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Winter segregation of migrant European robins *Erithacus rubecula* in relation to sex, age and size

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Birds often show some form of social segregation during winter, both at large geographical scales (a consequence of differential migration) and at the regional or local level, when comparing different habitats or micro-habitats. However, our understanding of the mechanisms underlying such patterns is still poor. These issues have been rarely investigated in migratory Old-World passerines, particularly with respect to differences between the sexes. In this study, we show that female European robins *Erithacus rubecula* (sexed by molecular techniques) greatly outnumber males in southern Iberia, which confirms that this species is a differential migrant with a strong latitudinal segregation of the sexes. Furthermore, sex, age and body size influence the habitat distribution of robins in winter. Subordinate birds (females, juveniles and small individuals) were generally more common in habitats with a greater shrub development, and comparatively scarce in woodlands with relatively little undergrowth. Birds wintering in woodlands were in better condition (assessed by breast-muscle scoring) than birds wintering in shrubland. These results are consistent with the hypothesis that proposes that social dominance, mediated by differences in size and experience, is important in determining the habitat segregation of sex and age classes. The alternative hypothesis (habitat specialization), although not specifically supported by our findings, cannot be ruled out on the basis of the available evidence.

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There are increasing evidence that differential migration and the habitat segregation of age and sex classes during the non-breeding season are widespread phenomena in birds (Ketterson and Nolan 1983, Greenberg 1986, Sherry and Holmes 1996), although the underlying mechanisms and consequences of such patterns are still poorly understood (Cristol et al. 1999). The most often invoked mechanism for segregation of age or sex classes in bird species is social dominance and competitive exclusion (e.g. Greenberg 1986, Cresswell 1994, Ardia and Bildstein 2001), but differences in habitat preferences, travel costs, previous knowledge and experience or other (unknown) factors may also play an important role in some species and migratory systems (Ketterson and Nolan 1983, Rogers et al. 1989, Morton 1990). Sex or age segregation can have consequences on the body condition and fitness of individuals occupying different habitats (Marra and Holmes 2001), which ultimately may be decisive in determining population dynamics (Rodenhouse et al. 1997, Marra et al. 1998).

The robin *Erithacus rubecula* is one of the most widespread and abundant birds in Europe, and it has been the object of several detailed ecological and behavioural studies (e.g. Lack 1945, Cramp 1988). Despite this, relatively little is known about the social structure of migratory populations during winter. Only recently, differences in habitat distribution of age classes have been described in the Iberian winter quarters

(Figuerola et al. 2001, Tellería et al. 2001). Evidence of latitudinal segregation of the sexes comes from studies showing that, in partially migratory populations, males have a greater tendency to remain on the breeding grounds during the entire annual cycle, while females move away (Adriaensen and Dhondt 1990). However, nothing is known about the sex-ratios of the important wintering populations in different habitats of the Mediterranean area. In a previous study, large and significant differences in wing-length of robins wintering in different habitats in southern Portugal were found (Catry et al. 1999). This prompted us to use molecular techniques to test the hypothesis that there could be differences in the sex composition of the wintering robins in different habitats. In this paper, we examine the sex ratio and the influence of age, sex and body size on the habitat distribution of robins wintering in southern Portugal, and assess the possible fitness implications by looking at body condition.

Methods

Study area and field methods

This study took place in Portugal, south of the Tagus river, during the winter of 2001–02, in areas where robins are absent as breeders, but very abundant during winter. Robins were trapped in 6 different study areas (3 shrubland and 3 woodland sites), in the provinces of Estremadura, Alentejo and Algarve. There was no systematic bias in the geographical position of woodland versus shrubland sites. Robins wintering on the Iberian Peninsula originate mostly from Scandinavia, Central Europe, the Low Countries and France (Bueno 1998). The majority (70%) of the robins we studied were trapped in December or January, with a further 30% in November. No robins were trapped during the main migratory periods, in October and February (Cuadrado 1992).

Birds were captured in mist-nets or (mostly, 74%) with spring-traps baited with mealworms. No tape-lures were ever used to attract birds to the traps or nets. Every newly trapped bird was ringed, and aged according to Svensson (1992). Maximum wing chord, a measure of body size (Gosler et al. 1998), was taken using a wing ruler and mass was measured using a Pesola spring-balance. The amount of subcutaneous fat reserves was assessed by visual inspection using a 6-point scale. Pectoral muscles were scored on a 3-point scale, with reference to the prominence of the sternal keel and muscle shape following Gosler (1991). Pectoral muscle scores can be used as an indicator of overall protein reserves (Gosler 1991) and may be a better indicator of condition than fat, reflecting long-term access to good quality diet instead of short-term strategic body mass regulation (Gosler 1991, 1996, Latta and Faaborg 2002). All muscle and fat scoring were done by a single observer.

The general habitat types where this study took place were: a) Medditerranean shrubland, growing on limestone, with dense shrub cover and with some low trees interspread with bare rock or soil. Fruit-producing robin food plants (see Herrera 1998) are abundant in these areas, particularly lentisc *Pistacia lentiscus* and wild olive *Olea europaea sylvestris*, but many others are also present. Robin density in these habitats is extremely high. b) Woodland. Slightly open woodland dominated by sessile oaks (either cork oak *Quercus suber* or holm oak *Q. ilex*) in many cases with some cultivated olive trees *O. e. europaea*, growing isolated or in small groves, and a certain amount of undergrowth or riparian vegetation. These species also produce fruit-foods eaten by robins (Herrera 1977).

Some birds were captured in other habitats, such as wetland margins or pine woodland. Because of the small sample sizes, they were not included in habitat analyses, but they were still used in other general summaries (for example, comparisons of adult and juvenile, or male and female measurements).

At each precise location where a robin was trapped, the following habitat variables were assessed visually in a radius of 20 m from the trap/net: a) mean canopy height, b) percentage canopy cover, c) mean height of the shrub layer (shrubs were defined as woody plants less than 3 m tall), d) percentage shrub cover, e) percentage bare ground or short-grass (< 10 cm tall) cover and f) percentage long-grass cover.

Sexing robins

A drop of blood was taken, from each bird caught, by puncturing the *vena ulnaris*. Blood samples ($n = 152$) were used for total genomic DNA extraction following the Sambrook et al. (1989) protocol. A region of the CHD genes located on the avian sex chromosomes was amplified by polymerase chain reaction (PCR) using the primers P2 and P8 (Griffiths et al. 1998). The thermal profile consisted of 3 min at 95°C followed by 30 cycles at 95°C for 30 s, 45°C for 30 s, and 72°C for 1 min with a 5 min extension at 72°C on the end of the reaction. PCR amplifications were performed in 10 µl total volume with 0.1 units of *Taq* polymerase (Promega), 3.5 pmol of each primer, 3 mM $MgCl_2$ and 0.2 mM of each dNTP. Successful PCR were electrophoresed in a T8C5 polyacrylamide gel with 1 X TBE buffer at a constant voltage of 300 V and constant temperature (8°C) for 3h. Results were visualised by silver staining. All the sexing work was carried out at the Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO) of the University of Oporto.

Data analysis

For each precise capture location, an index of *shrub volume* was obtained by multiplying shrub cover by its mean height.

Data on sex and age ratios in relation to habitat types were analysed using Hierarchical Loglinear analysis, with backward elimination of terms from the full model containing all interactions and main effects (Norusis 1994). Data concerning distribution of age and sex classes in relation to habitat measurements were assessed using logistic regression, with sex (male versus female) or age (juvenile/first year versus adult) as the dependent variables, and habitat characteristics as covariates. Wing length data was analysed using general linear models with habitat variables as continuous covariates and, sex and age as categorical factors.

Birds caught around sunset (i.e. possibly moving to roosts; $n = 9$) were excluded from the within-habitat analyses, which results in apparent inconsistencies in sample sizes. Because only 3% of all muscle scores had values of 1, we pooled values of 1 and 2, thus getting a two-point scale (1–2 and 3). This variable could then be analysed using Yates-corrected χ^2 (when comparing two groups of data) or logistic regressions. Using non-parametric tests on the original (not pooled) data set did not change the results of the analyses in any meaningful way. Fat score data were analysed using non-parametric tests. Means are presented with standard errors.

Results

Size, age, sex and habitat segregation

Both sex and age significantly influence wing length in robins (two-way ANOVA, Age effect: $F_{1,139} = 4.46$, $P = 0.036$; Sex effect: $F_{1,139} = 43.10$, $P < 0.001$). Adult males have the longest wings of all classes (75.3 ± 0.6 mm, $n = 9$) and juvenile females the shortest (72.2 ± 0.2 mm, $n = 76$). Juvenile males have longer wings (74.0 ± 0.4 mm, $n = 17$) than adult females (72.4 ± 0.3 mm, $n = 41$).

Of 152 robins caught during our study in several different habitats in southern Portugal, only 17.8% were males. Of 52 robins sampled and sexed in woodland, 29% (15) were males. In Mediterranean shrubland, the percentage of males was lower (13%; 12/89). A hierarchical loglinear analysis revealed that age structure did not differ between habitat types (although the power of the test was only 0.27), and this variable was therefore eliminated from the model (Fig. 1). On the other hand, there was a significant interaction between habitat type and sex (Likelihood ratio χ^2 change $= 4.8$, $P = 0.03$), showing that the proportion of male robins was lower in shrubland than in woodland communities (Fig. 1).

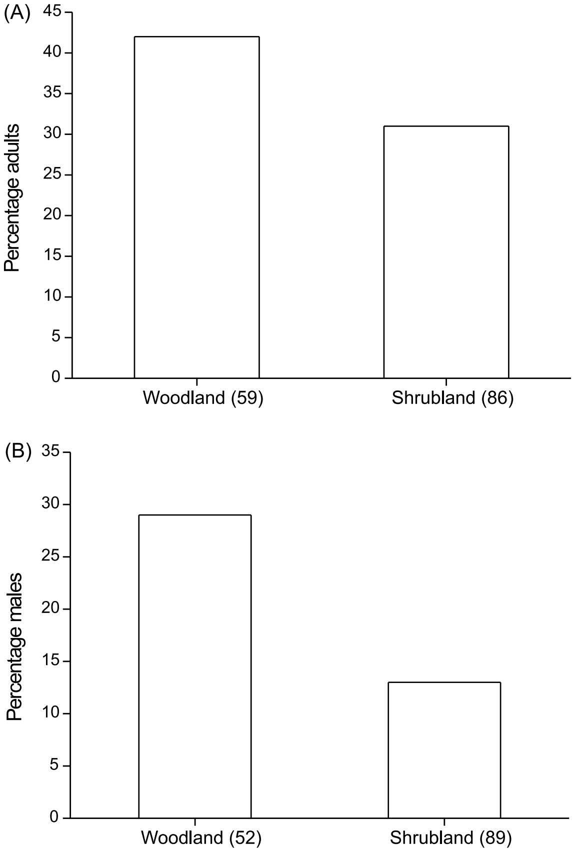

Fig. 1. Percentage of adult birds (A) and of male birds (B) in samples of robins wintering in woodland and in shrubland habitats in southern Portugal. Differences between habitats are significant in relation to sex, but not to age (see text). Sample sizes indicated in brackets.

Differences between habitat types were not simply the product of our (possibly subjective) habitat classifications. A logistic regression revealed that the probability of catching a female robin (instead of a male) at one location increased as the total shrub volume increased ($\beta = -0.010 \pm 0.0035$, $n = 135$, $P = 0.0028$, Fig. 2A). A similar and significant result is obtained when using shrub cover instead of shrub volume. The inclusion of other habitat variables did not significantly improve these models.

When a similar analysis was carried out with age (juveniles versus adults) as the dependent variable in the logistic regressions, the probability of catching a juvenile robin (instead of an adult) increased as the total shrub foliage volume increased ($\beta = -0.0058 \pm 0.0029$, $n = 132$, $P = 0.048$, Fig. 2B). This suggests that, although robins might not segregate by age amongst broad habitat types (see above), at a finer scale of analysis, juveniles were more frequently found in areas with more shrubs. Wing length correlated significantly (and negatively) with shrub volume in woodland habitats ($F_{1,49} = 6.3$, $r^2 = 0.11$, $P = 0.016$), further suggesting the

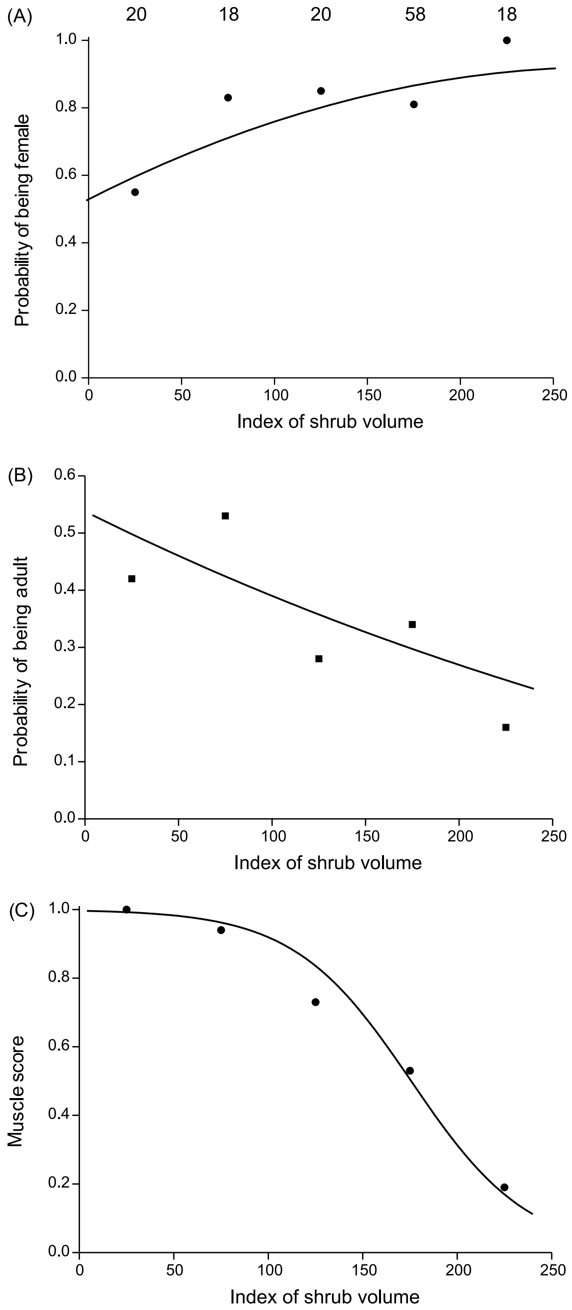

Fig. 2. Observed frequency (dots) and estimated probability (lines) of catching (A) female, (B) adult or (C) individual robins with maximum muscle-score, in relation to an index of shrub volume in a radius of 20 m around the trap. Observed values are grouped data (by 50 x-axis units). Sample sizes presented at the top. Lines estimated by logistic regressions on ungrouped data. The trends are highly significant (see text for statistics).

Table 1. Effect of the volume of shrubs in a radius of 20 m around the trap on the wing length of robins caught; the model that takes age and sex effects on body size into consideration. Non-significant interactions were removed from the model.

	df	F	P
Volume of shrubs	1	5.27	0.023
Sex	1	5.07	0.026
Age	1	47.38	<0.001
Sex × Age	1	4.34	0.039
Error	121		

existence of some form of segregation of robin classes at a finer scale within broad habitat types.

After accounting for the significant effects of age structure and sex composition of the samples in a general linear model, wing length still showed a dependency on shrub volume (Table 1), which shows that, within sex and age classes, smaller birds tend to occur in areas with greater shrub cover.

Consequences for body condition

Robins wintering in woodland had higher muscle scores than robins wintering in shrubland (Table 2). A negative relationship between muscle score and shrub volume (after controlling for age, see below) was also evident (logistic regression: $\beta = -0.028 \pm 0.006$, $\chi^2_1 = 48.5$, $n = 141$, $P < 0.0001$, Fig. 2C). No difference in fat scores could be found between the two habitats types (Table 2). Adult birds had higher muscle scores than juveniles, but there was no difference in fat scores (Table 2). The utility of our muscle scoring measurements can be confirmed by the following. After accounting for the significant effects of body size (wing length) and fat reserves (fat scores) in a general linear model, muscle scores significantly influenced body mass (muscle score effect: $F_{1,202} = 4.0$, $P = 0.047$).

Discussion

Our work shows that the habitat distribution of robins wintering in southern Portugal is probably determined by sex, age and body size. Generally, females, juveniles and small individuals tend to be associated with greater shrub development (see Tellería et al. 2001 for similar results concerning age).

Recent research on migrant birds wintering in the Neotropics revealed several cases of habitat segregation by sex in New World warblers *Parulidae* (e.g. Wunderle 1995, Sherry and Holmes 1996, Latta and Faaborg 2002). However, there is very little evidence of habitat segregation by sex in other families of passerines and in other geographical regions (but see Nisbet and Medway 1972, Smith et al. 1993, Herremans 1997). It might be no coincidence that New World warblers can often be sexed by plumage characteristics alone, making it easier to describe the above mentioned patterns. More studies on a diverse range of species, including sexually monochro-

Table 2. Percentage of birds with maximum muscle score and mean fat scores in relation to habitat types, sex and age. Comparisons of frequencies by Yates-corrected χ^2 and of medians by Mann-Whitney U tests.

	N	% with max. muscle score	Statistical comparison	Fat	Statistical comparison
Woodland	51	98	$\chi^2_1 = 51.9$	1.94±0.14	$U = 2048$
Shrubland	91	44	$P < 0.0001$	1.76±0.10	$P = 0.23$
Males	26	65	$\chi^2_1 = 0.11$	2.12±0.16	$U = 1174.5$
Females	121	62	$P = 0.74$	1.69±0.09	$P = 0.035$
Adults	49	73	$\chi^2_1 = 4.2$	1.78±0.17	$U = 2418$
Juveniles	101	56	$P = 0.04$	1.75±0.08	$P = 0.81$

matic and monorphic taxa, such as the robin, are needed to assess the generality of the pattern of sexual segregation.

Two main hypotheses could explain the segregation of age and sex classes of robins in a single geographical region, such as southern Portugal, in winter. The behavioural dominance hypothesis is consistent with the fact that robins can be strongly territorial in the winter quarters (Cuadrado 1995, 1997), which would provide a mechanism for the exclusion of subordinate birds from the areas preferred by the birds with a greater fighting ability. On the other hand, the habitat specialisation hypothesis may be potentially supported by the finding of (slight) differences in the foraging ecology related to robin sex and morphology (see Herrera 1978, East 1980). Our data, although still insufficient to reject any of these alternatives, provides important support for the behavioural dominance hypothesis. First, the coincidence that males, adults and large individuals (generally dominant over females, juveniles and small individuals; e.g. Piper 1997, Tobias 1997) tend to be found in greater numbers in the same habitats, suggests that there is a correlation between resource-holding potential and habitat type. Second, individuals occupying the habitats favoured by dominant birds were in a better condition than individuals found in places with more subdominant robins. This pattern is predicted by the dominance hypothesis, but not by the habitat specialization hypothesis (Marra and Holmes 2001). Only more observations coupled with experimental manipulations, such as removal experiments (e.g. Marra 2000), will allow a more complete clarification of the merits of the two hypotheses in explaining the patterns described in our study.

Cover (mostly provided by shrubs) is often seen as an important resource for robins (Cuadrado 1995, Johnstone 1998). In fact, robin winter territoriality has been suggested to be directly linked to the defence of cover, rather than to the defence of food sources (Cuadrado 1997). So, if males, adults and large birds generally have a greater resource-holding potential, we might have been expected to find them positively associated with shrub cover, exactly the opposite pattern to what we have reported. Below we present a hypothesis that might explain this apparent contradiction.

In spite of the common generalisation, not all robins are territorial in winter. Cuadrado (1997), for example, found that most birds he caught and marked in southern Spain were floaters. It is possible that, while territorial robins need only one or a few shrub patches for protection against potential predators, floaters need to live in areas with plenty of shrub cover that gives them protection, not only against predators, but also against the aggressive attacks from the holders of the several territories where they need to intrude everyday. If floaters are generally more numerous than territorial birds, then we would expect areas with great shrub cover to hold more individuals belonging to the subordinate than to the dominant classes. A detailed study of robin territoriality in such habitats will be necessary to confirm or refute these ideas.

Studies of captive robins originating from a population in southwestern Germany found only a small, and non-significant, difference in migratory restlessness between the sexes (Biebach 1983). In spite of this, 82.2% of the robins caught during our study in different habitats in southern Portugal were females. Females were the most abundant sex even in the habitats where the sex ratio was relatively more male-biased. In Belgium, near the other latitudinal extreme of the robin winter distribution, the reverse pattern was found, with the vast majority of the local birds remaining during winter being males (Adriaensen and Dhondt 1990). These studies, put together, provide the first unequivocal evidence for a strong latitudinal sexual segregation in Continental robins.

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