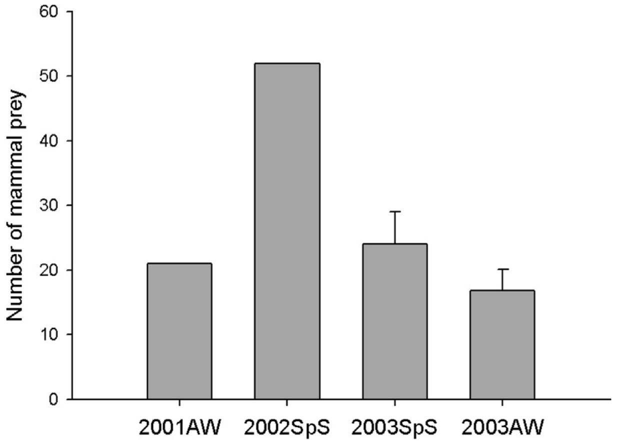

Fig. 1. Year (2001–2003) and season (AW = autumn-winter, SpS = spring-summer) variation on the mean number of mammal prey (+S.E.) consumed by Pygmy-owls in Parque Luro Reserve, central Argentina.

Table 2
Models explaining the consumption of the four vertebrate prey groups by pygmy-owls in caldén forests of Parque Luro Natural Reserve, Argentina. The intercept and coefficient for the variables included in the top-ranking model for each prey group are given with SE in parentheses. For each model, the corrected Akaike's Information Criterion (AICc), the difference in AICc between the current model and the best model (ΔAICc), and the Akaike weights (AIC*w*) are given.

Prey	Model	Intercept	Coefficients	AICc	ΔAICc	AIC*w*
Mammals	Year + season	532.29 (187.61)	−0.26 (0.09)	114.30	0.00	0.84
	Season		−0.63 (0.12)	117.59	3.29	0.16
Birds	Year + season + habitat	−1458.86 (547.92)	0.72 (0.27)	76.08	0.00	0.76
	Year + habitat		−0.75 (0.24)	79.73	3.64	0.12
	Season + habitat		−1.04 (0.26)	79.88	3.80	0.12
Reptiles	Null	−0.28 (0.33)	–	30.59	0.00	0.50
	Season			32.04	1.45	0.25
	Habitat			33.38	2.79	0.13
	Year			33.48	2.89	0.12
Insects	Habitat	356.67 (0.07)	−0.88 (0.12)	255.29	0.00	0.72
	Year + habitat			258.08	2.79	0.18
	Season + habitat			259.17	3.88	0.10

were more common in the diet in spring-summer than in autumn-winter. Small mammals were also more frequent in the diet of owls in 2002 than in the other years of the study. Although population dynamics of small mammals in dry forests of central Argentina and particularly those of sigmodontinae rodents (e.g. *Calomys* sp., *Graomys griseoflavus* and *Akodon molinae*) are not well defined, it is known that abundances of these rodent species fluctuate seasonally. Several studies, for example, have found peaks in field abundance of small mammals in autumn and spring with noticeable and marked declines during winter (Biseglia et al., 2011; Corbalán and Ojeda, 2004; Sarasola et al., 2007). Some of these studies also found differences in small mammal abundances between years, probably due to food availability/constraints, climate factors, or both (Corbalán and Ojeda, 2004). Birds were more frequent in the owl's diet in spring-summer than in autumn-winter. Density of birds in the caldén forest, and particularly those for the bird species found in the diet of owls except one (*Sturnella loica*), are also higher in warmer than in colder seasons (Sosa, 2008), suggesting that the owl's predation on birds is constrained by seasonal fluctuations. Thus, variation in the abundance of small mammals and birds in the diet of ferruginous pygmy-owls seems to reflect, at least in part, field availability and abundance. There is no available information on the effects of vegetal structure and habitat type on field abundance of these prey groups.

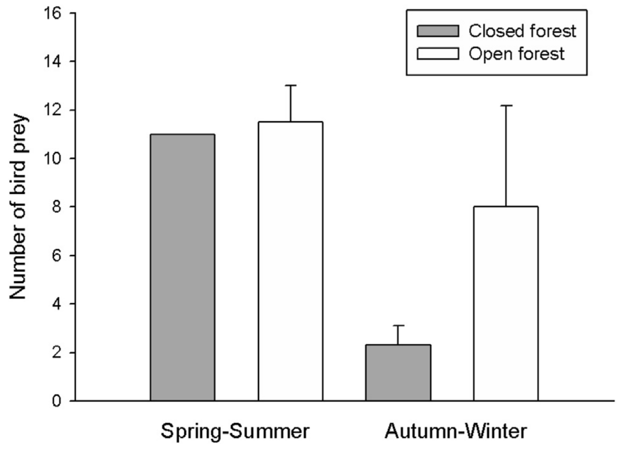

Fig. 2. Variation on the mean number of birds (+S.E.) consumed by pygmy-owls in different habitat types (open vs. closed forest) and seasons (autumn-winter vs. spring-summer) in the study area.

The frequencies of both birds and invertebrates in the diet were related to habitat characteristics, with higher abundances in open than in closed forest types. Invertebrate prey in the owl's diet was composed mostly of grasshoppers (Appendix 1, electronic version only), a group of insects more abundant in grasslands and open areas than in forests with dense bushes. Grasshoppers are a common prey in the diet of ferruginous pygmy-owls in North America (Proudfoot and Beasom, 1997) and also in the diet of related species (austral pygmy-owls, *Glaucidium nanum*) in Chile (Jimenez and Jaksic, 1993).

Although there are few studies on bird species diversity and abundance in the caldén forest related to differences in vertical plant structure, differences in bird prey intake by pygmy owls according to habitat types may by correlated with some particular behavioral and morphological traits of pygmy-owls rather than to fluctuations in field prey availability. Approximately 75% of the species in the genus *Glaucidium* ($n = 32$ species; Holt et al., 1999) exhibit eye-like patches or ocelli in their napes that resemble the face of an owl (Negro et al., 2007). These ocelli have been hypothesized to play a role in avian mobbing, an antipredatory behavior usually exhibited by small birds towards raptors. Two of the hypotheses for possible functions of ocelli, the “mobber manipulation” hypothesis (deflection of bird mobbing toward a frontal instead of posterior attack) and the “mobber census hypothesis (eliciting of bird mobbing by owls as a way to prospect local abundance of avian prey) posit that a false “face” helps predators detect or elude their avian prey (Negro et al., 2007). Support for the last hypothesis comes from a meta-analysis conducted by Negro et al. (2007) where species of pygmy-owls inhabiting open habitats had a higher proportion of birds in their diets. If owls are more conspicuous in open areas, the probability that they are detected by small birds could be greater, increasing the likelihood of both mobbing events and predation.

Seasonality, as well as inter-annual climatic variations, is commonly assumed to explain fluctuations in prey field abundances and subsequent dietary shifts of generalist predators. Our study shows that along with temporal variables, other environmental factors, such as habitat structure, may play an important role in prey choice and feeding ecology of ferruginous pygmy-owls. This is particularly true for bird and invertebrate prey, which comprise together ca. 20% of prey biomass in the diet of owls in our study area. The relative importance of these prey in some stages of the owl's life cycle, especially during the breeding period, require further studies to examine how habitat features may affect foraging ecology and breeding success of this small avian predator in caldén forests.

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Appendix A. Supplementary data

Supplementary data related to this chapter can be found at http://dx.doi.org/10.1016/j.jaridenv.2014.05.008.

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