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Seasonal interchange of the European Robin *Erithacus rubecula* populations in an evergreen holm oak forest

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Abstract. European Robins are found at "La Font Roja" Natural Park in SE Spain throughout the year. Analysis of recaptures of individually marked birds during 3 years strongly suggests that individuals breeding in the park abandon it during the winter, while a new wintering population occupies the park between November and March. We found that during 5 weeks in April and 3 weeks in October the two populations overlapped. We also analysed the biometry of the "local" (breeding) and "wintering" populations. The local population had significantly shorter wings, and longer tails and tarsi than the wintering population. In both populations, juveniles had shorter wings and longer tails than adults, but tarsus length did not differ between age classes. Among the local birds, males had longer wings and tails than females, but tarsus length did not differ between sexes (sex could not be determined in the wintering population). Biometric analyses supported the hypothesis of the occurrence of two separate populations in the study area, and also that the migratory tendency (as derived from wing and tail lengths) was higher among the wintering birds.

Key words: European Robin, *Erithacus rubecula*, biometry, flight-related morphology, migratory tendency, population replacement, wintering quarters

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INTRODUCTION

Mediterranean habitats constitute the wintering quarters of many birds breeding in central and northern Europe (Tellería 2004). Some of these wintering species have also breeding populations in the Mediterranean region, and the possible interactions between breeding and wintering individuals has recently received some attention (Pérez-Tris & Tellería 2002, Tellería & Pérez-Tris 2004). A consequence of both the migratory movements and the interactions between wintering and local (breeding) individuals is that a particular species could be present throughout the year in an area, but individual birds could change because of the arrival of immigrant ones (e.g. to overwinter) and possible departure of part or all of the local individuals. Therefore, if a species is

present in a particular habitat along the year, we might consider four possibilities (see e.g. Tellería 2004). First, only one (resident) population is present at the target habitat, while possible wintering individuals arriving to the region distribute over other habitats (i.e. breeding and wintering populations do not mix). In this case, individuals could be recaptured at any time along the year and, accounting for sex and age class differences, biometric measurements would have approximately normal distributions and relatively small variances. Secondly, there is a resident population, which receive individuals from other populations during winter. In this case, resident individuals could be captured all year round, while wintering ones (probably biometrically different from residents) could be captured only during the winter. Also, the distribution of biometric measurements

would tend to lose normality, and the variance in at least some of the measurements would increase. Another possibility is that there is a local population, part of which is displaced from the site during the winter by incoming competitively superior individuals. In this case, expected results would be similar to the previous case, but resident individuals captured during the winter would be a biased sample (in terms of sex or age ratios, biometry) of the population found in spring and summer. Finally, it is possible that there is a breeding population which abandon the area during the winter, being replaced by individuals arriving to the area for wintering. In this case, we would expect to have two groups of individuals temporally separated, so recaptures would occur either during the spring-summer period (for breeders) or during the autumn-winter (for wintering individuals). Breeding and wintering birds could also differ in biometric characteristics.

The European Robin (Robin hereafter) is a common species with western Palaearctic distribution, having the southern limit of its breeding area in North Africa. Northern populations are completely migrant, intermediate populations (the British Islands, central Europe) are partially migrant, and the species is resident in the southern part of its breeding area (Cramp 1988, Adriaensen & Dhondt 1990, Pérez-Tris et al. 2000b). Among partially migratory populations, females are more prone to migrate than males (Adriaensen & Dhondt 1990). Most populations from north and central Europe have their winter quarters in the Mediterranean basin (Cramp 1988). Thus, resident Robin populations of southern Spain receive northern individuals during the winter (Tellería et al. 1999, Pérez-Tris et al. 2000a, 2000b, Pérez-Tris & Tellería 2002).

This general picture could be fine tuned at a local scale, depending on the environmental characteristics of the place and on the populations which might reside at the site and arrive during the winter. Thus, the four possibilities described above, from having only one population throughout the year to having two distinct populations could in theory occur in Mediterranean habitats. To the best of our knowledge, the only study approaching this question with Robins has been done by J. L. Tellería, J. Pérez-Tris, and their co-workers (e.g. Tellería et al. 2001b, Tellería & Pérez-Tris 2004) in the Campo de Gibraltar, southern Spain, where the pattern found was that wintering birds arrive and displace part of the resident population to suboptimal habitats.

A basic aspect in this kind of studies is the ability to recognise individuals from different populations. To this end, mark-recapture data and biometry could be used. For example, mark-recapture studies are valuable to find out whether individuals are present at a study site during the target period (Belda et al. 2007). Also, different populations of the same species from different geographical regions are likely to differ in some morphometric characteristics (e.g. Tellería et al. 2001b, Campos et al. 2005).

At “La Font Roja” Natural Park, in SE Spain, Robins could be found throughout the year (Zaragozí & Izquierdo 2001, Cantó 2005). Traditionally, it has been thought that there was a single, resident population. However, any of the three other possibilities discussed above could theoretically occur at this area. Our target here was to determine the status of the birds present throughout the year, using recapture and biometric data from birds systematically captured along the year.

STUDY AREA AND METHODS

The study was performed at “La Font Roja” Natural Park, SE Spain (38°40'N, 0°32'W, 600–800 m a.s.l.). The park covers c.a. 2 300 ha and it is placed along a range with SW–NE orientation. The climate is Mediterranean, with a period of drought and high temperatures in summer and snow usually present in winter, from late November to early March. Mean temperatures are 4.2°C in January and 20.8°C in August (Ballester & Stubing 1990). Sampling was performed at the north face, where the dominant tree species was the Spanish holm oak *Quercus ilex* subsp. *rotundifolia*, with some deciduous tree species such as *Fraxinus ornus*, *Acer granatense*, *Quercus faginea*, *Sorbus aria* and *S. torminalis* scattered in the more humid areas. The undergrowth is well developed in most areas, including *Viburnum tinus*, *Amelanchier ovalis*, *Crataegus monogyna*, *Lonicera implexa*, *L. etrusca* and *Rosa* spp. Aleppo pines *Pinus halepensis* and traditional almond *Prunus dulcis* and olive *Olea europaea* plantations are found at the lowest parts of the park.

For the present study, Robins were captured at four different sites at the north slope of the park from January 2002 to September 2005. We used 5–6 mist nets 10 m long each, which were placed approximately once a week throughout the year and were open 4 h from sunrise each session.

The mean number of Robins captured per session per 100 m of net ($n = 4$ years, 2002–2005) was 7.1 ± 3.8 in January (an index of the wintering population) and 2.6 ± 0.9 in May (an index of the breeding population excluding young of the year).

Birds captured were ringed with individually numbered metal rings. Age class of the birds was determined by plumage characteristics (Jenni & Winkler 1994, Svensson 1996), discriminating between adults (birds having performed a complete post-nuptial moult; EURING codes 4 and 6) and “juveniles” (birds retaining juvenile feathers after their partial post-juvenile moult; EURING codes 3 and 5). Note that we include among “juveniles” all the birds until their first complete post-breeding moult.

Sex could be determined only during the breeding period using the presence of brood patch for females and cloacal protuberance for males. Therefore, both adult and “juveniles” (first-year breeders) could be sexed at this time. We took measurements of wing (maximum chord), 8th primary (P8), tail and tarsus length. Wing, P8 and tail length were measured with appropriate rulers to the nearest 0.5 mm, while the tarsus was measured with a digital caliper to the nearest 0.1 mm. All measurements were taken by the same author (JLC). In case of birds captured more than once, we used data taken at the first capture. P8 length was highly correlated with wing length, and the analyses involving this measure gave the same results than those including wing length, so they are not presented.

Mark-recapture data were used to explore the possible changes in the composition of the Robin population present at the park, determining periods of the year where the pool of birds present might differ. We used two-way ANOVAs to compare the biometric characteristics of different potential groups of birds, using group (population) and age class as factors. Sex could not be used in these analyses since it could not be determined outside the breeding period. We approached the possible biometric differences between sexes using birds captured during the breeding period, and sex and age as factors in two-way ANOVAs.

One of the possibilities was that the wintering population was a subset of the local population. Looking at previous results on other Robin populations (e.g. Adriaensen & Dhondt 1990), we explicitly tested the hypothesis that females might leave during the winter while males would stay.

In this case, biometric characteristics of local males should not differ from those of wintering birds.

Analyses were done with the SPSS 12.0 statistical package. Means are given \pm standard deviation (SD).

RESULTS

Mark-recapture data

We ringed 623 different Robins during the study period, and 66 of them were recaptured at least once. Most recaptures occurred within two annual periods clearly separated: birds first captured during autumn-winter (November to March) were never recaptured during spring-summer (May to September), while those first captured in spring-summer were no recaptured during autumn-winter (Fig. 1).

There were a few transitional weeks, also clearly separated, where an overlap occurred between these two groups of birds. One of them was in April (weeks 14 to 18) and the other in October (weeks 40 to 42).

Biometric differences between populations, age classes and sexes

Birds captured during spring-summer will be referred to as “local” birds hereafter, and those captured during autumn-winter as “wintering” birds. We excluded from the following analyses those birds captured at least once during the weeks where local and wintering birds overlapped (see above).

Wings were shorter in the local than in the wintering population (Table 1). However, both tails and tarsi were longer in the local population (Table 1). Wings and tails were shorter in juveniles than in adults in both populations, while tarsus length did not differ between age classes (Table 1).

Sex differences in biometry were explored in the local population, where adults and first-year breeders (“juveniles”) could be sexed (Table 2). Controlling for age, males had longer wings and tails than females (two-way ANOVAs, $F_{1,120} = 144.76$, $p < 0.001$). ($F_{1,113} = 24.96$, $p < 0.001$ respectively), while no significant differences were found in tarsus length ($F_{1,118} = 0.04$, $p = 0.84$). Controlling for age differences, wings, tails and tarsi were longer in local males than in wintering individuals (two-way ANOVAs: wing length: $F_{1,252} = 6.56$, $p = 0.011$; tail length: $F_{1,247} = 36.82$, $p < 0.001$; tarsus length: $F_{1,250} = 6.09$, $p = 0.014$; cf. Tables 1 and 2).

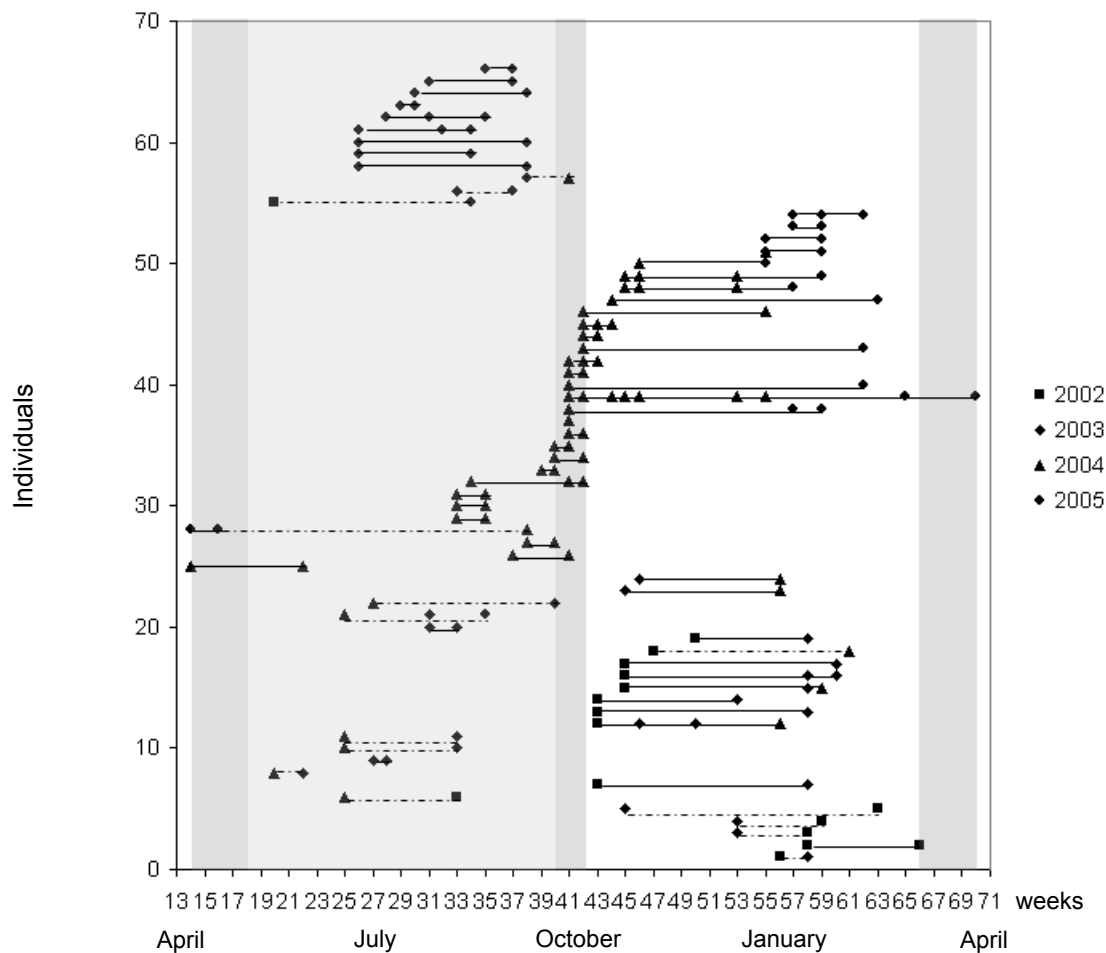


Fig. 1. Robins captured more than once at “La Font Roja” Natural Park between 2002 and 2005. The white band corresponds to the “wintering” period, the light grey bands to the “breeding” period, and the dark grey bands to the transitional periods. For the sake of clarity, we have duplicated the spring overlapping period (April) at the beginning and at the end of the graph; no bird trapped during the breeding period was captured during the winter or vice versa. Each line is a different bird and each symbol a capture event; a different symbol is used for each of the years of study. Solid lines join captures occurring during the same year, while broken lines join captures occurring at different years.

Table 1. Wing, tail and tarsus length (mean values \pm SD) of local and wintering European Robins at “La Font Roja” Natural Park, and results of the ANOVAs showing the effect of population (local/wintering), and age class (juveniles or adults) on these parameters. Sample size in parentheses, * — $p < 0.001$.

Population	Age class	Wing	Tail	Tarsus
Local	Juveniles	71.52 \pm 2.02 (298)	59.02 \pm 2.46 (294)	25.56 \pm 0.92 (296)
	Adults	72.51 \pm 1.73 (57)	59.67 \pm 2.89 (54)	25.75 \pm 0.71 (56)
Wintering	Juveniles	72.38 \pm 1.90 (132)	57.65 \pm 2.51 (132)	25.34 \pm 0.70 (132)
	Adults	73.62 \pm 2.07 (56)	59.00 \pm 2.31 (56)	25.06 \pm 1.07 (56)
Source of variation				
Population		$F_{1,539} = 21.64^*$	$F_{1,532} = 14.02^*$	$F_{1,536} = 23.74^*$
Age class		$F_{1,539} = 27.92^*$	$F_{1,532} = 13.51^*$	$F_{1,536} = 0.20$
Population x age		$F_{1,539} = 0.34$	$F_{1,532} = 1.68$	$F_{1,536} = 6.26$

Table 2. Wing, tail and tarsus length (mean values \pm SD) for the different sexes and age classes of local European Robins at "La Font Roja" Natural Park. Sample size in parentheses.

Sex	Age	Wing	Tail	Tarsus
Female	Juveniles	69.64 \pm 1.48 (39)	57.96 \pm 2.47 (38)	25.35 \pm 1.08 (39)
	Adults	70.94 \pm 1.50 (17)	58.50 \pm 1.03 (16)	25.81 \pm 0.80 (17)
Male	Juveniles	73.83 \pm 1.45 (46)	60.78 \pm 2.35 (43)	25.46 \pm 1.18 (45)
	Adults	73.59 \pm 1.41 (22)	60.67 \pm 3.42 (20)	25.61 \pm 0.74 (21)

DISCUSSION

Our results, both related to mark-recapture data and to biometry, clearly support the presence of two different Robin populations at "La Font Roja" Natural Park. One of the populations is formed by individuals that breed in the park and abandon it by October, while a different set of individuals arrive in the park by October to overwinter there, most of them leaving before next April. These results contrast with those from the other area for which this kind of data are available: in the Sierra de Ojén (southern Spain), local Robins stay at the area all year round, while wintering individuals arrive in by the autumn displacing part of the local Robins to peripheral areas (Pérez-Tris et al. 2000b).

Overlapping of the two populations at our study area occurred during two relatively short time windows. Peaks of pre- and postnuptial migration of Robins in Spain are detected in March and October respectively (Murillo & Sancho 1969, Bueno 1998, Tellería et al. 1999, J. Arizaga et al., unpubl. data). Thus, the autumn overlapping period found at "La Font Roja" adjusted well with the peak of the post-nuptial migration period of Robins in Spain, while the spring overlapping period was later than the peak, but still within the prenuptial migration period in Spain, which lasts from February to April (Bueno 1998, Tellería et al. 1999, J. Arizaga et al., unpubl. data). This strongly suggest that these are the periods when one population is leaving from and the other arriving to the study area, and both are related to migratory movements of the species.

Looking at the general picture of recaptures of this species in Spain (Bueno 1998), wintering birds are mainly coming from western Europe. However, we have no trapped any Robin ringed outside our study area, so the exact origin of the wintering population is unknown. Thus, we are talking about a wintering "population", but wintering individuals could come from different breeding populations or, on the other extreme, the birds wintering at "La Font Roja" could be only

part of a single breeding population (for example, males or females). On the other hand, none of the Robins ringed by us in the park has been recaptured outside, so we do not know where they spend winter. Tellería et al. (2001a), based on the analysis of flight-related morphology, suggested that Robins breeding in Spanish highlands may only make short, altitudinal movements to overwinter in nearby lowlands. Therefore, birds breeding at "La Font Roja" might be doing either local movements (e.g. altitudinal movements within the general area) or longer migrations towards southern areas.

Tellería et al. (2001b; see also Tellería & Pérez-Tris 2004) found that Robins arriving to winter at the Sierra de Ojén (S Spain) displaced part of the resident Robin population to peripheral areas. Especially, juveniles of the resident population were displaced from the forest areas (Pérez-Tris et al. 2000b, Tellería & Pérez-Tris 2004). They concluded that incoming wintering birds displaced competitively inferior juveniles from the forest areas, while adults were able to keep their territories throughout winter. It seems unlikely that a similar pattern occur in our study area since, during 3 years of weekly captures, no local bird was captured during any winter. Our data suggest that the local population left the park during the winter.

We could determine the sex and age class in the breeding population, and only the age class, but not the sex, of the wintering one. Since males were bigger (wing and tail length) than females, the possibility existed that the wintering population was composed mainly by males. Differential migration of the two sexes has been described in some passerines, with the proportion of females in the wintering areas increasing towards the south (reviewed by Cristol et al. 1999; see also Catry et al. 2005), and unbalanced sex ratios have been found in migrating and wintering Robin populations (Adriaensen & Dhondt 1990, Bueno 1998, Catry et al. 2004, J. Arizaga et al., unpubl. data). We do not think, however, that our data would support a wintering population mainly

formed by males. First, wing length was longer in the wintering than in the local population, but tail was shorter, against what would be expected. Second, tarsus length differed between wintering and local population, while it did not differ between sexes in the local population. Third, when explicitly comparing the biometry of local males with that of wintering birds, there were significant differences in all the three biometric parameters considered. As we shall see below, all these results are more coherent with an explanation involving populations with different migratory habits than with populations with different sex ratios.

Pérez-Tris & Tellería (2001) explored the relationship between wing shape, age and migratory tendency in Blackcaps *Sylvia atricapilla*. They found that migratory Blackcaps had longer and more pointed wings than sedentary ones, while juveniles had shorter and more rounded wings than adults in the migratory population but not in the sedentary one. The reason, they suggested (see also references therein), is that the main selection pressure acting on sedentary birds and migratory young would be the risk of predation, so a morphology which maximizes manoeuvrability (short rounded wings) would be favoured. However, the main pressure acting on migratory adults would be the challenges associated with long migratory flights, so long pointed wings would be favoured. Tail length is another key morphological trait to be taken into account when studying flying performance (e.g. Norberg 1995, Leisler & Winkler 2003). Thus, a combination of long and more pointed wings and short tails reduces energy consumption and increases speed (Mönkkönen 1995, Norberg 1995), which is crucial for long-distance migrants, while short rounded wings and long tails favoured manoeuvrability, important to avoid predation (e.g. Swaddle & Lockwood 1998). If this is true, we could hypothesize that the wintering Robin population of “La Font Roja” (longer wings, shorter tails) would make longer migratory movements than the local one. This is also consistent with the general migration pattern of the species, since birds arriving to winter at “La Font Roja” could come from northern Europe (e.g. Bueno 1998), while birds breeding at “La Font Roja” could move much shorter distances (i.e. to North Africa at the most). Alternatively, local birds might be only performing short altitudinal movements to nearby lowlands.

Pérez-Tris & Tellería (2001; see their Fig. 4), using Blackcaps as a model, suggested that optimal wing length would be similar for adults and

young in sedentary populations, while differences between adult and young wing length optima would increase progressively as the migration distance of the population increases. Our analysis showed that adults had longer wings than juveniles in both populations, but the difference was slightly larger in the wintering population (1.24 mm) than in the breeding one (0.99 mm, Table 1). Though these differences are not significant, they are in the expected direction, and again suggest that both populations would be migratory, and that the breeding one probably engages in shorter migration distances.

Results are more puzzling, however, for tail length measurements. If flight-related traits would be shaped by different selection pressures on adults and young, we would expect short wings to be related to long tails and long wings to short tails (e.g. Pérez-Tris et al. 2003, Winkler & Leisler 2005). Our data fitted this prediction at the between population level — the (probably) more migratory wintering population had longer wings and shorter tails than the (probably) less migratory local one. But, within populations, we would expect juveniles to have longer tails, and this difference to be more pronounced in the wintering population. Results were just the opposite: adults had longer tails in both populations, and differences were higher between adult and juvenile wintering Robins. Thus, at least at the within-population level, pressures other than flight performance should be behind the age-related differences in tail length, and perhaps the lower general investment of juveniles in plumage quality (e.g. Jenni & Winkler 1994), could better explain them. On the other hand, tail morphology is usually acknowledged to be less shaped by migration pressures than wing morphology (e.g. Winkler & Leisler 1992), and other aspects of the life style of the bird could be more important in shaping it.

In conclusion, we have two clearly separated Robin populations which are found at “La Font Roja” Natural Park in two different periods of the year, a local (breeding) and a wintering population, which overlapped during the pre- and post-nuptial migratory periods. To our knowledge, this is the first time that this temporal replacement of local and wintering populations is described in a passerine bird.

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STRESZCZENIE

[Okresowa wymiana populacji rudzika w zimozielonych lasach dębu kolcolistnego].

Badania prowadzono w rezerwacie “La Font Roja” w pół-wsch. Hiszpanii, w którym rudziki występują przez cały rok. Ptaki łapano były w latach 2002–2005 (łącznie 623 osobniki). Analiza ponownych złowień ptaków wskazuje, że ptaki gniazdujące w rezerwacie opuszczają go zimą, natomiast inna, zimująca populacja występuje na jego terenie w okresie listopad–marzec. Stwierdzono, że obie te populacje występują razem 5 tygodni w kwietniu i 3 w październiku (Fig. 1). Stwierdzono, że populacja lęgowa charakteryzuje się krótszymi skrzydłami, dłuższym ogonem i skokiem w porównaniu do ptaków występujących na badanym terenie zimą (Tab. 1). W obu populacjach osobniki młode miały krótsze skrzydła i dłuższy ogon niż ptaki dorosłe (Tab. 1). W populacji gniazdującej samce miały dłuższe skrzydła i ogon niż samice (Tab. 2).