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Abundance and diversity of small-bird assemblages in the Monte desert, Argentina

P.G. Blendinger*

CONICET-Unidad Zoología y Ecología Animal, IADIZA, CC 507, 5500 Mendoza, Argentina

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Abstract

Assemblages of small bird species (<90 g body mass) from the Monte desert in Argentina were studied to analyze spatial and temporal variation in abundance and species richness. Mean species richness was higher during breeding season than in non-breeding season. The same pattern was observed in aerial insectivores, while granivores and substrate insectivores did not differ between breeding and non-breeding seasons. Overall bird abundance was similar across seasons. Species richness was positively correlated with bird abundance and negatively correlated with dominance; bird abundance and dominance were not correlated. These patterns could be explained by distinct responses of functional groups of birds; dominant species were granivores in the non-breeding season and aerial insectivores during the breeding season, and bird abundance in functional groups changed according to food supply. Most species are residents or regular migrants, while there are few nomadic and transient species. Predictable annual fluctuations in rainfall and resource availability should favor a migratory strategy more than nomadic movements. Similarly, breeding is strongly seasonal and most species start breeding when the first summer rains have generally not yet fallen. Finally, concordances in assemblage structure at local and regional scale suggest that similar mechanisms are acting on the local bird assemblages across the Monte.

Keywords: Bird assemblage structure; Body mass; Breeding timing; Granivores; Insectivores; Monte desert; South America

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*Corresponding author. Present address: CONICET—LIEY, Universidad Nacional de Tucumán, CC 34, 4107 Yerba Buena, Tucumán, Argentina.

E-mail address: blendinger@birdecology.com.ar (P.G. Blendinger).

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1. Introduction

Bird faunas of many desert regions have been well studied, as in Australia (e.g. Schodde, 1982; Wiens, 1991b; Franklin et al., 2000; Morris and Wooller, 2001), Africa (Maclean, 1974; Dean, 1997; Robertson et al., 1998), Asia (Cowan, 1990; Newton and Newton, 1997; Khoury, 1998; van Heezik and Seddon, 1999) or North America (Wiens and Rotenberry, 1980; Wiens, 1991b; Naranjo and Raitt, 1993; Patten and Rotenberry, 1998). In contrast, ecological studies of bird assemblages from arid and semiarid lands of South America are limited. Examples include broad intercontinental comparisons based on generalizations from few samples (Orians and Solbrig, 1977; Schluter and Repasky, 1991), the influence of food shortage on local abundance of bird assemblages (Blendinger and Ojeda, 2001), studies on the seasonal fluctuation of avian populations, habitat use and bird abundance in two localities in the Monte desert (Marone, 1991, 1992; Marone et al., 1997; Blendinger and Alvarez, 2002) and Western Chaco (Capurro and Bucher, 1982, 1986), and the effect of livestock on bird abundance and distribution (Gonnet, 2001).

Bird species richness is usually lower in desert ecosystems than in more humid environments of the same region. Thus, birds in arid zones constitute an impoverished portion of the regional pool of species, including a reduced number of endemic species (Maclean, 1974; Schodde, 1982; Wiens 1991a, pp. 278–310; Stotz et al., 1996; van Heezik and Seddon, 1999). In these ecosystems, birds are faced with harsh environmental conditions, where daily and seasonal thermal fluctuations are pronounced, and where food and water availability is largely unpredictable. Consequently, the composition of dryland bird assemblages can be highly variable in both space and time (Schodde, 1982; Dean, 1997). Local abundances of many bird species can differ very strongly among neighboring localities or between years in the same area. Unpredictable rainfalls and their direct effects on productivity are causal factors of this variability in bird assemblage structure (Morton, 1993, pp. 159–169).

In contrast, the Monte desert of South America has a strong annual seasonality with a predictable rainy season, having potential consequences for the predictability of bird assemblages. To investigate this possibility, I analyzed seasonal changes and the relationships between a number of species and individuals for bird assemblages in the Monte desert. Specifically, I analyzed seasonal changes in bird abundance and species richness, and I explored the variations in abundance patterns for different functional groups of bird species. Also, a strong annual seasonality should affect the timing of reproduction. I expect a marked seasonality in reproductive activity, contrasting with other low elevation desert where inter-annual climatic differences strongly influence reproductive activity resulting in a breeding period expanded throughout the year (Maclean, 1974; Schodde, 1982).

Furthermore, I studied similarities and differences in assemblage structure between localities. Rabinovich and Rapoport (1975) suggested that bird species richness in the Monte desert changes along the latitudinal gradient as a consequence of diverse origins. Thus, it should be possible to differentiate between a southern bird fauna in the plains under Andean–Patagonian influence, and another one in the northern valleys (“bolsones”) and mountain slopes under Chacoan influence.

Consequently, I analyzed differences in species composition among valleys and plains, as well as related changes in the bird assemblage structure.

2. Study area

The Monte desert occupies an extensive sub-Andean latitudinal strip in western Argentina. Its climate is arid or semiarid, temperate or with cold winters. Morello (1958) defined two main latitudinal regions in the Monte determined by topography and annual rainfall patterns (a northern region between parallel 25° and 37° South and a southern region from 37° to 43° South), with strong differences in their flora and vegetation structure. The northern region is characterized by a marked climatic seasonality, with rainfall occurring primarily in summer, while rainfall is more evenly distributed throughout the year in the southern region (Morello, 1958; Mares et al., 1985). At lower latitudes, the northern region occupies closed basins, valleys and lower mountain slopes, whereas south of 32°, the desert stretches over large plains. More recently, Burkart et al. (1999) defined two ecoregions in the Monte desert, the Mountain and Close-Basin Monte north of 32° South, and a southern Plain and Plateau Monte. Thus, two different regions in the Monte meet the expected assumptions of strong annual seasonality and predictable rainy season, a Northern Monte (north of 32° South in valleys and mountain slopes) and a Central Monte (from 32° to 37° South in plains).

All four sampling localities are in the Northern and Central Monte, Amanao and El Balde are located in the lower valleys and Telteca and Ñacuñán occupy extensive alluvial plains with sand dune systems. Amanao (27°33′S, 66°31′W), to the northwest of the large Bolsón de Pipanaco, is a flat area crossed by many ephemeral watercourses. In inter-fluvial areas grows a low (shorter than 2 m in height) shrub steppe dominated by *Larrea cuneifolia*; the herbaceous layer is poor and dominated by annual grasses (*Bouteloua barbata* and *Bouteloua aristidoides*). Along temporary watercourses, vegetation shows greater diversity and higher structural complexity, with a sparse tree layer of *Prosopis chilensis* and *Acacia aroma*, and a shrub matrix of *Bulnesia retama*, *Cassia aphylla* and *Cercidium praecox* growing up to 4 m in height. Mean annual rainfall is 195 mm in Andalgalá, 13 km from Amanao ($n = 70$ years; Ezcurra et al., 1991). Orians and Solbrig (1977) have described this locality in detail.

El Balde (30°56′S, 68°39′W) is in the most depressed area of a narrow valley bounded by mountain ranges to the east and west. Cacti and sparse low shrubs of *Larrea divaricata*, *L. cuneifolia*, *B. retama*, *Mimozyganthus carinatus* and *Mimosa ephedroides* grow on a stony soil, where most shrubs are shorter than 2 m in height. A dense scrubland of *Grabowskia obtusa* and *Prosopis flexuosa* grows in the lower areas, forming a tight shrubby layer up to 4 m in height; the herbaceous layer is rich in annual herbs and grasses (*Flaveria bidentis*, *Pitraea cuneato-ovata*, *Chloris* sp., *Munroa mendocina*) and perennial grasses (*Trichloris crinita*). Mean annual rainfall is 90 mm ($n = 15$ years, Unidad de Información Hidrometeorológica, 1988).

The Telteca Flora and Fauna Reserve (32°21′S, 68°03′W) is located within a sand-dune system with scattered thickets of *L. divaricata*, *Tricomaria usillo* and *B. retama* usually less than 3 m in height; in the herbaceous layer *Panicum urvilleanum*, *Aristida mendocina* and *B. aristidoides* are dominant. In low inter-dune areas, there are patches of phreatophytic open woodlands of *P. flexuosa* of up to 8–10 m heights, with *Capparis atamisquea*, *B. retama* and *Lycium tenuispinosum* as frequent components of the shrub layer. Mean annual rainfall is 161 mm ($n = 21$ years) (Blendinger, 1999).

In the Ñacuñán Man and Biosphere Reserve (34°02′S, 67°58′W) the most conspicuous plant community is the open woodland of *P. flexuosa* of up to 6 m in height, with *L. divaricata*, *Geoffroea decorticans*, *C. atamisquea* and *Atriplex lampa* in the shrub layer. The herbaceous cover is dense and diverse, with abundant occurrences of *A. mendocina*, *Pappophorum caespitosum*, *Sporobolus cryptandrus*, *Chenopodium alba*, *Heliotropium mendocinum* and *Parthenium hysterophorus*. The mean annual rainfall is 328 mm ($n = 27$ years, data from CRICYT's Meteorology Program). Ojeda et al. (1998) provide a detailed description of this locality.

3. Methods

I performed a total of 23 field trips (Table 1) from November 1992 to August 2000. During these samples I used ground-level mist nets (36-mm mesh, 12.4-m long, 2-m tall) to sample bird species composition and relative abundance. All small birds (less than 90 g) captured were included in analyses. The probability of capture in mist nets varies among bird species depending on size, behavior and patterns of activity. Nevertheless, given the short stature of the vegetation covering most of the study areas, I would expect that mist nets covered the heights at which birds spent most of their time; and thus, captures can serve as indicators of relative bird abundance for each species between samples. Given that the bird species of the Monte show clear preference for different vegetation patches (Marone, 1991; Marone et al., 1997; Gonnet, 1998), I placed the nets on two sites at least 2 km apart on each visit to increase potential heterogeneity of sampled habitats. Nets were set apart as far as 20 m or more over an area of about 7 ha, near trees or shrubs to reduce their detectability in open environment with sparse vegetation. The number of nets varied between 13 and 20, depending on capture success and bird abundance. Mist nets were used at least two days per site until the total capture effort exceeded 300 net-hours, except during the last samples in Ñacuñán and Telteca where accumulated net-hours were lower (Table 1). Mist nets were opened at dawn, for approximately four hours, and before sunset for approximately three hours.

A likely shortcoming of this study is that Ñacuñán samples were not obtained at the same time that the remaining samples (Table 1) and bird abundance and species richness observed could be affected by year-to-year variations in resource availability. Nevertheless, rainfall in the Monte is very local and yearly productivity could differ greatly among close localities as was shown for seed supply (Blendinger and Ojeda, 2001). Thus, events at one year in a particular area could be very different to those at an area located a hundred kilometers away, justifying the inclusion of Ñacuñán samples in the analyses.

Table 1
Sampling effort, capture success, number of captured species and estimated species richness (Chao 1 estimator) in 23 samples of bird assemblages in the Monte desert; data of captures for each mist net were not available for Ñacuñán, precluding estimation of species richness

Locality	Date	Mist net hours	Captures in 100 net hours	Captured species	Estimated species
Ñacuñán	Nov. 92	441	33.1	32	—
Ñacuñán	Nov. 93	352	47.7	30	—
Ñacuñán	Apr. 95	188	45.2	15	—
Telteca	Jul. 95	374	29.7	15	24.0
Amanao	Aug. 95	482	19.1	16	20.2
El Balde	Sep. 95	459	24.8	17	25.2
Telteca	Dec. 95	618	18.1	27	35.1
Amanao	Dec. 95	417	12.5	14	23.0
El Balde	Jan. 96	405	31.4	21	41.3
Amanao	Aug. 96	377	16.2	12	14.7
Telteca	Aug. 96	412	11.7	13	17.5
El Balde	Sep. 96	433	16.6	16	19.1
Telteca	Nov. 96	353	24.6	22	23.3
El Balde	Dec. 96	411	10.5	14	23.0
Amanao	Dec. 96	382	17.0	16	17.6
Telteca	Jan. 97	326	24.5	30	54.5
Telteca	Mar. 97	341	25.0	26	30.1
Telteca	Jun. 97	418	15.1	15	19.0
Telteca	Aug. 97	385	16.1	18	36.0
Telteca	Nov. 97	386	26.4	30	54.5
Telteca	Dec. 97	196	26.6	19	23.5
Ñacuñán	Oct. 99	160	35.6	20	—
Ñacuñán	Aug. 00	244	32.4	26	—

Captured birds were weighed with a 100-g Pesola® scale with a precision of 0.1 g. For systematic and taxonomic arrangement I followed Sibley and Monroe (1990). Based on their diet and foraging behavior in the Monte desert (Blendinger, 2000), I grouped bird species into comprehensive functional categories (Appendix A). For the analysis, I placed granivores and granivores–insectivores together in one group as "granivores", species that capture insects in flight in another group as "aerial insectivores", and species that capture arthropods from branches, trunks, foliage or soil as "substrate insectivores".

4. Statistical analysis

As mist nets are less effective for larger birds, only those species weighing under 90 g were included in the analyses. I used capture rate (birds per 100 mist net hours) as the measure of bird relative abundance, to account for differences in number of mist net hours among samples. I combined spring and summer samples

(October–March) as well as autumn and winter samples (April–September) for seasonal comparisons. I expressed dominance per sample as the ratio between mean numbers of captures in 100 net hours of the most abundant species and mean number of all birds captured in 100 net hours.

To analyze seasonal changes in the species richness of bird assemblages, I estimated species richness from captures using the Chao 1 estimator (EstimateS Version 6, Colwell, R.K. 2000, http://viceroy.eeb.uconn.edu/estimates) based on the number of captures for each species. I used the same program to compute randomized species accumulation curves, with 100 randomized runs, to explore the adequacy of sampling effort for every locality. Seasonal differences in mean bird abundance (i.e. capture rate) and species richness were compared using *t*-tests. Relationships between dominance, species richness and capture rate were analyzed using Pearson correlation. Logarithmic transformations were used to normalize data when they did not satisfy parametric assumptions. Otherwise non-parametric tests were used. Relationships among the avifauna composition of the four localities considered were explored with correspondence analysis.

5. Results

5.1. Species richness

I captured 1999 birds representing 60 small (<90 g body mass) bird species in 8557 net-hours. These species represent 79% of all the small diurnal species that I recorded at the four sites during more than 200 days. Species that were not captured include three species that forage above mist net level (*Aeronautes andecolus*, *Tachycineta leucopyga*, and *Notiochelidon cyanoleuca*); six uncommon winter migrants (*Psilopsiagon aymara*, *Muscisaxicola capistrata*, *M. rufivertex*, *M. cinerea*, *Lessonia rufa*, and *Leptasthenura aegithaloides*) and seven other species recorded only a few times each.

At Amanao and El Balde captures included 71% of all small species recorded locally and from 78% to 80% of the species recorded at Telteca and Ñacuñán. Randomized species accumulation curves (Fig. 1) showed that new species were still being captured at all localities, including Telteca where sampling effort was greater. The increased rate in species accumulation was lower in El Balde and Amanao than in Telteca. Passerines account for 53 of the 60 captured species, of the remainder two were woodpeckers, two cuckoos, one owl, one hummingbird, and one dove (Appendix A). Estimated mean species richness (Chao 1 estimator) per sample was higher in the breeding season (mean ± S.D. $= 32.6 \pm 13.4$, $N = 10$) than in the non-breeding season (21.2 ± 6.6, $N = 9$) ($t = 2.30$, df $= 17$, $p = 0.034$). However, when species are split in functional groups, only the number of species of aerial insectivores differed among breeding and non-breeding seasons (aerial insectivores: $t = 6.01$, df $= 17$, $p < 0.0001$; granivores: $t = 0.39$, df $= 17$, $p = 0.70$; substrate insectivores: $t = 1.10$, df $= 17$, $p = 0.18$).

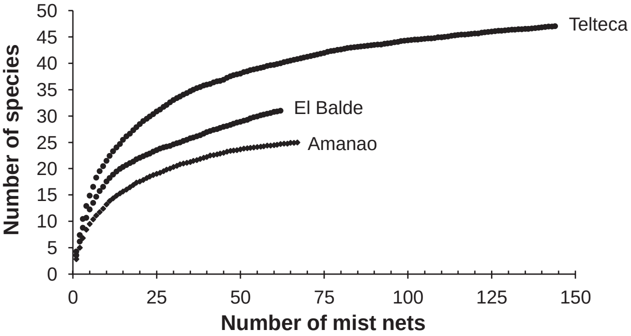

Fig. 1. Species accumulation curves in three areas of the Northern Monte desert based on numbers of mist nets used; data of captures for each mist net were not available for Ñacuñán, precluding computation of a species accumulation curve for this area.

5.2. *Bird abundance*

Mean capture rate showed no seasonal variations (Mann-Whitney *U*-test; $N = 10$, 13; $p > 0.1$) when samples from all localities were combined. A similar result was found for granivores and substrate insectivores (Mann-Whitney *U*-test; $N = 10$, 13; $p > 0.1$ in both cases). In contrast, aerial insectivores (Mann-Whitney *U*-test; $N = 10$, 13; $p < 0.0001$) were much more abundant in the spring–summer period.

The number of granivore species varies little throughout the year (Fig. 2a). Although 13 of 14 granivore species are resident in the Monte desert, capture rate was greater for granivores of 15–30 g body mass during the non-breeding season (Fig. 2a). Seasonal differences were stronger among aerial insectivores. For all size categories above 10 g, abundance and species richness were greater during the breeding season (Fig. 2b). The number of species of substrate insectivores and their abundance were more evenly distributed among body size categories (Fig. 2c). Number of birds and species richness of substrate insectivores did not vary between seasons.

Capture rate per sample was positively related with species richness ($r = 0.67$; $N = 20$; $p = 0.001$). This pattern was mainly due to changes in presence and abundance of smaller species with lesser body mass, which accounted for most species and captures in each season (Fig. 3). Furthermore, the frequency with which a species was present in the assemblages was positively correlated with mean capture rate of this species in both seasons considered (Fig. 4(a) and (b)).

5.3. *Dominance*

Five granivorous species (*Columbina picui*, *Diuca diuca*, *Poospiza ornata*, *Poospiza torquata*, and *Zonotrichia capensis*) and four insectivores (*Melanerpes cactorum*, *Elaenia albiceps*, *Stigmatura budytoides*, and *Myiarchus tyrannulus*) were the dominant species in the assemblages. During the non-breeding season, some granivorous species was always dominant in eight of ten assemblages, while in the breeding season ($N = 13$) granivores and insectivores were dominants in seven and six assemblages each.

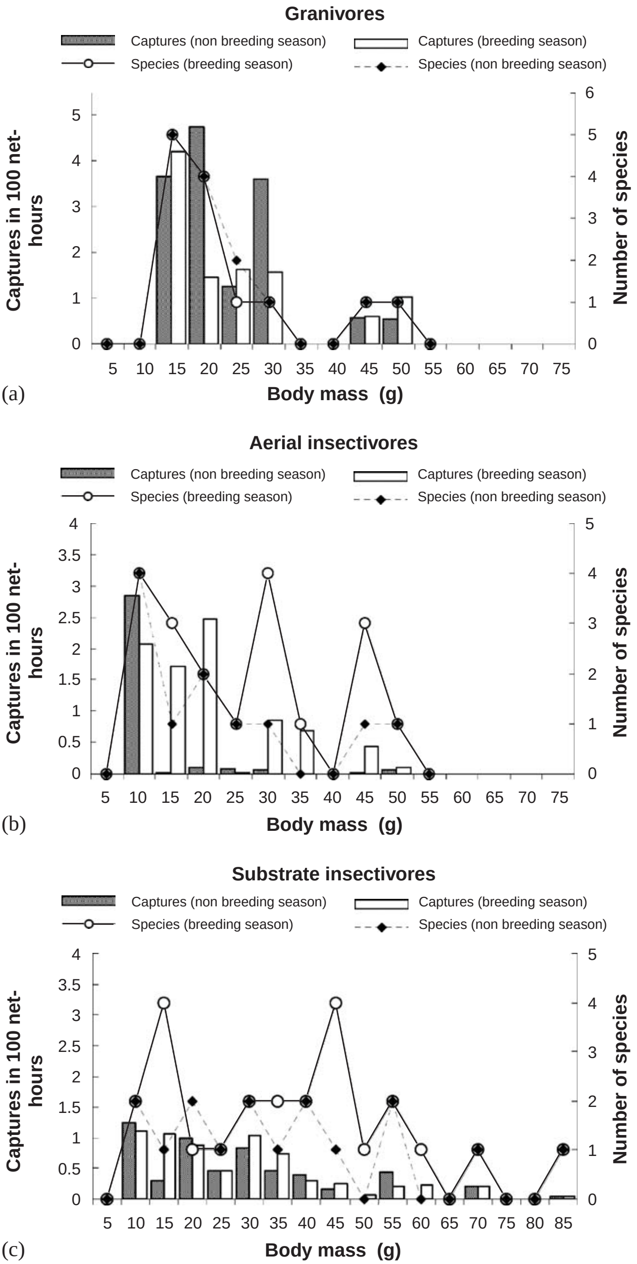

Fig. 2. Seasonal changes in abundance and species richness in three functional groups of birds assembled by body mass intervals; (a) granivores, (b) aerial insectivores, and (c) substrate insectivores.

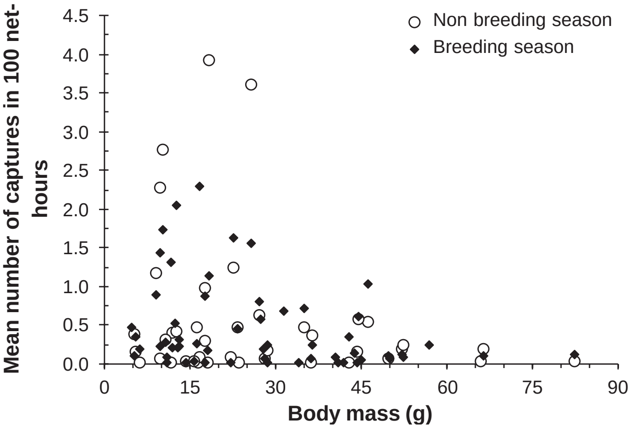

Fig. 3. Abundance distribution of bird species of the Northern Monte (measured as mean number of captures with a sampling effort of 100 mist net hours) in relation to body mass.

Dominance tended to diminish as the number of species in the assemblage increased ($r = -0.57$, $N = 23$, $p = 0.006$), although within season species richness and dominance were not correlated ($p > 0.20$ in both cases). Dominance was higher in the non-breeding season than in the breeding season ($t = 2.63$, df $= 21$, $p = 0.016$). I found a distinct inverse relationship between dominance and species richness for substrate insectivores ($r = -0.77$, $N = 23$, $p < 0.001$) and aerial insectivores ($r = -0.76$, $N = 23$, $p < 0.001$), but not for granivorous species ($r = -0.31$, $N = 23$, $p = 0.15$).

Bird abundance in an assemblage depends on the number of species as well as on the number of individuals of each species. As capture rate increased with species richness (see above), an inverse relation between dominance and capture rate would be expected in the assemblages. Nevertheless, dominance was not related to number of captures ($r = -0.08$, $N = 23$, $p = 0.70$), due to the samples with medium capture rate values showing a higher range of variation in dominance.

5.4. Reproduction

Nesting in the Monte desert is clearly seasonal. I recorded 43 species with reproductive activity (Appendix A) during this study. All breeding records corresponded to the October–February period (Fig. 5), with a peak in laying between late October and mid-December.

5.5. Bird assemblages of valleys and plains

A correspondence analysis based on presence and absence data tended to split assemblages of valleys and plains. Species composition was similar among plain sites and they clustered close together on the two first axes of the ordination (Fig. 6). The

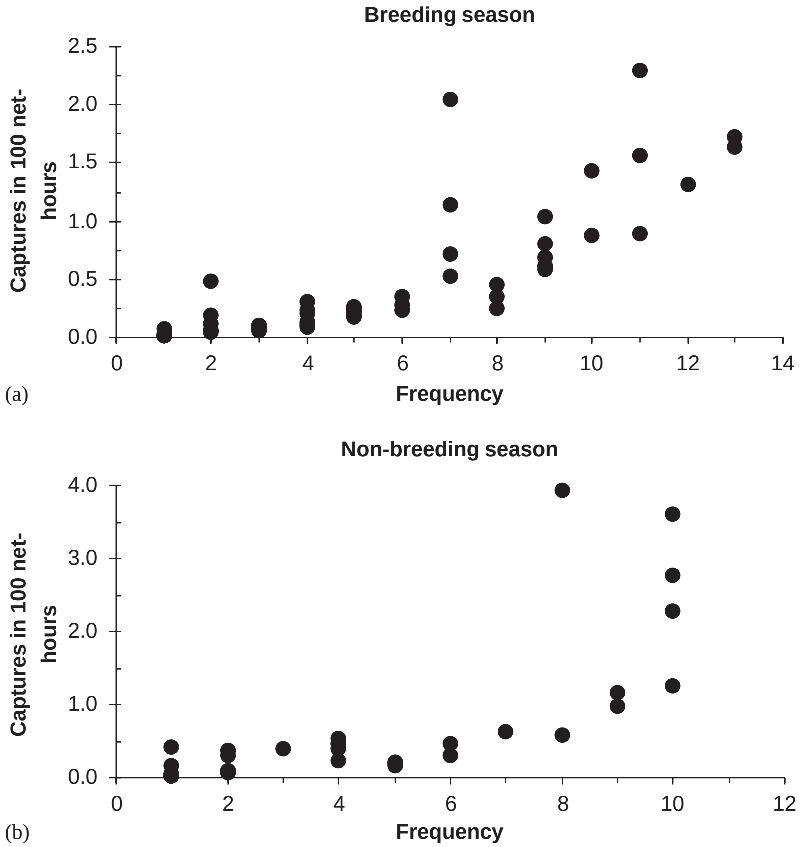

Fig. 4. Spearman correlation among species abundance (measured as mean number of captures per 100 mist net hours) and their frequency in bird assemblages in the Northern Monte: (a) breeding season, $r = 0.93$, $N = 57$, $p < 0.001$; and (b) non-breeding season, $r = 0.87$, $N = 41$, $p < 0.001$.

relationship among valley localities was not so clear. The axes 1 and 2 split the samples of El Balde and Amanao each from the rest due to a group of species captured only in these localities (Fig. 6). As well for Amanao as for El Balde, assemblage composition is more similar between seasons than between localities.

6. Discussion

Bird communities in desert areas exhibit considerable variation in species composition and richness throughout the year (Schodde, 1982; Wiens 1991a, pp. 278–310; Marone, 1992; Dean, 1997). In the Monte, the higher species number during the breeding season is partially due to the October arrival of latitudinal migrant species (*Coccyzus melacoryphus*, *Griseotyrannus aurantioatrocristatus*,

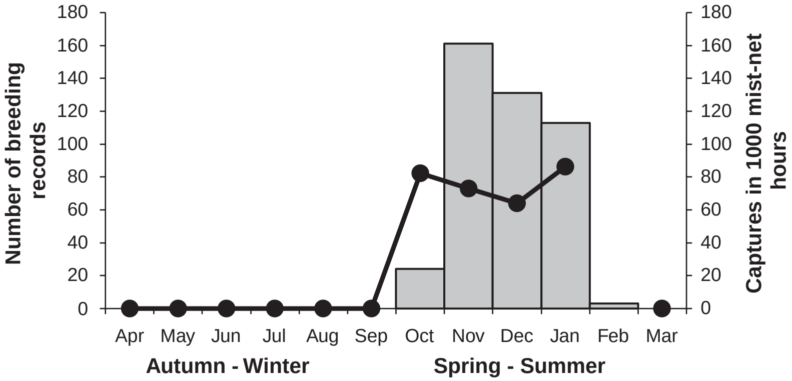

Fig. 5. Monthly breeding activity of birds in the Northern Monte desert; columns show the number of breeding evidences recorded throughout the year, points indicate the number of birds with cloacal protuberance or brood patch captured in 1000 mist net hours (no mist net data were available for February).

Myiarchus swainsoni, *M. tyrannulus*, *Serpophaga griseiceps*, *Sublegatus modestus*, *Synallaxis albescens*, *Progne elegans*, *Geothlypis velata*) from their wintering areas in central and northern South America. These species belong to various functional groups but are mainly aerial insectivores. *Chlorostilbon aureoventris* and *P. ornata*, two species with nomadic displacements superimposed on their seasonal movements, also arrive in the breeding season.

During the non-breeding season, arriving austral migrant species (*Anairetes flavirostris*, *Upucerthia dumetaria*, *Geositta cunicularia*) that breed to the south in the Patagonian steppe (Vuilleumier, 1993) and altitudinal migrants (*Muscisaxicola maculirostris*, *Catamenia analis*) that descend from the mountains are outnumbered by the departure of summer migrants. Also, some insectivorous species that are present in the region all year had a lower density in the non-breeding season as a consequence of partial displacements of their populations (e.g. *Agriornis microptera*, *Xolmis coronata*, *Serpophaga munda*, *Mimus triurus*), lowering the probability of finding these species in the non-breeding season at the local scale in the Monte desert. Similar results emerge when this study is compared with a long-term study performed at the local scale in the Monte desert by Marone (1992). The increase of species richness during the breeding season due to the arrival of insectivores, and the arrival of austral migrants in winter were also reported locally (Marone, 1992; Marone et al., 1997).

Most species in the Monte desert are residents or regular migrants between breeding and wintering areas, while there are only a few nomadic species (i.e. species with irregular movements whose arrival site change among years; Davies, 1984). In this regard, the Monte is more similar to temperate deserts from North America (Wiens, 1991b) than it is to African or Australian deserts, where nomadic species are an important fraction of the regional pool of species (Maclean, 1974; Schodde, 1982;

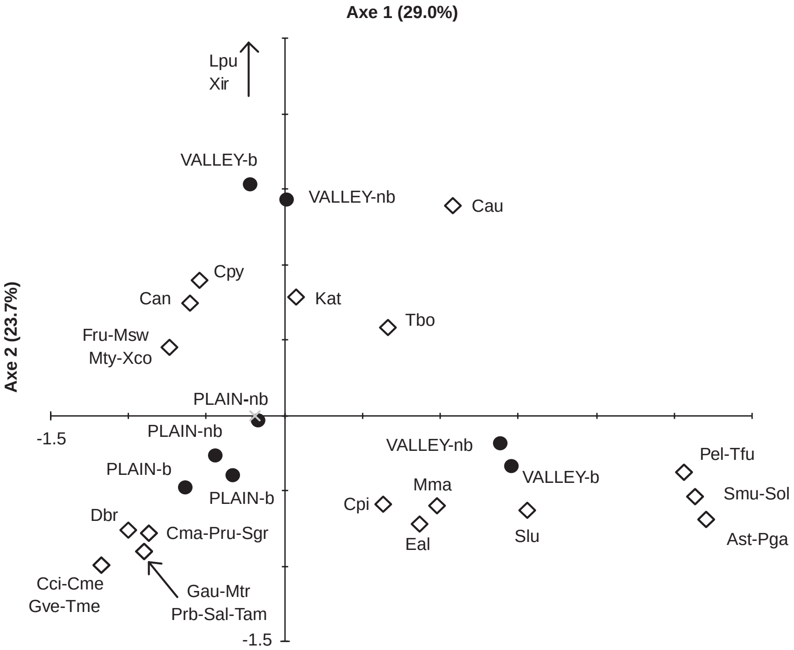

Fig. 6. Diagram of the two first axes in a correspondence analysis showing the ordination of plains and valleys bird-assemblages (closed circles) based on species composition; -nb and -b refer to non-breeding season and breeding season, respectively. Only species explaining most of the variation (open diamonds) are depicted in the diagram: Ast = *Asthenes steinbachi*, Can = *Catamenia analis*, Cau = *Chlorostilbon aureoventris*, Cci = *Coccyzus cinereus*, Cma = *Carduelis magellanica*, Cme = *Coccyzus melacoryphus*, Cpi = *Columbina picui*, Cpy = *Cranioleuca pyrrhophia*, Dbr = *Drymornis bridgesii*, Eal = *Elaenia albiceps*, Fru = *Furnarius rufus*, Gau = *Griseotyrannus aurantioatrocristatus*, Gve = *Geothlypis velata*, Kat = *Knipolegus aterrimus*, Lpu = *Lophospingus pusillus*, Mma = *Muscisaxicola maculirostris*, Msw = *Myiarchus swainsoni*, Mtr = *Mimus triurus*, Mty = *Myiarchus tyrannulus*, Pel = *Progne elegans*, Pga = *Phrygilus gayi*, Prb = *Pyrocephalus rubinus*, Pru = *Phytotoma rutila*, Sal = *Synallaxis albescens*, Sgr = *Serpophaga griseiceps*, Slu = *Sicalis luteiventris*, Smu = *Serpophaga munda*, Sol = *Sicalis olivascens*, Tam = *Turdus amaurochalinus*, Tbo = *Thraupis bonariensis*, Tfu = *Teledromas fuscus*, Tme = *Tyrannus melancholicus*, Xco = *Xolmis coronata*, Xir = *Xolmis irupero*.

Davies, 1984; Dean and Milton, 2001). Nomadism could be selected when extreme conditions are frequent and unpredictability forces birds to move from areas with low to high availability of resources (Dean, 1997). Thus, the cyclic fluctuations in resource availability observed in the Monte should favor a migratory strategy more than nomadic movements.

When all assemblages were considered together, species richness was correlated negatively with dominance, but this relationship disappeared within seasons. Although high dominance in assemblages with few species is unavoidable (Wiens and Rotenberry, 1987), when the number of species increases the dominance is less predictable, because species with distinct requirements could be affected by different factors. Dominant species were usually granivores during the non-breeding season in the Monte desert. Although the number of species did not vary in this group, there was a strong increase in local abundance of some granivorous species during the non-breeding season, coincident with increases in seed supplies (Blendinger and Ojeda, 2001). On the other hand, aerial insectivorous species increased in abundance in the breeding season, when arthropods are much more abundant (Debandi, 1999; G. Debandi and P.G. Blendinger, unpublished manuscript). Among insectivores, winter migration was proposed as an effective strategy to avoid food shortage periods in the Monte desert (Marone, 1992). In the cold non-breeding season, only species less than 10 g of body mass were abundant, mainly *S. budytoides*. This species modifies its foraging behavior in the cold season, taking larger number of prey from leaves (Blendinger, 2000).

Granivores were the most numerous functional group, as in different arid lands around the world (Maclean, 1974; Capurro and Bucher, 1982; Wiens 1991a, pp. 278–310; Morton, 1993; Dean, 1997). Changes in granivorous species abundance in the Monte desert could explain why mean bird abundance in assemblages did not increase during breeding season as did species richness. When insectivorous migrant species arrive in summer, most granivorous species are less abundant than in winter despite being present in many samples. However, in the non-breeding season when overall species richness decreases, granivores show a greater abundance than in the breeding season (Blendinger and Ojeda, 2001).

Body mass is a good predictor of abundance variation, and tend to show a negative correlation with population density in arid environments. This trend was also evident in the small-bird assemblages analyzed in this study. Most granivorous species belong to the same family, thus an inverse relationship between body size and local abundance would be expected to remain when the effects of phylogenetic relatedness are controlled. Similarly, all, except one, species of aerial insectivores belong to the same family. Lower abundance in larger species of granivores and aerial insectivores could be a consequence of food shortage in the Monte desert. More than 95% of seeds found in the soil bank were too small to be efficiently manipulated by large passerines (P.G. Blendinger, unpublished data), imposing a potential upper limit to granivores body size. Similarly, only some of the smallest species of aerial insectivores were abundant in winter, when arthropod abundance and biomass are very low in the Monte desert (G. Debandi and P.G. Blendinger, unpublished manuscript). In contrast, substrate insectivore abundance was more evenly distributed between body size intervals.

A positive association between local abundance and regional distribution is one of the more general macroecological patterns (Gaston and Blackburn, 2000), and a detailed treatment of this issue is not within the scope of this paper. However, it is pertinent to discuss which species do not fit this pattern. A positive association between the mean capture rate of a species and its frequency in the assemblages was found in both seasons. Four of the five more abundant species were granivores. *Z. capensis* was the most abundant species (3.9 birds per 100 net-hours) but it was absent from some assemblages. At least three geographical races of *Z. capensis* can occur in the same area during the non-breeding season, but local abundance of this species is highly variable among successive years (P. Handford, personal communication; P.G. Blendinger, personal observation). Two species, *E. albiceps* and *P. ornata*, had a high capture rate (2.3 and 2.2 birds per 100 net-hours, respectively) compared with other species present with the same frequency in breeding assemblages. The first species does not breed in the Monte desert; it is a transient migrant that was captured in great numbers from late October to early November. No other species showed this behavior, in contrast with other temperate deserts where transient migrants can be a major component of bird assemblages (Newton and Newton, 1997; Wardman and Warrington, 1997; van Heezik and Seddon, 1999). On the other hand, *P. ornata* is a nomadic species that can breed in some years in high densities in a locality, and be completely absent the next breeding season in the same place (Marone, 1992; Blendinger, 2000).

In the Monte desert, the beginning of the reproductive activity coincides with the arrival of spring and with the increase in both temperature and photoperiod. Most species start laying between mid-October and mid-November, when the first summer rains have generally not yet fallen. This marked seasonality of the reproductive period contrasts with other deserts of low elevation at latitudes similar to the Monte desert. In Africa and Australia, although a seasonal pattern exists with periods of higher reproductive activity, nesting extends throughout the year when all bird species of assemblages are considered (Maclean, 1974; Schodde, 1982; Dean, 1997). Factors that determine the beginning of reproductive activity in these deserts are controversial (Schodde, 1982; Wiens 1991a, pp. 278–310; Dean, 1997), and the importance of rainfall, food availability, temperature, or length of the photoperiod will probably differ depending on whether species are sedentary or nomadic. Although monthly and annual rainfall values in the Monte are highly variable between years, rains always are concentrated between late spring and early autumn (Morello, 1958; Le Houérou, 1999). Despite the fact that rainfall amounts are unpredictable, annual seasonality is predictable and well defined. Also, thermal seasonality is well delimited in the Monte, with warm summers and cool winters (Morello, 1958; Le Houérou, 1999). In the Monte desert the temporal coincidence of increased photoperiod, temperature and rainfall does not allow a determination of which is the primary factor or factors that control the beginning and duration of reproductive activity; likely all contribute.

Geographical and historical processes acting at the regional scale affect the composition of local bird assemblages (Ricklefs and Schluter, 1993). Although I sampled too few sites to reach firm conclusions, differences in species composition among assemblages of valleys and plains provide evidence of the heterogeneity of the Monte. According to Rabinovich and Rapoport (1975), in the Monte desert it might be possible to differentiate a bird fauna of the plains under the Andean–Patagonian influence, and another one in the northern valleys and mountain slopes under the Chacoan influence. However, their hypothesis does not explain differences in composition among plain and valley sites. While plains in the southern region of the Monte (south of 35° South) host bird assemblages clearly influenced by Andean and Patagonian species (e.g. Blendinger and Alvarez, 2002), northern plain sites were mainly characterized by the occurrence of a group of species broadly distributed in the contiguous Chaco thorny-woodlands, such as *G. aurantioatrocristatus*, *Phytotoma rutila*, *Drymornis bridgesii*, *Upucerthia certhioides*, *S. albescens*, *Rhinocrypta lanceolata* and *Turdus amaurochalinus*. Finally, species more related with mountains (*Muscisaxicola* spp., *Asthenes steinbachi*, *Sicalis olivascens*, *C. analis*, *Phrygilus gayi*) were more frequent in valleys, suggesting that the valleys have a stronger Andean and Patagonian influence than the northern plains. Thus, these preliminary data suggest that three coarse areas could be differentiated in the Monte desert according to bird species composition and their biogeographical affinities, a Northern Monte valleys area, a Central Monte plains area and an Austral Monte plain and plateau area.

Desert assemblages composition is highly variable between localities (Schodde, 1982; Dean, 1997), determined mostly by individualistic responses (Wiens 1991a, pp. 278–310) and modified by biological interactions such as competition (Grant, 1986), comensalism (Genise et al., 1993; Blendinger, 1999) or predation (Lima and Valone, 1991; Schluter and Repasky, 1991; Watts, 1991). For the Monte desert, it was suggested that idiosyncratic responses of granivorous species explain most of the changes in their diets (Blendinger, 2000) and abundance (Blendinger and Ojeda, 2001). Relative importance of each of these factors for determining assemblage composition and structure are scale dependent. Nevertheless, coincident patterns found between local and regional scales suggest that similar processes are acting on bird assemblages of the Monte, despite the heterogeneity of environments presents in the region.

Additional information on other local assemblages is needed to determine the generalities for the Monte desert of these conclusions. For comparison, plain areas close to the sub-Andean foothill and foothill areas in northern valleys should be a priority. Likewise, long-term studies are needed to address how the strong year-to-year changes in resource availability as a result of variations in rainfall affect assemblage structure and diversity at local and regional scale.

7. Summary

The strong seasonal changes in rainfall and temperature in the Northern and Central Monte desert affect directly and indirectly the bird assemblage structure. The breeding season is clearly delimited between middle spring and early summer. Although overall bird abundance did not show seasonal changes, important variation existed at the level of functional groups of species. Aerial insectivores and granivores showed opposite patterns of change in their regional abundance, responding to seasonal variations in food supply. Finally, bird assemblages of valleys and plains areas in the Monte could be differentiated due to their species compositions. Nevertheless, similarities in assemblage structure at local and regional scale suggest that similar mechanisms are acting on the local bird assemblages across the Monte.

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Appendix A. Bird species captured with mist nets in four areas of the Northern Monte, classified in broad functional categories based on their diet and foraging behavior

Species	Common name	Body mass (g)	Capture localities	Functional category
*Melanerpes cactorum**	White-fronted Woodpecker	35.0	ñ,t	SI
*Picoides mixtus**	Checkered Woodpecker	28.5	a,b,ñ,t	SI
Coccyzus cinereus	Ash-colored Cuckoo	41.0	t	SI
*Coccyzus melacoryphus**	Dark-billed Cuckoo	50.0	t	SI
Chlorostilbon aureoventris	Glittering-bellied Emerald	4.7	a,b	N
Glaucidium brasilianum	Ferruginous Pygmy-Owl	66.0	t	C
*Columbina picui**	Picui Ground-Dove	46.3	b,ñ,t	G
*Sublegatus modestus**	Scrub Flycatcher	11.7	a,b,ñ,t	AI
Elaenia albiceps	White-crested Elaenia	16.7	b,ñ,t	AI
*Serpophaga munda**	White-bellied Tyrannulet	6.1	b	AI
*Serpophaga griseiceps**	Gray-crowned Tyrannulet	5.4	ñ,t	AI
*Stigmatura budytoides**	Greater Wagtail-Tyrant	9.8	a,b,ñ,t	AI
Anairetes flavirostris	Yellow-billed Tit-Tyrant	5.2	a,b,ñ,t	AI

*Pyrocephalus rubinus**	Vermilion Flycatcher	13.0	ñ,t	AI
*Xolmis coronata**	Black-crowned Monjita	42.9	a,ñ,t	AI
Xolmis irupero	White Monjita	22.2	a	AI
*Agriornis microptera**	Gray-bellied Shrike-Tyrant	49.7	ñ,t	AI
*Agriornis murina**	Least Shrike-Tyrant	28.1	ñ,t	AI
Muscisaxicola maculirostris	Spot-billed Ground-Tyrant	11.0	b,ñ	SI
Knipolegus aterrimus	White-winged Black-Tyrant	18.2	a,b,ñ,t	AI
*Myiarchus swainsoni**	Swainson's Flycatcher	31.4	a,ñ,t	AI
*Myiarchus tyrannulus**	Brown-crested Flycatcher	27.4	a,ñ,t	AI
*Tyrannus melancholicus**	Tropical Kingbird	40.4	t	AI
Tyrannus savana	Fork-tailed Flycatcher	28.6	ñ	AI
*Griseotyrannus aurantioatrocristatus**	Crowned Slaty-Flycatcher	27.8	ñ,t	AI
*Phytotoma rutila**	White-tipped Plantcutter	36.5	ñ,t	F
*Upucerthia certhioides**	Chaco Earthcreeper	23.4	ñ,t	SI
Upucerthia dumetaria	Scale-throated Earthcreeper	44.2	a,b,ñ,t	SI
*Furnarius rufus**	Rufous Hornero	45.0	a,ñ,t	SI
*Leptasthenura platensis**	Tufted Tit-Spinetail	9.1	a,b,ñ,t	SI
*Synallaxis albescens**	Pale-breasted Spinetail	12.3	ñ,t	SI
*Cranioleuca pyrrhophia**	Stripe-crowned Spinetail	10.8	a,ñ,t	SI
*Asthenes pyrrholeuca**	Lesser Canastero	13.2	b,ñ,t	SI
*Asthenes baeri**	Short-billed Canastero	17.5	a,b,ñ,t	SI
Asthenes steinbachi	Chestnut Canastero	16.5	b	SI
*Pseudoseisura lophotes**	Brown Cacholote	66.5	a,ñ,t	SI
*Drymornis bridgesii**	Scimitar-billed Woodcreeper	82.3	ñ,t	SI
*Lepidocolaptes angustirostris**	Narrow-billed Woodcreeper	27.2	a,ñ,t	SI

*Rhinocrypta lanceolata**	Crested Gallito	52.4	ñ,t	SI
Teledromas fuscus	Sandy Gallito	34.0	b,t	SI
*Turdus amaurochalinus**	Creamy-bellied Thrush	56.8	ñ,t	SI
*Mimus patagonicus**	Patagonian Mockingbird	52.3	b,ñ,t	SI
*Mimus triurus**	White-banded Mockingbird	43.8	ñ,t	SI
*Troglodytes aedon**	House Wren	9.7	b,ñ,t	SI
Progne elegans	Southern Martin	42.0	b	AI
*Carduelis magellanica**	Hooded Siskin	12.8	ñ,t	G
*Zonotrichia capensis**	Rufous-collared Sparrow	18.4	a,b,ñ,t	GI
Geothlypis velata	Masked Yellowthroat	11.0	t	SI
Thraupis bonariensis	Blue-and-Yellow Tanager	36.3	a,b,ñ	SI
*Saltatricula multicolor**	Many-colored Chaco-Finch	22.6	a,b,ñ,t	GI
Phrygilus gayi	Gray-hooded Sierra-Finch	23.5	b	GI
*Phrygilus carbonarius**	Carbonated Sierra-Finch	16.2	b,ñ,t	GI
Lophospingus pusillus	Black-crested Finch	14.3	a	GI
*Diuca diuca**	Common Diuca-Finch	25.7	a,b,ñ,t	GI
*Poospiza ornata**	Cinnamon Warbling-Finch	12.7	b,ñ,t	GI
*Poospiza torquata**	Ringed Warbling-Finch	10.1	a,b,ñ,t	GI
*Sicalis olivascens**	Greenish Yellow-Finch	17.7	b	GI
*Sicalis luteiventris**	Misto Yellow-Finch	15.7	b,ñ	GI
Catamenia analis	Band-tailed Seedeater	11.9	a,ñ,t	GI
*Saltator aurantiirostris**	Golden-billed Saltator	44.6	a,b,ñ,t	GI

AI: aerial insectivore, C: carnivore, F: folivore, G: granivore, GI: granivore–insectivore, N: nectarivore, SI: substrate insectivore.

*Species recorded breeding.

a = Amanao; b = El Balde; ñ = Ñacuñán; t = Telteca.

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