Movement patterns of three species of sparrow in the central Monte Desert, Argentina: differences between and within species

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Accurate knowledge of the movements of passerine populations in the southern hemisphere is limited, in part owing to differences in movements between and within species and between and within populations. In temperate South America, descriptions of patterns of movements are often based on reports of local changes in abundance and occurrence of species and there have been few detailed studies of movements at the population level. We banded and monitored individuals of three species of sparrow – the Many-coloured Chaco-Finch (*Saltatricula multicolor*), Ringed Warbling-Finch (*Poospiza torquata*) and Rufous-collared Sparrow (*Zonotrichia capensis*) in a temperate site in the central Monte Desert, Argentina, to evaluate differences in site-attachment between and within species. We found resident populations of all three species, the juveniles of which showed little site-attachment. We also observed a large influx of mobile Ringed Warbling-Finches and Rufous-crowned Sparrows during the non-breeding season. We confirmed partial migration of two subspecies of Rufous-collared Sparrows (and, possibly, a third otherwise resident subspecies), and possibly also within Ringed Warbling-Finches. The influxes of mobile individuals during the non-breeding season may be in response to unpredictable climate and consequent availability of resources, as has been found in arid regions of Australia and Africa. Our results provide a basis for a better understanding of the evolution of movement patterns of birds in temperate South America.

(Lay summary).

Introduction

There is little accurate knowledge of the movements of many passerine populations in the southern hemisphere in part because the avifauna exhibit a wide variety of movement patterns, including residence, nomadism and partial migration, in which there may be both migratory and

resident populations within a species (population partial migration) or migrant and resident individuals within populations (intra-population partial migration) (Hockey 2000; Chan 2001; Jahn *et al*. 2004). This wide range of movements within the southern hemisphere possibly occurs because of the lack of extreme climatic conditions and the lack of important barriers between northern and southern locations (e.g., extreme deserts, oceans, mountains), which confers little relative costs or benefits to migrating, or migrating long distances (Jahn *et al*. 2004; Dingle 2008). Further, given that changes in environmental conditions are more usually linked to rainfall than to temperature, migration routes may be complex and variable (Chesser 1994; Hockey 2000; Chan 2001). Two-thirds of known migrant bird species in South America have wintering ranges that overlap with resident populations of the same species (Stotz *et al*. 1996; Jahn *et al*. 2004). Such overlap of migratory and resident populations has also been observed in some birds of Africa and Australia (Chan 2001). It has been suggested that resident populations of birds can persist in regions where severe climatic conditions and shortages of food do not extend for long periods but when severe weather and abundance of food varies between years, as in many arid systems of the southern hemisphere, partial migration may be beneficial. Partial migration may have evolved in systems where migration would be selected during bad years and residence during good years, with no relative benefits of one strategy over the other, resulting in the occurrence of both migrant and resident populations and individuals (Dhondt 1983; Chan 2001). Similarly, in species with wide geographical ranges, as with many species of birds in South America, mobile strategies may be beneficial in regions where climate or abundance of food are unpredictable or adverse but residence may be beneficial in regions with less severe conditions. Knowledge of intraspecific differences in movements is important because it allows within-species comparisons of mobile and sedentary individuals when trying to understand physiological adaptations to migration and the evolution of migratory behaviour (Chan 2001). There have been a number of important studies of migratory birds in South America (Chesser and Levey 1998; Joseph *et al*. 2003; Jahn *et al*. 2004, 2006, 2010, 2012; Jahn and Cueto 2012), although most were of species within a single family of passerines (Tyrannidae), and there remains a lack of basic knowledge about the patterns of movements of many species and populations within South America.

There have been few medium to long-term studies of individually marked populations of passerines in the arid zone of Argentina (e.g. Blendinger and Ojeda 2001; Blendinger 2005*a*; Jahn *et al*. 2009; Cueto *et al*. 2011). The claimed patterns of movements of many species are often based on the assessment of local changes in abundance and occurrence of species (e.g. Capurro and Bucher 1988; Marone 1992*a*; Codesido and Bilenca 2004; Cueto *et al*. 2008; Lopez de Casenave *et al*. 2008) or data from museum specimens or banding studies combined with visits to study sites varyingly dispersed in space and time (e.g. Zimmer 1938; Ortiz and

Capllonch 2007, 2011; Capllonch *et al*. 2011; Areta *et al*. 2012). However, the continued presence of a species at a site is not evidence of residence by individuals at a site throughout the year.

In the central Monte Desert of Argentina, three of the most common species of sparrow are present throughout the year: the Many-coloured Chaco-Finch (*Saltatricula multicolor*), Rufous-collared Sparrow (*Zonotrichia capensis*) and Ringed Warbling-Finch (*Poospiza torquata*). The latter two species show seasonal changes in abundance, with greater numbers in the desert in winter (Marone 1992*b*; Lopez de Casenave 2001; Blendinger 2005*a*). It has been suggested that these changes in abundance are a result of partial migration of the species, but this has never been examined. The comparative study of a system with resident and mobile populations may provide insight into the evolution of migratory behaviour. We banded and monitored Many-coloured Chaco Finches, Ringed Warbling-Finches and Rufous-collared Sparrows in the central Monte Desert over 5 years and describe species-specific differences in site-attachment among adults and juveniles, and explore the occurrence of resident and mobile populations within these species.

Methods

Study site and species

We conducted our study in open mesquite woodland of the Biosphere Reserve of Ñacuñán (34°03'S, 67°54'W), a UNESCO Man and Biosphere Programme reserve in the central Monte desert, Mendoza Province, Argentina (Fig. 1). The open woodland is dominated by Mesquite (*Prosopis flexuosa*) and Chañar (*Geoffroea decorticans*) trees, scattered within a matrix of Creosote (*Larrea divaricata*) shrubs, other tall shrubs with low cover-scores (e.g. *Capparis atamisquea*, *Atriplex lampa*, *Condalia microphylla*), perennial grasses and annual forbs. Ñacuñan's climate is dry and temperate, with hot summers (mean and absolute maxima of 31.5°C and 42.5 °C, respectively) and cold winters (mean and absolute minima of -0.1 °C and -13 °C, respectively). On average >75% of annual rainfall occurs during spring and summer (October–March) but rainfall varies between years (mean annual rainfall ± s.d. 333 ± 116 mm, range 91–585 mm, *n* = 32 years; see Lopez de Casenave 2001 for a more detailed description).

We studied three species of sparrow: the Many-coloured Chaco-Finch (*Saltatricula multicolor*, hereafter MCCF), the Ringed Warbling-Finch (*Poospiza torquata*, RWF) and the Rufous-collared Sparrow (*Zonotrichia capensis*, RCS). All three species were formerly in the family Emberizidae but the MCCF and RWF are now placed in Thraupidae (tanagers and allies; see Webster and Webster 1999; Lougheed *et al*. 2000; Klicka *et al*. 2007). All species are core species of the Ñacuñán avifauna and are present throughout the year (Lopez de Casenave 2001; Lopez de Casenave *et al*. 2008). During the non-breeding season, all three species are mainly granivorous; in the breeding season, the RWF completely changes its feeding behaviour to

become almost exclusively insectivorous, but the other two species remain primarily granivorous, although they may include other food items in their diet (see Lopez de Casenave 2001; Lopez de Casenave *et al*. 2008; Marone *et al*. 2008; Milesi *et al*. 2008).

Survey methods

We conducted capture and observational surveys of the three species during spring (late November), summer (mid-February), autumn (mid-May) and winter (early August), from the spring of 2004 to the winter of 2009, except for the autumn of 2009 (a total of 19 survey periods). Birds were captured in mist-nets (12 m long, 38 mm mesh), arranged in three parallel lines of 10 nets (total of 30 mist-nets) each 50 m apart on a permanent 10-ha plot within the Mesquite woodland. Nets were opened for 4–5 h after sunrise on 6 consecutive days provided that weather conditions were not adverse (i.e. not rainy, windy or extremely cold or hot). Mean sampling effort per survey period was 735.2 ± 18.5 mist-net hours ($n = 19$ survey periods).

Birds were classed as juveniles (i.e. fledglings that were likely to have been produced at the site) or as adults. In RCS, adults have a rufous hindneck-collar, grey half-crest and cheeks, black head-stripes, and clean greyish breast and abdomen; whereas juveniles lacks grey and rufous, hindneck-collar and head-stripes are brown, and have dark-mottling on the breast and abdomen. In RWF, adults have a black collar (typically wider and darker in males than in females) and clean white breast and abdomen, whereas juveniles have only a few yellow or grey feathers on the collar and dark mottling on the chest and abdomen. In MCCF, juvenile and adult plumages are very similar, although the black facial mask is slightly less distinct in juveniles, but the colour of the bill is pale yellow in juveniles and bright yellow in adults. Juveniles of all species could also be distinguished by soft, swollen and yellow gape at the base of the bill. We are aware that some of these features may be also shown by adults or subadults (e.g. inconspicuous collars in the RWF, pale beak in the MCCF) so a birds with these characteristics was only classed as juvenile when it also showed soft gape at the base of the bill. In cases where a bird could not be aged unequivocally, it was classed as an adult.

Subspecies of RCS are generally morphologically indistinguishable (Handford 1985) and have not shown genetic correlates (Lougheed *et al*. 2013). However, we identified three classes of RCS based on the pattern of their head plumage (particularly the paired black lateral stripes on each side of the crown) and size: Group 1 – heavy birds (mean = 19.1 g, range 15.3–25.0 g, n = 228) without black lateral crown-stripes, and with longer wings (mean = 77.5 mm, range 70–85 mm, n = 228); Group 2 – heavy birds (mean = 19.8 g, range 16.8–23.0 g, n = 86) with thin lateral crown-stripes (1– 2 mm wide) and longer wings (mean = 77.7 mm, range 71–88 mm, n = 86); and Group 3 – lighter birds (mean = 17.8 g, range 14.5–22.5 g, n = 374) with thick black lateral crown-stripes (generally >3 mm wide), and shorter wings (mean = 73.6 mm, range 65–82 mm, n = 374). These groups appear to correspond with several subspecies of RCS (Chapman

1940; Keve and Kóvacs 1971; King 1974; Handford 1985; Piloni 2002): Group 1 comprises *Z. c. australis*, and Group 2 has features of *Z. c. choraules*. Group 3 has characteristics intermediate between those of *Z. c. choraules* and *Z. c. hypoleuca*. Eight museum specimens from eastern Mendoza Province were *Z. c. choraules* (all collected before 1980), and the contact area subspecies *choraules* and *hypoleuca* is in San Luis Province, east of Mendoza (Piloni 2002). Whether the wider lateral crown-stripes and shorter wings of birds in the Group 3 compared with corresponding measurements typical of *Z. c. choraules* are a result of latitudinal variation, as previously suggested (King 1974), or the result of expansion of the presumed contact area with *Z. c. hypoleuca* is not known and beyond the scope of this study. For the purposes of this study, and to distinguish the three groups present at the study site, we classified Group 1 as *Z. c. australis* (hereafter RCSa), Group 2 as *Z. c. choraules* (RCSc), and Group 3 as *Z. c. hypoleuca* (RCSh), but we are aware that the taxonomy of the latter needs to be clarified.

Individual MCCF, RWF and RCSh captured for the first time were banded with individually numbered aluminium bands (Aves Argentinas, Buenos Aires, Argentina) and unique combinations of coloured bands (A. C. Hughes, Hampton Hill, United Kingdom). Individuals of RCSa and RCSc were colour-banded only during the autumn and winter of 2005 owing to their high abundance, low rate of recovery, and the logistics of the limited number of colour combinations available for individual identification. We decided to give priority to the individual marking of RCSh.

After the 6-day mist-netting period, we conducted intensive daily searches for banded birds in the permanent 10-ha study plot and for 50–100 m beyond its boundaries (a minimum total search area of 18 ha) during the first 4 h after sunrise and the last 2 h before sunset, for a minimum of 10 days or until no new banded individuals were seen after 10 h of searching. The mean search effort per survey was 51.3 ± 5.4 h ($n = 19$ survey periods). Searches were conducted by systematically walking through the search area at least once per day. We also included data from individuals relocated outside of the study plot (two other 10-ha plots, used for other studies, 800 m from our plot) and in the vicinity of the research station (350 m from our plot), where we searched occasionally (at least twice per survey period).

Site-attachment of birds

We determined locations and movements of birds from both recaptures in mist-nets and resighting of colour-banded individuals, which we term collectively as resightings. This could underestimate the values of relocation for RCSa and RCSc because resightings would only include mist net captures. However, over the entire study we only resighted three individual RCSa or RCSc with aluminium bands and, when considering only mist-net recaptures, found that relative differences in recapture rate of species or subspecies remain the same, despite

relocations being lower. Analyses of data for adults and juveniles were undertaken separately. Birds initially banded as juveniles that remained in the study area for 1 year were then treated as adults.

For our analyses, we included only resightings from survey periods after that in which an individual was first captured, and we did not include individuals first captured in the last year of the study (i.e. spring 2008, and summer and winter 2009). Our first step in evaluating site-attachment for each species, subspecies and age-class was to calculate the total number of resightings for each class and species or subspecies as a percentage of the total number of birds captured for that class and species or subspecies (total resightings). To estimate the proportion of birds resighted at least once (probable residents that remain at the site), we recalculated the percentage of resightings of adults of each species and subspecies but excluding individuals that were never relocated (probable transients). To evaluate within-season persistence of adult birds during the breeding and non-breeding seasons we calculated the proportion of birds that were encountered at the beginning and at the end of either the breeding or non-breeding season (e.g. within-breeding season persistence is the percentage of birds captured or relocated during the spring that were also recorded during the following summer as a percentage of the birds captured at the spring). For this calculation, we pooled the data from each season for the entire study. Finally, to evaluate the turnover of individuals between the breeding and non-breeding season, we calculated the proportion of birds present during the breeding season that were resighted during the subsequent non-breeding season, and proportion of birds present during the non-breeding season that were resighted during the subsequent breeding season (e.g., turnover of birds from the breeding to the non-breeding season is the number of birds resighted during the breeding season that were also resighted during the following non-breeding season as a percentage of the birds captured during that breeding season). We assessed turnover for all adults of each species that were captured and for those birds that were recorded as owners of territories. Territorial birds were defined as those adult birds inside the plot or adjacent to the plot that were seen consistently singing or with a consistently singing mate in a fixed area at least during one breeding season of the study.

Data analysis

To evaluate differences in overall and within-season resightings in species and subspecies, differences in within-season resightings between breeding and non-breeding seasons, and differences in juvenile relocations between species, we performed either a Test for Differences for Two Proportions (Tests DTP), Test for Differences for More than Two Proportions (Tests DMTP) or Multiple Comparisons for Proportions (Zar 2010). To compare turnover between seasons we used a two-way analysis of variance (ANOVA; season × species), and *post hoc*

Tukey comparisons when needed. Data were log-transformed to meet the assumptions of normality and homoscedasticity.

Results

We captured a total of 1229 individual adult birds (excluding recaptures; Table 1). RCSh, RWF and MCCF were present throughout the year (Table 1), and are considered resident species or subspecies; RCSa and RCSc were present only during the non-breeding season (Table 1), and are considered as migrant subspecies. The two migrant subspecies had similarly low values for the proportion of total resightings (Table 1; Test DTP: $\chi^2_1 = 3.18$, $P = 0.074$) and a similarly low tendency to remain at the study site in the non-breeding season (Table 1; Test DTP: $\chi^2_1 = 1.94$, $P = 0.164$). Values for the proportion of total resightings differed between the resident species and subspecies but values were higher and more similar when transients were excluded from the analyses (Table 1). Abundance of RWF and RCSh was greater, and site-attachment lower, within the non-breeding season than within the breeding season (Table 1; Test DTP: RWF $\chi^2_1 = 10.65$, $P = 0.001$; RCSh $\chi^2_1 = 9.58$, $P = 0.002$), but abundance and site-attachment of MCCF were similar in the breeding and non-breeding seasons (Table 1; Test DTP: $\chi^2_1 = 1.08$, $P = 0.298$). Further, few RWF and RCSh present during the non-breeding season remain in the area until spring, whereas more individuals present during the breeding season remained in the area the rest of the year (Fig. 2a). In contrast, MCCF were equally likely to be recorded throughout the year (Fig. 2a). However, considering only territorial individuals (see Methods), turnover of individuals between seasons was lower (Fig. 2a cf. Fig. 2b), and the pattern was the same for the three resident species or subspecies (Table 2; no interaction).

We captured a total of 149 juveniles (48 MCCF, 62 RWF, 39 RCSh). Six juvenile MCCF (12.5% of those captured) were resighted at least once after first capture (two after the first year), and four (6.5%) juvenile RWF and one juvenile RCSh (2.6%) were resighted (none seen after first year). There were, however, no significant differences in resightings between species (Test DMTP: $\chi^2_2 = 2.30$, $P = 0.224$).

Discussion

The high level of site-attachment of territorial individuals at Ñacuñán throughout the year strongly suggests resident populations of MCCF, RWF and RCSh. However, the lower levels of site-attachment of RWF and RCSh during the non-breeding season needs closer analysis (see below). We also found two subspecies of RCS (RCSa and RCSc) were present only in the non-breeding season (autumn–winter). There were few resightings of juveniles of any species (near 0 after 1 year), suggesting they have either higher mortality than adults or low fidelity to their natal sites. Studies of tropical populations of RCS have found low persistence of juveniles, which tend to disperse in search of new areas to establish territories or fill territorial vacancies

within established territories in their natal areas (Miller and Miller 1968; Handford 1980). There are, however, no published studies of temperate South American populations of juvenile RCS or the other species studied here. At the end of the summer, we twice observed small groups of presumed young MCCF (with duller plumage and bills) and, on several occasions, we observed aggressive interactions between territorial males and juveniles within their territories (at least for MCCF and RCSh; M. C. Sagario, pers. obs.). These aggressive interactions, together with the high level of territorial fidelity and survival of adults of the three species at the site (Sagario 2011) may be promoting a high rate of dispersal of juveniles to other areas (Greenwood and Harvey 1982; Wheelwright and Mauk 1998; Fajardo *et al*. 2009).

Large numbers of the two migrant subspecies, RCSa and RCSc, were observed foraging actively in the study site during the non-breeding season, often in mixed flocks with the other species and subspecies we studied, but these birds left to breed elsewhere in spring–summer. These subspecies have been considered both long- and short-distance migrants, breeding in Patagonia (with RCSa breeding as far south as Tierra del Fuego, and RCSc breeding in Neuquén and Río Negro) but leaving these breeding areas during the non-breeding season (Chapman 1940; King 1974; Ortiz and Capllonch 2011). The occurrence of population partial migration involving resident and migrant subspecies has been documented for many South American tyrant-flycatchers, with resident subspecies in the tropics and migrant subspecies moving between temperate and tropical regions (e.g., *Myiarchus swainsoni*, *Tyrannus melancholicus*, *T. savana*, see Joseph et al. 2003; Stiles 2004; Jahn et al. 2010). Our results show that partial migration, with resident and migrant subspecies, may also involve resident subspecies in south-temperate latitudes, as we found two migrant subspecies of RCS (RCSa and RCSc) and a resident subspecies (RCSh) occurring at the study site. Further, influxes of RWF and RCSh to the study site during the non-breeding season but which do not subsequently breed there suggests that there may also be partial migration within these species and subspecies. The occurrence of resident populations of RWF and RCSh was confirmed by both the presence of territorial individuals and, when transients were excluded, the similar values of site-attachment to those of MCCF, which showed little change in abundance and site-attachment between the breeding and non-breeding seasons. The fluctuations in abundance in RWF and RCSh in Ñacuñán seem to be mostly associated with the high proportion of transient individuals, as suggested for an assemblage of insectivorous birds in a tropical semi-arid environment (Poulin *et al*. 1993), indicating that the seasonal variation may be caused by the movement of individuals between different areas. The differences in site-attachment between seasons that we observed may have also resulted from mortality of adults and emigration of juveniles (Newton 1998), particularly if most mortality occurred during the non-breeding season or if we were unable to identify dispersing juveniles (and thus treated them as adult birds). Inter-annual

survival among breeding adults of the three species was high and similar throughout the study period (Sagario 2011), and we have no *a priori* expectations that mortality among non-breeding birds may be so differentially high. Also, site-attachment of juveniles did not differ between species (this study). Hence, although levels of site-attachment may be underestimated during the non-breeding season, we believe this bias would not be enough to explain the large seasonal and between-species differences we observed.

We were not able to determine whether the influx of individuals to the study site during the non-breeding season derived from local movements or movements from more remote areas. Because the study area is only a small patch within the potential range of these birds, the large number of new individuals occurring at the site may result from local movements of birds, especially because these birds usually forage in highly mobile flocks during the winter (Marone 1992*a*; MCS, VRC and JLdC, pers. obs.). Some banded birds were resighted outside the study plot during winter, mainly at sources of water, indicating local movements are occurring. However, we did not resight banded birds far from the plot during the breeding season, implying birds banded during the non-breeding season may not be breeding locally (Sagario 2011). Further, in later surveys of marked birds in three plots 800–3000 m from each other over 3 years, we never recorded adults at a site other than that in which they were captured (A. Zarco, V. R. Cueto and M. C. Sagario, unpubl. data), which suggests that few birds, if any, are moving locally in the non-breeding season. We therefore suggest that as well as resident populations of RWF and RCSh, which remain in Ñacuñán throughout the year, other individuals of these species undertake large-scale movements during the non-breeding season.

Movements of arid-zone granivorous birds in response to the availability of seeds have been observed in Australia (Davies 1984; Dean 2004; but see Dingle 2008) and Africa (Dean 1997, 2004). In South America, a correlation between the abundance of granivorous birds and the availability of seeds during the non-breeding season (winter) has been found at several sites in the Monte Desert (Marone 1992*b*; Blendinger and Ojeda 2001), and Cinnamon Warbling-Finches (*Poospiza ornata*) in Argentina may also undertake movements in response to the availability of seeds (Marone 1992*a*; Cueto *et al*. 2011). RWF and RCS observed during this study may also be moving within the Monte Desert in winter in response to the availability of seeds. Further, both RWF and RCS have wide geographical distributions that extend beyond the Monte Desert, and changes in occurrence and abundance of these species have been reported in ecoregions adjacent to the Monte Desert, such as the Chaco (e.g. Capurro and Bucher 1988; Codesido and Bilenca 2004); birds may be moving to or from those areas into the Monte Desert. Overall, however, we do not know either the destination or origin of birds moving through our study site, and can say only that the species are mobile but their patterns of movement are not known (Chan 2001).

The rather mild and predictable climate of Ñacuñán and the Monte Desert may favour the occurrence of resident populations of the three granivorous species we studied (Blendinger 2005a). In addition, the more extreme temperatures of locations further south of Ñacuñán and the high abundance of seeds during autumn–winter in Ñacuñán (Marone and Horno 1997; Marone et al. 1998) may support the influx of mobile individuals of RWF and RCS (RCSh, RCSa and RCSc) and other granivores (e.g. *Phrygilus carbonarius*, *P. gayi*, *Catamenia analis*) during autumn–winter. In 2009, the mean abundance of seeds in the study site dropped dramatically, from $13\,240 \pm 1038$ seeds m^{-2} ($\pm$s.e.) in 2005–08 to 494 seeds m^{-2} (Sagario 2011). Although we have no data for autumn 2009, in winter 2009 we did not capture a single RCSa or RCSc, and the numbers of RWF and RCSh captured were much lower than in previous years (RWF: 27.8 ± 7.4 individuals (in winter 2005-08) and four individuals in winter 2009; RCS: 65.8 ± 15.4 individuals (in winter 2005-08) and 13 individuals in winter 2009). Further, in searches for banded birds in the study site, we recorded unbanded and banded individuals of the resident species and subspecies but no RCSa or RCSc. Hutto (1985) found that transient insectivorous birds in semi-arid Arizona may 'test' food abundance in several patches before deciding to stay in one of them or to move on. Also, the movements of many granivorous birds were suggested to be a function of food abundance in Australia and Africa (Dean 2004). Thus, variation in climate and abundance of resources may in turn promote inter-annual changes in the density and occurrence of both granivorous and insectivorous birds in the Monte desert (e.g. Marone 1992b; Lopez de Casenave 2001; Blendinger and Ojeda 2001; Blendinger 2005a; Cueto et al. 2008; Sagario 2011, this study) as well as their low wintering and breeding site-fidelity (Jahn et al. 2009; Cueto et al. 2011; M. C. Sagario, V. R. Cueto and J. Lopez de Casenave, unpubl. data).

The 'winter-crowding' of resident and mobile individuals in South America was noted long ago (Zimmer 1938) and has been observed for granivorous birds at sites in the Monte Desert and Chaco region (e.g. Blendinger 2005a; Capurro and Bucher 1988; but see Codesido and Bilenca 2004). The overlap of resident and migratory species or subspecies in winter was a driver of much research into the Afro-Tropical migration system and a search for interspecific differences that might provide evidence of niche-partitioning and characteristics that could explain costs and benefits of mobile or sedentary strategies (see Salewski and Jones 2006 for a review). For example, benefits of residency include earlier onset of breeding (Dingle 2008; Newton 2008) and maintenance of territories (Hinde 1956; Stamps 1987; Dearborn and Wiley 1993). Advantages of a mobile strategy include movement from unfavourable conditions, presumably based on efficiency in exploring new environments (but see Shochat et al. 2002), and opportunistic exploitation of resources as an ultimate or proximate result of wider diets, higher rates of consumption, and morphological differences (Salewski et al. 2003; Salewski and

Jones 2006; Newton 2008). Of the species we studied, MCCF have low aerodynamic efficiency for long-distance flight (Blendinger and Ojeda 2001), a restricted seed diet in the field (Marone *et al*. 2008) and high selectivity for seeds of grasses in laboratory experiments (Cueto *et al*. 2006). RWF also have a restricted seed diet during the non-breeding season (Marone *et al*. 2008), mainly taking seeds from panicles, but during the breeding season completely change feeding behaviour to forage almost exclusively for foliage insects (Lopez de Casenave *et al*. 2008; Milesi *et al*. 2008). RCS has a broader granivorous diet than MCCF and RWF (Marone et al. 2008) and preferred seeds of both grasses and forbs in laboratory experiments (Cueto et al. 2006). The broader diet of RCS may be explained by its higher tolerance to secondary compounds (at least in comparison with MCCF, Rios et al. 2012a; 2012b). RCS may also has higher rates of consumption than MCCF because, unlike MCCF, it has the capacity of encounter and consume seeds buried or trapped in litter (Cueto et al. 2013). It is not known, however, if differences in diet and foraging are related to the mobility of the species (Salewski *et al*. 2003). The relationship between diet and foraging and patterns of movements has not been studied in temperate South America . Our research indicates the taxa studied provide a useful system for comparisons between and within species in order to understand the processes and mechanisms that lead to mobile strategies at these latitudes of South America.

In summary, we have shown that populations of MCCF, RWF and RCSh are resident in the central Monte Desert, with juveniles of those species showing low site-attachment. Further, we also observed partial migration involving subspecies of RCS (RCSa, RCSc) and evidence of possible partial migration by both RWF and RCSh. Patterns of movement of passerine populations of semi-arid temperate South America have seldom been examined using marking and monitoring, and our results were consistent with expectations for the study region and the southern hemisphere in general. However, there are many questions left unanswered, including: the source of the large influx of birds that was recorded during winter and where they go after departure; whether juveniles move with migratory individuals in search of breeding opportunities elsewhere; whether there are behavioural or physiological differences between migrant and resident individuals during the non-breeding season; and whether those differences, if they exist, provide some competitive advantage. This lack of knowledge is true of most South American birds, and answers are difficult to obtain. The combination of increased local studies and collaborative large-scale studies are necessary for determination of the patterns of movements of avian species throughout their South American range, but detailed local studies identifying the patterns of movements of populations and the occurrence of resident and mobile individuals within such populations, can still provide the basis for the development of successful conservation strategies (Chan 2001; Faaborg *et al*. 2010), more appropriate assessment of the dynamics of populations (Newton 1998), and planning of comparative studies

to determine ecological, physiological or behavioural factors involved in the evolution of migration (Chan 2001; Jahn *et al*. 2006).

Acknowledgements

References

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Table 1. **Captures and relocations for adult individuals of three species of sparrows in the central Monte desert**

Number of captures and percentage of relocations during spring and summer (breeding season), and autumn and winter (non-breeding season) for Many-coloured Chaco-Finch (MCCF), Ringed Warbling-Finch (RWF), and three subspecies for the Rufous-collared Sparrow (see Methods for more details): *Zonotrichia capensis hypoleuca* (RCSh), *Z. c. choraules* (RCSc), and *Z. c. australis* (RCSa). Different letters indicate significant differences (Test for Difference between More than Two Proportions and Multiple comparisons for Proportions when needed, p<0.05) between resident species / subspecies.

	MCCF	RWF	RCSh	RCSc	RCSa
BREEDING SEASON					
Number of new captures	57	99	132		
Within season relocations (%)	51.6	39.7	17.5		
NON-BREEDING SEASON					
Number of new captures	43	161	420	87	230
Within season relocations (%)	42.1	17.1	6.7	4.8	1.5
TOTAL RELOCATIONS (%)	35.5[a]	21.9[b]	11.8[c]	6.9	2.6
Excluding transients (%)	63.6[a]	42.3[a]	63.5[a]		

Table 2. **Comparison of between-season turnover of adult individuals of three species of sparrows in the central Monte desert**

Anova results for comparisons of between-season turnover of adult individuals for Many-coloured Chaco-Finch, Ringed Warbling-Finch, and Rufous-collared Sparrow (here refers to the subspecies *Zonotrichia capensis hypoleuca*; see methods for more details) including all the adult birds and only territory owners. For mean values and standard errors see Fig. 2.

Source of variation	MS	Df	F	p-value
ALL BIRDS				
Season	0.52	1	21.23	<0.001
Species	0.49	2	19.89	<0.001
Interaction term	0.20	2	8.09	0.003
Error	0.02	18		
TERRITORIAL BIRDS				
Season	0.10	1	8.03	0.011
Species	0.002	2	0.20	0.818
Interaction term	0.01	2	1.02	0.379
Error	0.01	18		

Fig. 1. Map showing the location of the Biosphere Reserve of Ñacuñán (Ñ) in the Monte desert
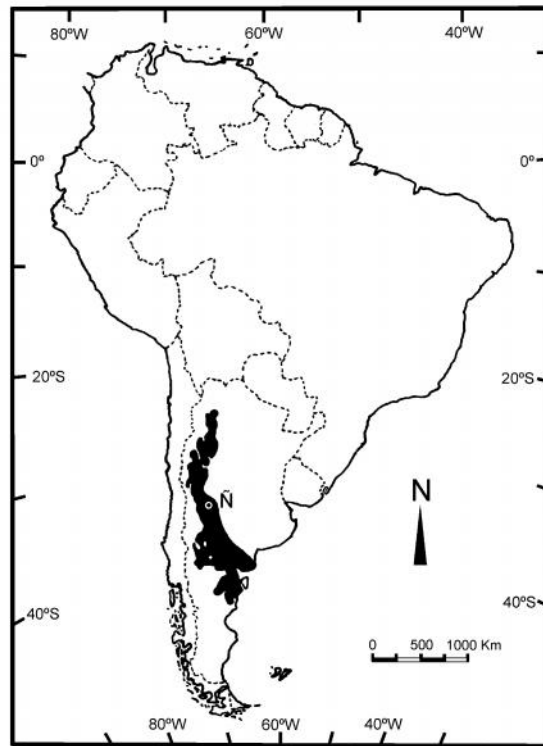
of Argentina (black area).

Fig. 2. Between-season turnover of individuals of three sparrow species in the central Monte desert including all the adult birds (A) and only territory owners (B). Values are percentages (Mean ± S.E.) of individuals present during one season (non-breeding or breeding season) that were relocated during the following season (breeding or non-breeding season, respectively). Rufous-collared Sparrow here refers to the subspecies *Zonotrichia capensis hypoleuca* (see methods for more details). Note scale differences between (A) and (B). Different letters indicate significant differences (*post hoc* Tukey comparisons p <0.05, see Anova results in Table 2).