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How do Robins *Erithacus rubecula* resident in Iberia respond to seasonal flooding by conspecific migrants?

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Capsule The majority of Robins in Iberia are sedentary and stay in their nesting areas despite the presumed increased competition that results from the seasonal flooding of the area by conspecific migrants.

Aims To evaluate if Robins in Iberia are displaced from their nesting areas by the presence of large numbers of competitors originating from higher latitudes.

Methods Data from constant effort ringing sites were used to estimate the proportion of Robins that are strictly sedentary and the seasonal variation in Robin numbers. Hydrogen stable isotope ratios ($\delta^2\text{H}$) in feathers, and sex ratios determined through molecular techniques, allowed an insight into the numerical importance of invading Robins from higher latitudes.

Results Robins were more numerous outside the breeding season, with clear influxes in autumn. Around half of the locally nesting Robins were captured during winter, indicating they are truly sedentary. $\delta^2\text{H}$ in feathers suggests that a wide mixture of Robins from all European latitudes were present in winter, and these data, together with sex ratios, suggest that there may be similar numbers of local and foreign individuals in winter at the main study site.

Conclusion Despite the occupation of their range by migrants, local birds are largely sedentary.

For many widely distributed bird species in the northern hemisphere, migratory and resident populations share common wintering grounds in the southern part of their range (Newton & Dale 1996). This raises questions about the way individuals from different geographic origins co-exist in a scenario of presumed increased intraspecific competition, resulting from the co-occurrence of several populations in the same areas (Cox 1968, Greenberg 1986, Pérez-Tris & Tellería 2002a).

Such questions have the potential to reveal insights into the evolution and maintenance of migratory systems and for the regulation of different populations (Bell 2005, Newton 2008).

Few studies have examined this issue at the local and individual level. For example, while it is often assumed that southern populations are mostly sedentary (with backing-up evidence from ringing recoveries), it remains unclear whether southern individuals are displaced by migratory conspecifics (for example, by moving to different habitats), or whether they manage

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to secure the winter sites of their choice despite increased levels of intraspecific competition.

Studies of Blackcaps *Sylvia atricapilla* and European Robins *Erithacus rubecula* (hereafter Robins) have documented that local populations largely hold onto their nesting habitats, while migrants predominate in habitats where no locals breed. While this pattern of (partial) population segregation has been clearly established (Tellería *et al.* 2001, Pérez-Tris & Tellería 2002a, Tellería & Pérez-Tris 2004), the studies inferred the breeding origins of previously unmarked individuals from morphological data and so responses at the individual level are uncertain (e.g. resident birds could still disperse within/between breeding habitats).

Robins are small (ca. 15–19 g) passerines with a range of movement strategies from year-round residents to long-distance migrants. They are common breeders in most of Iberia. In autumn, Robins from across much of Europe, particularly from the large Scandinavian and central European populations, move south to winter in Iberia and other Mediterranean areas (e.g. Cramp 1988, Bueno 1998, Remisiewicz 2002). Both migratory and resident birds often defend individual territories during the non-breeding season, while others behave as floaters. In mostly non-migratory populations, some adult Robins move from the nesting territories once the reproductive season is complete, either just before or just after the post-breeding moult (Cramp 1988). Juveniles can settle into winter territories either before or after the adults (Cramp 1988). During winter in Iberia, Robins feed on a mixture of invertebrates and fruits such as berries and acorns (Herrera 1977, 1998).

A recent study in mountain habitats of SE Spain showed that, in an area where Robins are present year-round, nesting individuals seasonally disappeared during the autumn–winter and were replaced by conspecifics from more migratory populations (Domínguez *et al.* 2007). These findings raise the question of whether southern resident populations generally are truly sedentary, or whether they get shifted around as a result of increased intraspecific competition caused by the arrival of migrants and by changes in available resources. Ringing data suggest that individual Iberian Robins can be strictly sedentary, while populations from more seasonal environments, such as mountains, show a greater tendency to move (Pérez-Tris & Tellería 2002b). However, there is little information on the relative numbers of truly sedentary birds in Iberian habitats. Could their spatial ecology be more similar to Robin populations in Ireland and Great Britain, where little seasonal flooding takes place and where many Robins

stay on the same site all year round (Burkitt 1926, Lack 1943, Jackson 1958, Wernham *et al.* 2002), or is the pattern described by Domínguez *et al.* (2007) the one that more widely applies to Iberian individuals?

In the present study we determined capture rates, sex ratios and stable isotope ratios in the feathers of nesting and wintering populations of Robins in Iberia. We show that, despite being seasonally confronted by large numbers of incoming foreign individuals, a large proportion of Iberian Robins remain on their breeding territories over winter. Previous studies of partially migrant Robin populations also found that altitude, or type of habitat of the nesting areas, can have a strong influence on the proportion of individuals that display a truly sedentary behaviour (Adriaensen & Dhondt 1990, Pérez-Tris & Tellería 2002b). In light of this we also assessed whether Robins from different sites vary in their propensity to move away from breeding territories in winter.

MATERIALS AND METHODS

Constant effort sites

Data were obtained from Bird Ringers (Bird Banders) participating in the Portuguese Constant Effort Site bird ringing programme, in which ringers trap birds regularly (about every 2 weeks) using mist-nets at specific study sites. Net placement and capture effort are kept constant in trapping sessions that are regularly distributed within the annual cycle. Trapped birds are ringed and recaptures recorded. Where possible, the age (juvenile versus adult) of the trapped individuals is determined. Brood-patch development is also recorded, which, in the case of Robins, allows the sexing of some individuals during the breeding season. The occurrence of wing-moult is also noted. For the present study, we used data from five constant effort sites (CES) where Robins were known to breed. Sites covered a range of latitudes, altitudes, and habitat types, and had been in continuous operation over a period of at least 36 months (Table 1).

Details on the location and sampling period of each CES are presented in Table 1. The main study site was at Mata da Margaraça, Serra do Açor, an area covered mostly by deciduous forest of oaks *Quercus robur* and chestnut trees *Castanea sativa*, with an undergrowth of several evergreen bushes, including *Arbutus unedo* and *Virburnum tinus*. Robins feed on the fruits of *Virburnum* in autumn and winter. Other study sites were: Parque Biológico de Gaia, a large suburban park with open

Table 1. Location, main habitat, and sampling period in each of the Constant Effort Sites (CES) included in this study.

Local	Location	Altitude (m a.s.l.)	Main habitat	Sampling period
Margarça	40° 12'N, 07° 55'W	500–600	Deciduous forest	March 2003–July 2007
Gaia	41° 05'N, 08° 33'W	60	Suburban park	October 2006–October 2009
Madriz	40° 07'N, 08° 38'W	25	Wetland margin	January 2004–July 2007
Azóia	40° 06'N, 08° 41'W	30	Abandoned Orchards	March 2002–July 2007
Tornada	39° 26'N, 09° 08'W	24	Wetland margin	January 2003–June 2007

lawns and woodland patches, mostly deciduous (*Quercus*, *Castanea*, *Alnus*), and diverse shrubs including *Rubus* spp., *Sambucus nigra* and *Frangula alnus*; Paul da Madriz, a wetland margin with willows *Salix atrocinerea* and brambles *Rubus* spp. fringing a large reedbed; Carvalhal da Azóia, an area of old abandoned orchards bordered with oaks *Quercus faginea*, pines *Pinus pinaster* and bramble edges; and Paul de Tornada, a wetland margin with willows and brambles fringing a reedbed area.

Complementary sampling

To compare the breeding and the wintering Robin communities, data from constant effort programs were supplemented at Margarça by trapping birds with mist-nets and baited spring-traps in January and June 2008. This took place after the cessation of the constant effort trapping at this site, and it did not interfere with the CES programme. Note that this sampling was made for purposes other than recapturing previously marked individuals and birds captured on these occasions were not used to study individual behaviour, but rather to assess social composition at the population level. Feathers (innermost secondary) and blood samples were collected. They were used for stable isotope analysis and for molecular sexing respectively. Because Robins grow secondary feathers on the nesting grounds and very rarely lose them accidentally (which would imply replacement growth), the isotope composition of the metabolically inert feather keratin reflects that of the breeding area. The hydrogen isotope (deuterium) ratios ($\delta^2\text{H}$) in rainwater (and in bird feathers) show a strong gradient across Europe, with a depletion occurring in a northeast direction (Hobson *et al.* 2004). Hence hydrogen isotope ratios provide a useful tool for avian migration research (e.g. Bearhop *et al.* 2005), as they can differentiate the geographical origins of birds.

We also took feather samples for isotope analyses from Robins from northern Europe, to help put isotope values from Margarça into context. Robins were sampled

during migration through the southern tip of Sweden at Falsterbo (55° 23' N, 12° 50' E), where migrant individuals originating from all over Sweden and (less so) from Finland occur during autumn (Karlsson *et al.* 1988). There have been many recoveries in Portugal of Robins which originate in Scandinavia, and these are likely to contribute to a large proportion of the wintering birds in Portugal (Bueno 1998, Catry *et al.* 2010). Trapping took place at Falsterbo on five different dates from mid-September to mid-October 2007, to ensure a broad coverage of the main migratory period. It is therefore likely that each of the 36 individuals sampled here came from a different breeding site.

Laboratory and data analysis

Feathers were washed, dried, finely cut, and then weighed (0.1 mg) into small silver capsules, and analysed for hydrogen isotope ratios ($\delta^2\text{H}$) using continuous flow isotope ratio mass spectrometry. Sexing from blood samples was done through the amplification by PCR (polymerase chain reaction) of a fragment of the *CHD* gene, using the primers P2 and P8 (Griffiths *et al.* 1998).

For analyses of site fidelity and residency we did not consider Robins that were captured only once at constant effort sites. Our aim was to exclude individuals that might be passing through on migration, engaged in post-breeding dispersal, or that were 'floaters' only incidentally visiting the CES. This procedure also helps to exclude (temporarily) resident individuals whose home range only marginally overlapped with the CES, hence making capture probability very low. Furthermore, for Robins captured more than once, we only considered birds that stayed at the study area for at least 21 days, to further exclude birds that might be just stopping over at the study site; studies of Robin migration suggest that most stopover durations are shorter than this (e.g. Polak & Szewczyk 2007). Finally, captures of young of the year during the period of juvenile dispersal (until the end of September) were not included in these analyses, as such individuals

might have chosen to settle permanently in areas outside the CES.

Based on the migration and breeding phenology of Robins in Portugal (Bueno 1998, Catry *et al.* 2010, this study) we divided the annual cycle into four periods: Winter, 1 November until 28 February; Spring (breeding season), 1 April until 31 July; the period between 1 and 31 March, and the period between 1 August and 31 October. The latter were defined as transitional and cover the main migration periods as well as much of the post-juvenile dispersal and adult moulting season.

Robins selected according to the above criteria were then classified into six different categories. (1) Sedentary: individuals that were captured both in spring and in winter; (2) Spring–single: individuals captured during one single spring season (and possibly also during a transitional period); (3) Spring–return: individuals captured in more than one spring season; (4) Winter–single: individuals captured during one single winter season (and possibly also during a transitional period); (5) Winter–return: individuals captured in more than one winter season; (6) Uncertain: individuals only captured in transitional periods. We were especially interested in comparing the numbers of individuals classified as Sedentary (1) and as spring visitors (the sum of individuals classified as Spring–single (2) and Spring–return (3)).

RESULTS

Captures were high in October and November, when the main autumnal flux of migrants was felt, and were particularly low in March–May, when few movements occurred and only local nesting birds were present (Fig. 1). The very first juveniles did not appear before May or sometimes June, with large influxes in July (at Madriz, reproduction appeared to be earlier, with many juveniles in May in each year). Juveniles, apparently in post-fledging dispersal, continued to be captured in August and September. Adults were recorded moulting flight feathers from June until mid-September.

At each of the five study sites, at least some of the Robins were apparently sedentary (Table 2). Overall, of the Robins that settled in the study area and were present in the breeding season (adding sedentary birds and spring visitors, $n = 66$), 52 % were also captured in winter (34 individuals classified as sedentary). Birds staying for winter, at each of the five sites, included not only adults, but also juveniles of the year that were

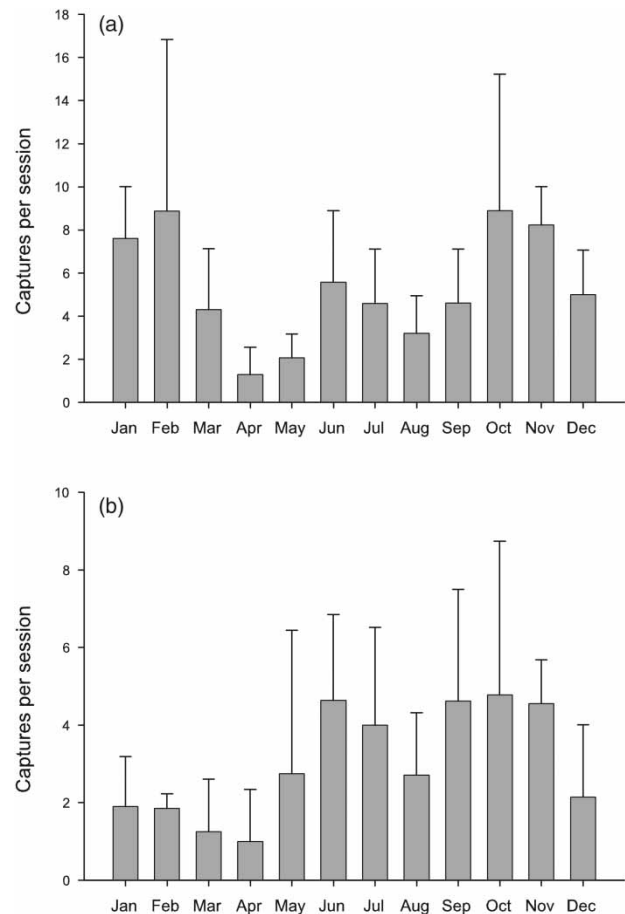


Figure 1. Monthly variation in the numbers (mean \pm sd) of Robins mist-netted at the two Constant Effort Sites (CES) with larger numbers of captures. Totals include both new captures and recaptures of birds ringed on previous occasions. Data from four years pooled. (a) Margaraça, (b) Madriz.

captured in their first summer (excluded from statistics presented in Table 2, see Methods).

Comparing Margaraça (500–600 m a.s.l.), where 33 % of the Robins that settled in the breeding season ($n = 27$) were classified as Sedentary (Table 2), with the other four (low-altitude) sites (64 % Sedentary, $n = 39$), a significant difference in year-round site fidelity was found (Fisher's Exact Test, $P = 0.024$). Among the low-altitude sites, there was no difference in the proportion of Sedentary birds found at the suburban park in Gaia (78 %, $n = 9$) versus the other habitats (69 %, $n = 26$; Fisher's Exact Test, $P = 1.0$).

Among birds that settled in winter (Sedentary plus Winter visitors), the proportion of birds classified as Winter visitors in Margaraça (81 %, $n = 48$) differed from the proportion of Winter visitors at the four other sites (61 %, $n = 64$; Fisher's Exact Test, $P =$

Table 2. Numbers of individual Robins captured at five Constant Effort Sites (CES) and classified in each phenological category. Figures in brackets represent numbers of sexed individuals (male : female). Male and female numbers do not add to total in categories because many individuals were not sexed.

CES	Sedentary	Spring–single	Spring–return	Winter–single	Winter–return	Uncertain
Margaracha	9 (4 : 1)	10 (3 : 5)	8 (3 : 2)	31	8	1
Gaia	7 (1 : 1)	0	2	4	2	1
Madriz	9 (2 : 3)	2 (0 : 1)	5 (2 : 3)	11	0	1
Azóia	3 (1 : 2)	2 (1 : 1)	2 (0 : 2)	6	4	1
Tornada	6 (3 : 1)	1 (0 : 1)	0	8	4	2
Total	34 (11 : 8)	15 (4 : 8)	17 (5 : 7)	59	18	6

0.024). Comparing Gaia (46 %, $n = 13$) with the other low-altitude sites (65 %, $n = 51$), no significant difference was found when considering the same statistic (Fisher's Exact Test, $P = 0.34$).

At Margaracha, the distribution of feather $\delta^2\text{H}$ values had a much higher dispersion in winter ($\delta^2\text{H} = -79.2 \pm 15.5$ ‰, $n = 57$) than in spring ($\delta^2\text{H} = -70.9 \pm 9.1$ ‰, $n = 37$; Homogeneity of Variance Test: Levene Statistic = 14.1, $P < 0.001$), with a clear increment of the proportion of Robins with more negative $\delta^2\text{H}$ values (Fig. 2). The winter feather $\delta^2\text{H}$ values from Margaracha also had a much higher variance than $\delta^2\text{H}$ values of Robins from Scandinavia ($\delta^2\text{H} = -93.5 \pm 8.1$ ‰, $n = 36$; Homogeneity of Variance Test: Levene Statistic = 21.5, $P < 0.001$).

Individuals sampled at Margaracha with more negative $\delta^2\text{H}$ values had longer wing-lengths (Pearson correlation: $r = -0.35$, $n = 57$, $P = 0.008$).

The sex ratio of Robins at Margaracha during winter was fairly even, with 55 % male ($n = 57$ sexed individuals). There were no significant differences in the variance or in the mean of isotopic composition of feathers of males ($\delta^2\text{H} = -78.4 \pm 13.2$ ‰, $n = 31$) and females ($\delta^2\text{H} = -81.1 \pm 17.6$ ‰, $n = 25$; Levene Statistic = 2.75, $P = 0.10$; ANOVA $F_{1,55} = 0.41$, $P = 0.5$). Among Robins that became sedentary during the wintering period, only 23 % were recorded in more than one autumn/winter (Table 2).

DISCUSSION

This study documents for the first time a geographically widespread sedentary behaviour by a passerine confronted with large numbers of conspecific visitors. Using an approach broadly similar to Domínguez *et al.* (2007), we have shown that their result of a full population interchange of Robins is not generally applicable in Iberia. Our study sites encompass a range of altitudes, habitats, and local climates that is likely to be

representative of much of the large nesting Robin population in Western Iberia (Equipa Atlas 2008). The existence of fully sedentary birds in Iberian populations had previously been demonstrated by Pérez-Tris & Tellería (2002b), but from that study it was unclear whether such individuals were the rule or the exception in the sampled populations, or whether the study sites had indeed been flooded by foreign competitors. It had also previously been shown that local Robins partially segregated from migrant visitors in southern Spain during winter (Tellería *et al.* 2001, Tellería & Pérez-Tris 2004), with 'local birds' being more abundant in those habitats where they also nested. However, those studies did not assess the behaviour of individuals and took a broad population approach instead. The present study suggests that the pattern of general population segregation is caused to a large extent by a majority of local Robins (52%, in our overall sample) that are present in the immediate vicinity of their presumed nesting sites over winter. Nevertheless, there were differences between sites in the proportion of sedentary birds. Those differences may have been related to altitude (and local climate), as previously suggested by Pérez-Tris & Tellería (2002b).

Substantial numbers of Robins that apparently nested near the CES were not captured in winter. This may be explained by three factors. Some birds may have died or permanently emigrated (this obviously does not apply to those captured in subsequent springs). Other birds may have been present, but were not captured because of their familiarity with the net sites and trap-shyness. Finally, some birds may have moved away for the winter. The fact that some birds are indeed likely to have moved away (they were captured multiple times in the breeding season but never in winter) does not necessarily mean that they were forced to do so by increased competition from migrants, as this type of behaviour is present even in populations subjected to no autumnal influx of long-distance migrants. For

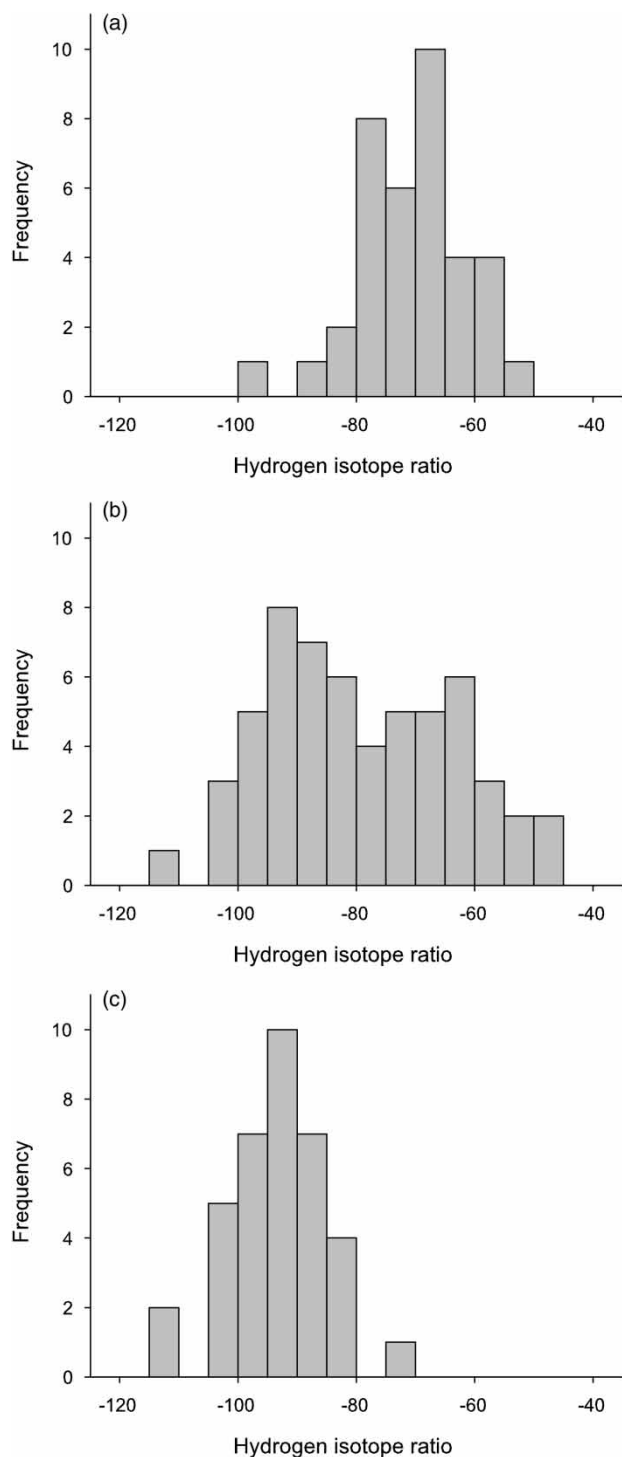


Figure 2. Frequency of isotopic signatures of Robins (feathers) at Margarça in (a) spring (June) and (b) winter (January) and (c) during autumn migration at Falsterbo, Southern Sweden.

example, around 50% of the broadly resident Robins in Ireland and England move away from their breeding territories in autumn and early winter, and return in the

following nesting season (Burkitt 1926, Lack 1943, Jackson 1958), and the British Isles is a region with very small numbers of migratory Robins (Remisiewicz 2002, Wernham *et al.* 2002). If migrants strongly influenced local birds, we should have expected that our study would have experienced very different results from those from the British Isles, which clearly was not the case.

Are Robins from our study sites truly confronted with significant numbers (relative to the local population) of incoming migrants during the non-breeding season? The higher capture rates in the non-breeding season do suggest this, as do the large numbers of recoveries of foreign Robins scattered through Iberia (Bueno 1999). Data from the intensively studied site of Margarça provide new evidence on this subject. The negative correlation between wing-length and hydrogen isotope ratios in wintering Robins is in line with the assumption that Robins coming from higher latitudes (which have longer wings) also have lower $\delta^2\text{H}$ (see Materials and Methods). This is also confirmed by $\delta^2\text{H}$ values from our Scandinavian sample. The widely contrasting distribution of isotopic signatures of Robins sampled in spring and winter at Margarça clearly indicates that there is an important influx of Robins from other breeding origins in the cold season. Furthermore, the large variance of winter $\delta^2\text{H}$ values suggests that Robin populations from various sources are simultaneously present at this site. The range of values is consistent with measurements obtained from almost the full distributional range of Robins (Fig. 2), suggesting that the wintering population includes both local birds (also confirmed from CES data) and long-distance migrants from northern Europe.

To get an estimate of a plausible value for the proportion of long-distance migrants at Margarça in winter, it is possible to use the isotope data presented in Fig. 2. If it is assumed that all of the birds with $\delta^2\text{H} < 80$ are migrants (a few locals have values < 0.80 , but these will be compensated by migrants which have $\delta^2\text{H} > 80$), then the proportion of migrants would be 53 %. Of course, this is a crude estimate, because Robins from mid-latitudes in Europe will also be present, probably contributing birds to both sides of the cut-off line.

On the other hand, the wintering sex ratio of birds at Margarça suggests that many local Robins are present. The sex ratio of Robin populations in autumn–winter, at Iberian sites where no Robins nest, is generally heavily female-biased, with 69% females reported in northern Spain (Arizaga *et al.* 2010) and 71–87% in southern Portugal (Catry *et al.* 2004). This results from

Robins being differential migrants, with a tendency for females to move farther and males to winter at more northerly latitudes (Adriaensen & Dhondt 1990). The fact that, at Margaraça, females represented only 45% of the captures does not support the idea that foreign Robins largely dominate the wintering community, because in this case the sex ratio should be more female-biased. For example, if we assume that sedentary birds were 80% male (a figure obtained from local CES data and that is consistent with results obtained in the British Isles; Burkitt 1926, Lack 1943, Jackson 1958) and that 75% of the wintering migrants were female, an overall winter proportion of 45% females at Margaraça implies that only 46% of the wintering individuals were migrants. Overall, these two fully independent tentative estimates of 53% and 46% (of the winter population as long-distance migrants) give an order of magnitude and suggest that there is not a great imbalance between the numbers of residents and of migrants in the mid-winter Robin population at Margaraça.

The low frequency of individuals classified as Winter–return, as opposed to Winter–single, is well in line with multiple studies documenting that Robins wintering in Iberia have low between-year site fidelity (e.g. Cuadrado 1992, Herrera 1998, Catry 2005). To some extent, Robins spending the winter in Iberia track spatial variations in fruit abundance (Tellería *et al.* 2008) and this may explain the low interannual site fidelity of wintering individuals and possibly also the movements of some individuals of the local population.

In conclusion, this article suggests that incoming migratory populations do not force local Robins to vacate nesting territories and redistribute themselves in the shared wintering range. Whether this happens because local Robins are somewhat dominant over incoming conspecifics or for other reasons, such as different Robin populations having distinct ecological requirements or adaptations, will have to be clarified by further research.

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