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Emu
http://dx.doi.org/10.1071/MU13082

Short Communication

Trophic ecology of the Ringed Warbling-Finch (*Poospiza torquata*) in Neotropical semi-arid scrublands

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Abstract. Seed-eating birds in temperate deserts must cope with great variation in the availability of their food resources. We studied the trophic ecology of Ringed Warbling-Finches (*Poospiza torquata*) in semi-arid scrublands of the Monte Desert, Argentina. We assessed seasonality in the availability of seed and in the consumption of arthropods and seeds at a regional scale, and evaluated the composition of the granivorous component of the diet and the seed dietary breadth. Ringed Warbling-Finches had a granivorous–insectivorous diet consisting largely of arthropods in summer and seeds and arthropods in winter. The granivorous component of the diet consisted mainly of grass seeds, but with low breadth of the winter seed diet. To deal with seasonal variation in the availability of food resources, Ringed Warbling-Finches switched opportunistically between different resources, exploiting alternating seasonal patterns of food abundance. This seasonal switching is a well-established strategy in the behaviour of the species and was observed in all Ringed Warbling-Finch populations studied across the Monte Desert. Our results show the flexibility of foraging strategies of Ringed Warbling-Finches, an opportunist species that adjusts their relative consumption of seeds and arthropods in response to the spatial and temporal variations in these food resources.

Additional keywords: dietary switch, granivory, Monte Desert, resource channels, seed-eating birds.

Received 12 March 2013, accepted 9 December 2013, published online 7 April 2014

Introduction

Seed-eating birds that inhabit arid environments must cope with significant temporal changes in the supply of seeds. In such environments, climatic seasonality and rainfall determine primary productivity and pulses of seed production (Reichman 1984; Gutiérrez *et al*. 2000). In turn, the often local nature of rainfall increases regional heterogeneity in seed production (Le Houérou *et al*. 1988; Facelli *et al*. 2005). Seed-eating birds use different ecological strategies in response to the temporal variability and scarcity of seed resources, such as switching to other types of food or making regular or unpredictable movements to obtain seed resources (e.g. Díaz 1996; Dean and Milton 2001; Burbidge and Fuller 2007).

In the Monte Desert of Argentina, grasses account for most of the total seed supply of the region, with an annual peak in seed production in summer followed by a decrease in the soil seed-bank over time owing to germination and consumption of seeds (Marone *et al*. 2000; Blendinger and Ojeda 2001). Similarly, the abundance of arthropods peaks during the warm and wet summer season and decreases during the cold and dry winter (Flores *et al*. 2004). These seasonal changes in resource availability affect consumption of arthropods and seeds by birds in the Monte Desert. Granivores as a group track changes in the abundance of seeds in winter but not during the spring breeding period (Blendinger and Ojeda 2001), when insects become the major component of their diet (Milesi *et al*. 2008). Reduced consumption of seeds in spring and summer in bird species with mixed diets of seeds and arthropods has been attributed to increased demand for resources of high nutritional value during the breeding season or to an opportunistic strategy to exploit alternating patterns of seed and arthropod abundance in seasonal regions (Díaz 1996; Holland *et al*. 2006).

One of the most ubiquitous seed-eating birds of the Monte Desert is the Ringed Warbling-Finch (Thraupidae : *Poospiza torquata*). The little known about its diet comes almost wholly from the Biosphere Reserve of Ñacuñán, in the central Monte Desert (e.g. Cueto *et al*. 2006; Marone *et al*. 2008; Ríos *et al*. 2012). This locality is characterised by high annual rainfall and high annual productivity compared with most of the northern and central Monte Desert (Abraham *et al*. 2009) and the diet of the Ringed Warbling-Finch here may not be representative of the whole of this vast and heterogeneous ecosystem. We studied three populations of Ringed Warbling-Finches, each several hundred kilometres apart, in arid and semi-arid environments of the Monte Desert. The distance between study sites allowed us to evaluate the existence of regional patterns in the trophic ecology of the species. We assessed changes in seed availability, seasonality in the consumption of arthropods and seeds by Ringed

Warbling-Finches at a regional scale, and the composition and breadth of the granivorous component of the diet. Specifically, we (1) assessed the seasonal availability of seeds, (2) the seasonal consumption of seeds and arthropods at a regional scale, and evaluated (3) the composition of the granivorous component of the diet and the seed dietary breadth.

Materials and methods

Study area

The study was conducted between 1995 and 1996 at three sites in the northern and central Monte Desert of central-western Argentina: Amanao (27°33′S, 66°31′W), in Catamarca Province, Posta El Balde (30°56′S, 68°39′W), in San Juan Province, and the Telteca Flora and Fauna Reserve (32°21′S, 68°03′W), in Mendoza Province. The climate is arid and semi-arid with strong seasonal variation in temperature and precipitation, and cold and very dry winters. During the coldest months, minimum absolute temperature can fall below −10°C (Red Ambiental IADIZA, CONICET, www.cricyt.edu.ar/ladyot/red_iadiza/index.htm, accessed on July 2013). Amanao and El Balde are located in low valleys, and Telteca Reserve occupies extensive alluvial plains with sand-dune systems (see Supplementary material for a more detailed description of the study sites).

We conducted four sampling trips to each of the study sites: two during the austral summer (December 1995–January 1996, November–January 1997), coinciding with the breeding season and the beginning of the rainy season, and two during the austral winter (July–September 1995, August–September 1996), which coincides with the dry season.

Study species

The Ringed Warbling-Finch occupies arid and semi-arid habitats at the eastern foot of the Andes and in lowlands of southern South America, ranging from central Bolivia and western Paraguay to central Argentina (Ridgely and Tudor 1994). In Argentina, the species occurs in open woodlands, shrubby grasslands and shrub-steppes of the northern and central portion of the country, where it is one of the dominant birds in avian assemblages (Blendinger 2005*a*; Sánchez *et al*. 2013). Its foraging behaviour varies seasonally: in winter Ringed Warbling-Finches take seeds from standing herbaceous vegetation, without descending to the ground, and obtain arthropods and sap by perching in trees and shrubs; in summer, they forage primarily upon arthropods by perching upon the foliage of shrubs and trees (Blendinger 2005*b*; Lopez de Casenave *et al*. 2008; Milesi *et al*. 2008). Local abundance of Ringed Warbling-Finches is correlated with total seed abundance. Population size would thus appear to be limited by seed supply, and this limitation could promote regional and seasonal movements to concentrate populations in areas of higher productivity (Blendinger and Ojeda 2001).

Sampling of birds

Birds were captured in winter and summer using mist-nets (36-mm mesh, 12.4 m long, 2 m high) set at ground level. During each sampling trip at each study site, we mist-netted at two netting sites at least 2 km apart, to increase potential heterogeneity of sampled habitats. At each netting site, 13–20 mist-nets were set at least 20 m apart over an area of ~7 ha, and placed near trees or shrubs to reduce their detection in open environments of sparse vegetation. The number of mist-nets used depended on capture success and abundance of birds. The nets were opened at dawn for ~4 h and before sunset for ~3 h. Mist-netting took place on at least 2 days at each netting site until the total capture effort exceeded 300 net-hours. Most birds (65%) were captured early in the morning, but all captures were pooled for the analyses. Males and females, of both adults and juveniles, were pooled in the analysis because sample sizes were small and sexes cannot be distinguished outside the breeding period.

We determined the diet of birds by stomach flushing, using warm water injected with a syringe and a plastic tube to force regurgitation of stomach contents (Rosenberg and Cooper 1990). Stomach samples were stored in individual containers with 70% ethyl alcohol until laboratory analysis. Only one sample per individual was taken in any one sampling trip.

Availability of seeds

We estimated the availability of seeds on standing plants during each sampling trip. We sampled thirty 1-m^2 quadrats placed along a transect in each of the two mist-netting sites at each study site. The starting point and direction of each transect was determined randomly and a quadrat placed every 30 m along the transect. Seeds were identified to species and their density per quadrat was assigned to one of the following categories: 1–5, 6–10, 11–50, 51–100, 101–500, 501–1000, 1001–5000 and 5001–10 000 seeds m^{-2}. We transformed categorical samples of seed density in a continuous variable of seeds per square metre. First, we estimated the mean value of the interval of each categorical data (e.g. from 1–5 to 3, from 6–10 to 8); then, we summed the estimates values of all plants into a quadrat to obtain the density of seeds per square metre. Only seeds of ripe fruits and spikes were counted because Ringed Warbling-Finches always forage on standing plants and do not feed on fallen seeds on the ground.

Diet

Stomach contents were analysed under a binocular magnifying glass in the laboratory. We placed the entire sample in a Petri dish (50-mm internal diameter) and scored presence in 50 fields, each of 25 mm^2. In each field we determined the presence of food items, classified as seeds, flowers (fragments or whole), leaves and arthropods, and determined relative frequency (ranging from 0 to 50) of each type of food item . This method has the advantage of compensating for coarse differences in biomass between seeds and arthropods, as larger items (whole or in fragments) occupied more fields than smaller ones. Seeds were identified to species level using reference catalogues of seeds of the study sites and catalogues of the Herbarium of the Instituto Argentino de Investigaciones de las Zonas Áridas (Mendoza, Argentina). We did not identify arthropod taxa.

Statistical analyses

We tested for differences in the availability of seeds using a generalised linear model (GLM), with a factorial design that included the main effects and interactions for categorical predictors to a two-way degree. Season, year and site were included as fixed factors. To analyse dietary consumption, we calculated the mean frequency of each type of food item consumed for each sampling trip. In the analyses of the granivorous proportion of the diet we only included data from the same site and season if we had three or more samples of stomach contents that contained seeds. We evaluated the granivorous portion of the diet using the Levins' index (Krebs 1989), only for data from winter because we obtained fewer than three samples of stomach contents that contained seeds per site for summer. The Levins' index is a minimum value when only one category of resource is consumed and at a maximum value when all categories are consumed in equal proportion. We used simple linear regressions to relate seed consumption to seed availability per season. To improve normality of residuals, seed availability was $\log_{10}$ transformed.

Correspondence analysis (CA) was used to describe the structure of dietary patterns among the three populations of Ringed Warbling-Finches in winter and summer. Analysing the ordination of population diets in the multidimensional space generated by the items consumed allows for exploration of resource preferences and their variation in space and time. CA provides information on the importance of every food item for population ordination, allowing for the interpretation of the causes that determine their dispersion in the ecological space.

All means are given ±standard deviation.

Results

We obtained 63 samples of stomach contents (including two recaptures at the same site in different years) from the three study sites: 8 winter samples and 14 summer samples from Amanao; 11 winter and 15 summer samples from El Balde; and 9 winter and 6 summer samples from Telteca Reserve. Of these 63 samples, 50.8% contained seeds, 95.2% arthropods and 19.0% fragments of leaves and flowers.

Seasonal changes in diet

During winter, both arthropods and seeds were important components of the diet of Ringed Warbling-Finches (Fig. 1*a*). In winter, consumption of arthropods and seeds (mean frequency of items per stomach sample) was approximately equal at Amanao and El Balde, whereas Telteca differed from the other study sites, with the mean frequency of seeds per stomach sample greater than that of arthropods (Fig. 1*a*). In summer, mean frequency of seeds per stomach sample fell sharply, leaves and flowers were recorded in samples, and the mean frequency of arthropods per sample was much greater than in winter, forming the main component of the diet at all three study sites (Fig. 1*b*).

Availability of seeds was significantly lower in summer (0.90 ± 1.06 seeds m^{-2} ($\log_{10}$-transformed data)) than winter (1.50 ± 1.24 seeds m^{-2} ($\log_{10}$-transformed)) (GLM cross-factorial design: $F_{1,350} = 27.40$, $P < 0.0001$). Seasonal differences in density of seeds per quadrat did not differ between sites and years (sites: $F_{2,350} = 2.43$, $P = 0.09$; years: $F_{1,350} = 2.42$, $P = 0.12$), but there was a significant interaction between site and year (site × year: $F_{2,350} = 22.24$, $P < 0.0001$). At El Balde and Telteca Reserve, the availability of seeds (all figures $\log_{10}$ transformed) was greater in the first year of the study (El Balde: 1.26 ± 1.36 seeds m^{-2}; Telteca: 1.78 ± 1.41 seeds m^{-2}) than in the second year (El Balde: 0.81 ± 1.04 seeds m^{-2}; Telteca: 0.84 ± 1.04 seeds m^{-2}), whereas the opposite pattern was observed at Amanao (first year: 0.82 ± 0.86 seeds m^{-2}; second year: 1.68 ± 0.97 seeds m^{-2}).

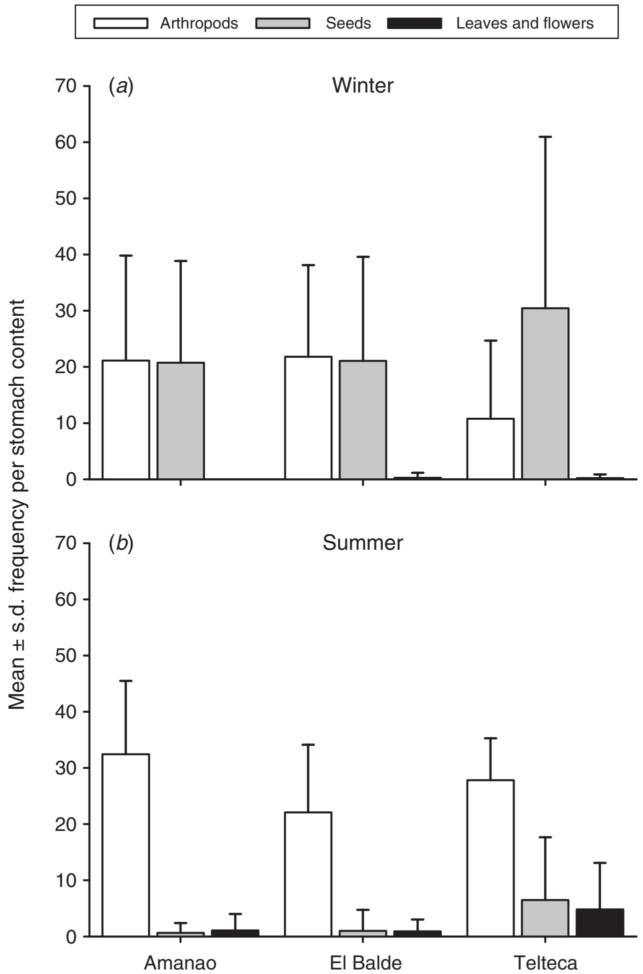

Fig. 1. Mean frequency of arthropods, seeds, and leaves and flowers (±s.d.) consumed by Ringed Warbling-Finches at three sites in the Monte Desert, Argentina, in (*a*) winter and (*b*) summer.

Composition and breadth of the granivorous diet

We recorded 28 seeding species in the study sites (from standing plants), of which 15 were grass seeds. At Amanao, the number of grass seeds comprised 60% of the total seed availability in winter and summer. At El Balde and Telteca Reserve, grasses comprised >90% of the total abundance of seeds per square metre in winter and summer. In winter, Ringed Warbling-Finches consumed different seed species at each site (Fig. 2), with the presence and abundance of seed species varying greatly between sites (Fig. 3). Ringed Warbling-Finches consumed 14 of the 28 available seed species: 5 of 8 seeding species at Amanao, 3 of 16 at El Balde and 9 of 19 at Telteca Reserve.

The granivorous component of the diet consisted almost exclusively of seeds of grasses (12 species, 85.7% of seeds consumed; Table S4 of the Supplementary material). Seeds were not consumed according to their availability in summer (Fig. S2 of the Supplementary material), when the diets of the three populations of Ringed Warbling-Finches was similar because they all

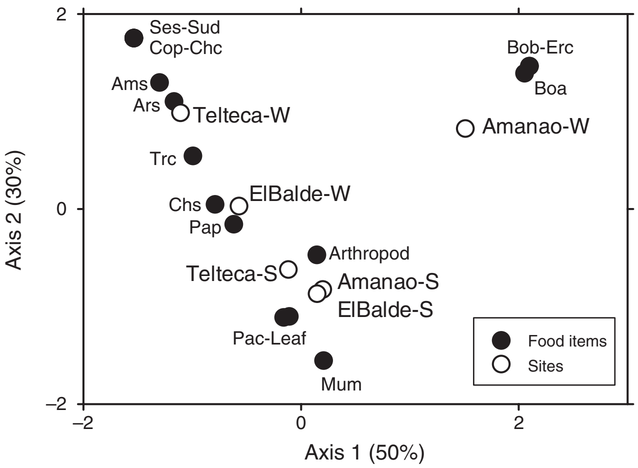

Fig. 2. Ordination diagram in a correspondence analysis of the diet of Ringed Warbling-Finches on the space defined by food items consumed at three sites in the Monte Desert in winter (W) and summer (S). Seed species: Ams, *Amaranthus* sp.; Ars, *Aristida* spp. (includes *A. adscencionis* and *A. mendocina*); Boa, *Bouteloua aristidoides*; Bob, *Bouteloua barbata*; Chc, *Chloris castilloniana*; Chs, *Chloris* sp.; Cop, *Cottea pappophoroides*; Erc, *Eragrostis cilianensis*; Mum, *Munroa mendocina*; Pac, *Pappophorum caespitosum*; Pap, *Pappophorum phillippianum*; Ses, *Setaria* spp. (includes *S. leucopila* and *S. mendocina*); Sud, *Suaeda divaricata*; Trc, *Trichloris crinita*.

relied primarily upon arthropods and leaves (Fig. 2). The breadth of the winter seed diet was slightly greater at Amanao ($B = 1.40$ 0.55, $n = 5$) than the other two sites (El Balde: $B = 1.00 \pm 0.00$, $n = 10$; Telteca Reserve: $B = 1.22 \pm 0.85$, $n = 9$). At El Balde, *Trichloris crinita* was the only species of seed recorded in stomach contents. In winter, the seed species with the highest mean frequency per stomach sample were those with the highest availability at both Amanao (*Bouteloua aristidoides*) and El Balde (*Trichloris crinita*) (Fig. 3). At Telteca, of the four seed species with the highest availability, two were frequently consumed (*Aristida* spp. and *Trichloris crinita*) and two were eaten little (*Bouteloua aristidoides* and *Setaria* spp.) (Fig. 3).

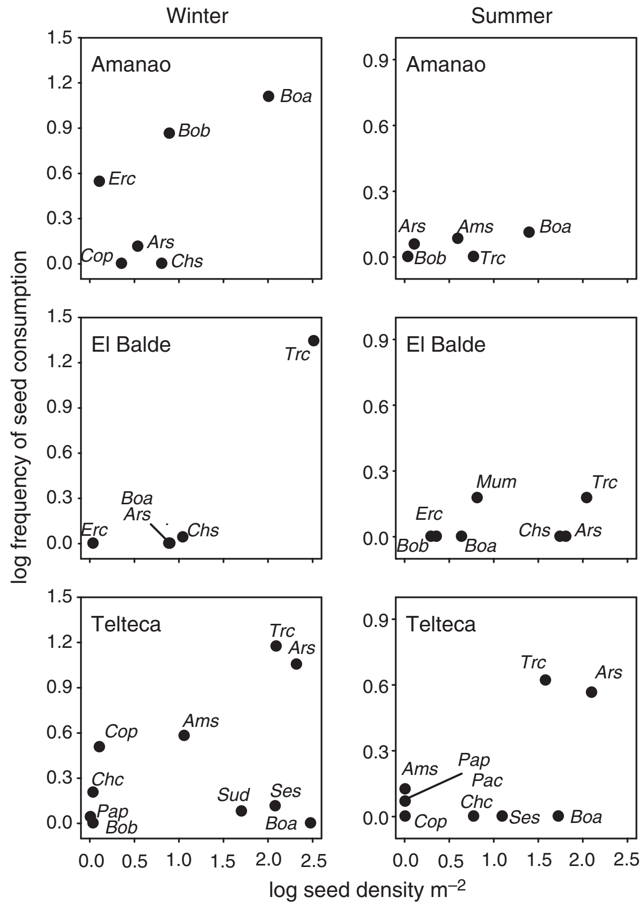

Fig. 3. Mean density of seeds on standing plants of species recorded at least once in stomach contents of Ringed Warbling-Finches, in relation to the mean frequency of seeds recorded in stomach contents in winter and summer. See Fig. 2 for abbreviations.

Discussion

The mixed granivorous–insectivorous diet of Ringed Warbling-Finches showed a well-marked seasonality. During winter, when the availability of seeds was greater than in summer, Warbling-Finches had a mixed diet of seeds and arthropods, whereas in summer they switched to a diet largely of arthropods. The granivorous component of the diet was largely seeds of grasses, with the dietary composition varying regionally with the pool of available seed species. As is typical of desert environments, where heavily variable local rainfall results in complex spatial patterns of productivity, years of high and low availability of seeds varied among sites. However, availability of seeds was always higher in winter than in the preceding summer. The importance of seeds in the diet depended on the availability of seeds, suggesting that Ringed Warbling-Finches are opportunists that adjust their relative consumption of seeds and arthropods in response to the spatial and temporal variation in their availability.

The ability to shift from a diet based on one set of resources to another has been reported for several opportunistic species of bird (e.g. Díaz 1996; McWilliams and Karasov 2001; Podlesak *et al*. 2005; Carnicer *et al*. 2008). This flexibility in diet may have evolved in response to uncertainty in the availability of food resources (Parrish 2000). For seed-eating birds, a strategy of switching between food types avoids the need to move to other areas of higher seed availability, so long as the dietary change to a different trophic channel allow birds to meet their daily energy requirements. The observed change in the diet of Ringed Warbling-Finches to one dominated by arthropods in summer, coincides with the time of year of greatest abundance of arthropods in the Monte Desert (Flores *et al*. 2004; Fig. S3 of the Supplementary material).

In winter, when seeds are an important part of the diet, Ringed Warbling-Finches fed mainly on the most abundant seed species available. It is noteworthy that at Telteca, where seeding species were more abundant than at the other sites, Ringed Warbling-Finches consumed at high levels only some of the abundant seeding species, suggesting a hierarchy of foraging decisions in which preference for seeds is secondary to availability of food. In addition to the importance of seed availability, seed preferences seem to involve nutritional mechanisms. Seeds of *Trichloris crinita*, one of the species most frequently consumed at El Balde and Telteca Reserve, are a very nutritious food resource, with the highest level of starch of all seeds in the Monte Desert that have been tested chemically, as well as high levels of protein and low levels of secondary compounds (Ríos *et al*. 2012). Likewise, *Setaria* seeds, which contain very low levels of starch, had a low ratio of consumption to availability at Telteca Reserve despite their high abundance. Because starch can be easily digested, Ringed Warbling-Finches might show a dietary preference for maximise rates of energy intake by selecting seeds that can be processed faster (Ríos *et al*. 2012). Moreover, the high levels of protein in seeds of *Trichloris crinita* may also compensate for lower nitrogen intake when arthropods are less abundant, allowing birds to maintain nitrogen balance and nutritional status during winter.

In summary, the feeding ecology of Ringed Warbling-Finches suggests that this tanager should not be classified as a seed eater, but rather as an opportunistic, primarily insectivorous species, that shifts to a mixed diet in winter when the availability of arthropods decreases and standing seeds are available in large quantities. The seed component of the diet of Ringed Warbling-Finches largely reflects opportunistic consumption of locally abundant species, although seed preferences of more nutritious seeds could arise when seed availability is high enough. These strategies are deeply rooted in the behaviour of the species, because they were consistently observed in localities spread across >500 km of latitude in the northern and central Monte Desert of Argentina.

Acknowledgments

We are grateful to the members of the Laboratorio de Ecología de Aves of the Instituto de Ecología Regional for their comments on an earlier draft of the manuscript. Fieldwork was supported by a grant to P. G. Blendinger and a research grant by CONICET, Argentina (PIP 4684, to R. Ojeda). All parts of this study comply with the current laws of Argentina. We appreciate the improvements in English usage by Phil Whitford through the Association of Field Ornithologists program of editorial assistance.

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