# Consequences of the settlement of migrant European Robins *Erithacus rubecula* in wintering habitats occupied by conspecific residents

JOSÉ LUIS TELLERÍA* & JAVIER PÉREZ-TRIS†

*Departamento Zoología y Antropología (Vertebrados), Facultad de Biología, Universidad Complutense, 28040 Madrid, Spain*

In wintering areas where migrant birds meet sedentary conspecifics, early settlement of local residents in the best habitat patches might reduce the availability of suitable sites for arriving migrants. We studied how sympatric migratory and sedentary European Robins *Erithacus rubecula* occupy two wintering habitats of different quality (forests and shrublands) in southern Spain, and how such a distribution affects individuals of each population sector. In September, before migrants arrived, Robins were only found in forests, and they had already saturated these habitats, so that rather than increasing Robin abundance in these habitats, the arrival of migrants caused a massive occupation of the previously vacant shrublands. During the winter, we captured Robins and identified them as migrants or residents using a discriminant function based on morphological traits. Residents always predominated in forests, and migrants in shrublands, but through the winter around 35% of residents (mainly juveniles) moved to shrublands, having been replaced by some migrants in forests. Although food was more abundant in shrublands, Robins had better body condition in forests, suggesting that other factors determined habitat preferences (e.g. shelter availability or food diversity, which were higher in forests). In addition, we observed a greater variance in body mass relative to body size in forests, suggesting that energy management was less constrained in this habitat (for example owing to a lower exposure to predators or a higher food predictability). Our results suggest that sedentary Robins benefit from an early occupation of the best habitats in the wintering grounds, forcing migrants to colonize apparently less suitable sites. This would explain the persistence of these small southern populations despite the yearly flooding of the area by huge numbers of migrant conspecifics.

Migratory bird populations are thought to be intensely regulated through the settlement of individuals in wintering habitats of differing quality (Fretwell 1980, Greenberg 1986, Sherry & Holmes 1996, Rodenhouse *et al.* 1997). According to theoretical models, the first migrants to arrive on the wintering grounds should occupy the best habitat patches available, thereby increasing conspecific interactions, which cause the displacement of subordinates to less suitable habitats (Brown 1969, Fretwell & Lucas 1970, Fretwell 1980, Pulliam & Danielson 1991).

Given that habitat occupancy may be affected by intraspecific interactions, sedentary birds already settled in wintering areas could reduce the prospects for conspecific migrants to occupy high-quality sites. In these circumstances, competition should lead to the regulation of migratory and sedentary populations. The final outcome of this would be the persistence of residents, migrants or both depending on the recruitment of each population (Bell 2000), the advantages that residents could obtain from early occupation of the best sites (Cox 1968, 1985) and the competitive ability of each population in relation to the characteristics of individuals (e.g. differences in body size; Pérez-Tris & Tellería 2002a). The study of such interactions contributes to our understanding of how extant sedentary populations have persisted despite annual 'flooding' of their ranges by migrant conspecifics (Bell 2000, Pérez-Tris & Tellería 2002a).

European Robins *Erithacus rubecula* wintering in southern Spain provide a good opportunity to study

*Corresponding author.
Email: telleria@bio.ucm.es

†Present address: Department of Animal Ecology, Lund University, Ecology Building, SE-223 62 Lund, Sweden.

which factors affect the habitat distribution of sympatric migratory and sedentary populations. In some areas in southern Spain, migrant Robins join sedentary conspecifics during winter (Pérez-Tris *et al.* 2000a). An earlier study of the distribution of Robins between different habitats in the Gibraltar area (well-developed forests and largely unsheltered shrublands) found that forest sites were the first to be occupied and the last to be abandoned in the non-breeding period (Tellería *et al.* 2001a). In addition, this study found habitat segregation in relation to migratory behaviour (resident Robins were more abundant in forests, their breeding habitats in the area, whereas migrants predominated in shrublands, where Robins are extremely rare as breeders), and it also found a different distribution of birds in relation to age, with adults predominating in forests and juveniles in shrublands (Tellería *et al.* 2001a).

If, as suggested by previous studies, forests are better habitats than shrublands (Tellería *et al.* 2001a), settling in one or other habitat might have different fitness consequences for Robins. This would contribute to the non-breeding regulation of both migratory and sedentary populations (Sherry & Holmes 1996). However, given that Robins are territorial in winter and adults are likely to be dominant over juveniles, habitat segregation in relation to age suggests that social dominance affects the distribution of Robins in the area. In this case, conspecific interactions might lead to the exclusion of most migrants from high-quality habitats (forest), as well as to the displacement of some residents from these sites by the best-competing migrants (i.e. adults). However, this interpretation still requires empirical support (for a review, see Pérez-Tris & Tellería 2002a).

In this study, we address the causes and consequences of habitat segregation in wintering Robins. In particular, we tested whether conspecific interactions underlie habitat segregation in relation to age and migratory behaviour by asking three basic questions:

### Do migrants and residents affect each other's distribution?

That some residents are found in shrublands during winter does not necessarily mean that they have been pushed out from forests by arriving migrant conspecifics. Neither does the predominance of migrants in shrublands necessarily mean that residents prevent them from occupying forests. For example, some residents could disperse to suitable wintering sites in shrublands before the arrival of migrants, and migrants could colonize forests if the carrying capacity of these habitats increased after the autumnal primary production typical of Mediterranean environments.

To address this, we studied the non-breeding distribution of residents before the arrival of migrants, and how the arrival of migrants affected population density in each habitat. In the absence of competition, residents should have settled in shrublands before migrants arrived, and population density should increase in forests when migrants joined residents already settled in these habitats. However, if migrants and residents compete for forest sites, the settlement of migrants in forests should affect the distribution of residents, with some of these residents being displaced to shrublands, without this changing the overall population density from what it might have been if the forests were saturated before the arrival of migrants.

### Does habitat quality explain habitat preferences?

We still do not know why most resident Robins remain in forests and migrants seem also to prefer this habitat (Tellería *et al.* 2001a). Differences in habitat quality between forests and shrublands could explain this apparent preference. For example, food availability and predation risk are two major determinants of habitat quality for wintering birds (e.g. Walther & Gosler 2001). Because wintering Robins are intensive frugivores (Herrera 1981, 1984, 1998, Jordano 1989), fruit abundance is a good candidate to affect habitat preferences in relation to nutritional quality (Rey 1995). Fruit diversity may also be important; indeed, Mediterranean winter frugivores actively search for rare fruits or invertebrates. This has been interpreted as a way to maintain nutrient balance (Herrera 1985). In relation to predation risk, vegetation cover may be important for Robins, as they prefer sheltered territories where they are less exposed to predator attacks (Cuadrado 1997, Johnstone 1998). We studied between-habitat differences in fruit abundance, fruit diversity and vegetation cover, in an attempt to understand how birds may benefit from occupying forests or shrublands in relation to nutrition and predator avoidance.

### Does habitat distribution affect body condition?

At mid to high latitudes, birds need to accumulate body reserves to survive during winter nights or periods of food scarcity: the more fat stored, the smaller the starvation risk (Blem 1990). However, to gain and maintain energy resources is costly, as food searching takes time that could otherwise be used

for anti-predatory behaviours, and carrying a large amount of fat may impair escape flight in some circumstances (McNamara & Houston 1990, Metcalfe & Ure 1995, Lind *et al.* 1999). According to these ideas, birds should be in better condition in the habitat that provides more abundant food resources if food is limiting, but they should reduce their body mass if they perceive a high predation risk (Witter & Cuthill 1993, Gosler *et al.* 1995). Consequently, if birds were eventually forced to accumulate fat under predation risk, they should show a stabilized distribution of body mass relative to body size: to be light would increase the probability of starvation, and to be heavy might compromise anti-predatory behaviours (Adriaensen *et al.* 1998, Tellería *et al.* 2001b). Therefore, we analysed the body condition of Robins (fat storage, body mass and variation in body mass relative to body size) as a comprehensive approach to the consequences of habitat segregation.

## METHODS

### Study area, habitat quality and the distribution of Robins

We studied Robins in an area of 200 km² at the northern side of the Strait of Gibraltar (36°01′N, 5°36′W). In this area, hills are dominated by forests (Cork Oak *Quercus suber* woods with mixed Mirbeck's Oaks *Quercus canariensis*), contrasting with the surrounding shrublands, which are dominated by Lentiscs *Pistacia lentiscus* and wild Olives *Olea europaea sylvestris* (Tellería 1981, Tellería *et al.* 2001a).

In two consecutive winters (between December and January in 1998/99 and 1999/2000), we studied variation between and within habitats in fruit abundance and availability of shelter, and how this variation affects the distribution of Robins at both spatial scales. To do so, we used a set of linear transects distributed along a 20-km-wide belt ranging from the mountains in Sierra de Ojén (250 m elevation) to the surroundings of Tarifa (at sea-level), in which forests and shrublands were almost equally represented (23 and 20 transects, respectively). The same transects were used in both study years. In each transect (500 m long), we counted Robins within a 50-m-wide band (25 m at either side from the observer), and the number of fruiting shrubs within a 10-m-wide band (5 m at either side from the observer). Shrubs holding unripe fruits were not counted as they did not supply suitable food. We also noted the number of raptors detected in each

transect to assess actual predation risk. To measure the availability of shelter, we recorded tree cover (vegetation above 2 m in height) and shrub cover (below 2 m) in each transect, for which we estimated visually the percentage of ground covered by each type of vegetation in three 25-m-radius plots evenly spaced along the transect (Larsen & Bock 1986). In order to determine the non-breeding distribution of residents before the arrival of migrants, we repeated all transects in September 1999, well within the non-breeding season but still before the first migrant Robins appeared in the area (see also Bueno 1998). In these late-summer censuses we measured fruit abundance, but because of time restrictions we did not estimate vegetation cover. Within-transect vegetation cover did not change between years (see Table 1 in Results), so we used the average cover recorded in each transect to evaluate the effect of habitat structure on Robin density during late summer.

### Capture and measurement of Robins

At the same time that we counted birds, we mist-netted, measured and ringed Robins in five forest sites and four shrubland sites. We aged most birds, distinguishing between juveniles (first-winter birds) and adults (Svensson 1992). We were unable to age three birds, which were excluded from the analyses. As Robins cannot be sexed in the hand during winter (Svensson 1992), we did not consider this in our study. We measured all individuals to identify them as residents or migrants by using a discriminant function based on morphology (wing length, tail length and wing formula; Pérez-Tris *et al.* 2000b). This function allows us to identify as migrant or resident more than 80% of Robins breeding in the Iberian Peninsula, and increases its reliability dramatically during winter, when sedentary residents in the Gibraltar area are joined by Robins, mostly from northern Europe, which have much more exaggerated migratory-like morphology than Iberian migrants (for further details see Pérez-Tris *et al.* 2000b). We also measured tarsus length (to the nearest 0.01 mm, using a digital calliper) and weighed birds with a digital balance (0.1 g precision). We derived an index of structural body size from measures of wing length, tail length and tarsus length using principal component analysis (PCA). The first component in this analysis weighed all body dimensions with positive loading (tarsus = 0.209, wing = 0.892, tail = 0.906, eigenvalue = 1.66), so we used it as a measure of

structural body size (Rising & Somers 1989). We analysed between-habitat variation in structural size, fat storage and body condition by means of ANOVA or ANCOVA. These analyses controlled for possible confounding effects of age, year and daily fat storage by including time of day in the analysis (Blem 1990, Brown 1996). We used the variation in body mass (the absolute value of residual mass once other factors contributing to explain body mass in previous analyses were controlled for) as an indicator of the restrictions imposed on mass variation in different habitat types.

## RESULTS

### Habitat quality of forests and shrublands

When studying between-habitat variation in protective cover, predator abundance and food availability, we took into account possible within-transect variation between years. For example, forestry could have changed vegetation cover in some transects. More importantly, fruit production may vary greatly in space and time and hence might have caused differences between years in food availability measured in our transects. To control for these changes, we used two-way repeated measures ANOVAs with habitat as a between-transect factor and year as a within-transect factor. In both years, the tree cover was much higher in forests than in shrublands, although shrub cover did not differ significantly between habitat types (Fig. 1, Table 1).

Excluding Eurasian Griffon Vultures *Gyps fulvus*, we only observed 11 'raptors' and owls in shrubland transects (three Eurasian Sparrowhawks *Accipiter nisus*, three Common Kestrels *Falco tinnunculus* and five Common Buzzards *Buteo buteo*) and 16 in forest censuses (nine Common Buzzards, three Tawny Owls
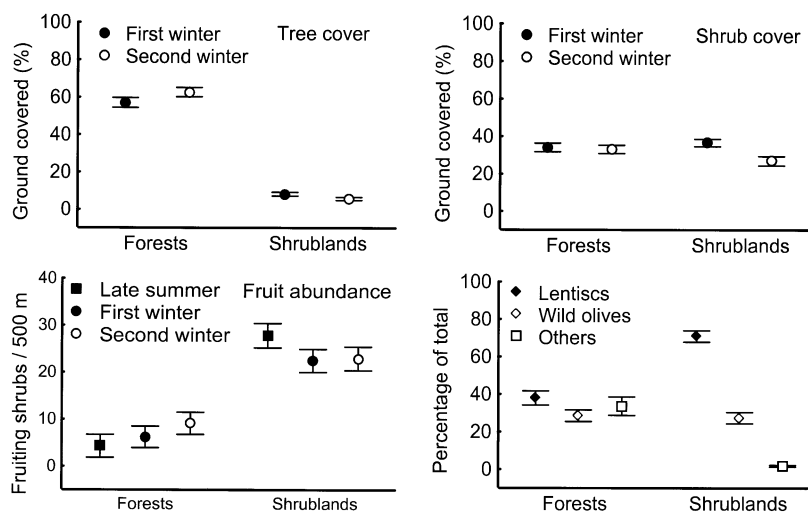


**Figure 1.** Variation in the cover of trees and shrubs and in the abundance of fruiting shrubs between habitats (forests, *n* = 23 transects; shrublands, *n* = 20 transects) and years. Means and standard errors are shown. Fruit abundance in late summer (September 1999) is also given.

**Table 1.** Results of two-way repeated measures ANOVA analysing changes in habitat features between habitat types (forests and shrublands, a between-transect factor) and periods (within-transect factor). The term period tests for differences between the winters 1998/99 and 1999/2000 in the case of covers, and for differences between both winters and late summer (September 1999) in the case of fruit abundance.

|  | Tree cover | | | Shrub cover | | | Fruiting shrubs | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | *df* | *F* | *P* | *df* | *F* | *P* | *df* | *F* | *P* |
| Habitat type | 1,41 | 137.95 | < 0.0001 | 1,41 | 0.13 | 0.72 | 1,41 | 50.32 | < 0.0001 |
| Period | 1,41 | 0.02 | 0.90 | 1,41 | 2.52 | 0.12 | 2,82 | 1.47 | 0.24 |
| Habitat × period | 1,41 | 1.28 | 0.26 | 1,41 | 1.66 | 0.21 | 2,82 | 3.31 | 0.041 |

**Table 2.** Results of ANCOVAs analysing the variation in population density in relation to habitat features (abundance of fruiting shrubs, and cover of shrubs and trees), taking into account variations between habitat types. Different models have been used to analyse which factors affect abundance in late summer (measured in September 1999) and in each winter.

| | Late summer | | | First winter | | | Second winter | | |
|---|---|---|---|---|---|---|---|---|---|
| | $F_{1,38}$ | $P$ | β | $F_{1,38}$ | $P$ | β | $F_{1,38}$ | $P$ | β |
| Habitat type | 36.01 | < 0.0001 | – | 0.43 | 0.51 | – | 0.02 | 0.90 | – |
| Tree cover | 0.69 | 0.41 | 0.120 | 2.98 | 0.092 | 0.213 | 1.30 | 0.26 | 0.152 |
| Shrub cover | 7.09 | 0.01 | 0.390 | 1.21 | 0.28 | 0.109 | 0.21 | 0.65 | −0.062 |
| Fruits | 1.51 | 0.23 | 0.181 | 16.34 | 0.0003 | 0.519 | 17.99 | 0.0001 | 0.579 |

*Strix aluco*, two Eurasian Sparrowhawks, one Common Kestrel and one Peregrine Falcon *Falco peregrinus*) during both study winters. The number of raptors per transect ranged between none and three, regardless of habitat type, so we analysed variation in raptor abundance by comparing the frequency of occurrence of raptors in each habitat. We detected predators in nine out of 20 forest transects and in 12 out of 23 shrubland transects ($\chi_1^2 = 1.09$, $P = 0.30$), suggesting that any between-habitat difference in predation risk should be more dependent on the availability of sheltered sites in each habitat type than on the abundance of predators.

Shrubs holding ripe fruits were more abundant in shrublands than in forests (Fig. 1, Table 1). Fruit abundance showed little variation from summer to winter or between winters. However, between-habitat differences were larger in September (in 1999) than in either winter, as shown by a significant interaction between habitat and period (Table 1). This was explained by a greater abundance of Lentisc in shrublands than in forests (see below), as this species fruits earlier than other shrubs and holds ripe fruit from late summer (Herrera 1984, 1985).

Lentiscs and the wild Olives were much more frequent than any other fruiting species in the area (Fig. 1). A two-way repeated measures ANOVA, with habitat type as a between-transect factor and year as a within-transect factor, showed that the percentage of Lentisc was much greater in shrublands than in forests ($F_{1,31} = 20.54$, $P < 0.0001$; year $F_{1,31} = 2.60$, $P = 0.12$; interaction $F_{1,31} = 1.08$, $P = 0.31$). Wild Olives were equally frequent in forests and shrublands (habitat $F_{1,31} = 0.69$, $P = 0.41$; year $F_{1,31} = 1.75$, $P = 0.20$; interaction $F_{1,31} = 0.40$, $P = 0.53$), and other fruiting species were too rare in shrublands to be considered an important food source (habitat $F_{1,31} = 18.18$, $P < 0.001$; year $F_{1,31} = 0.001$, $P = 0.97$; interaction $F_{1,31} = 0.42$, $P = 0.52$). The variety of plants other than Lentisc and wild Olives was also greater
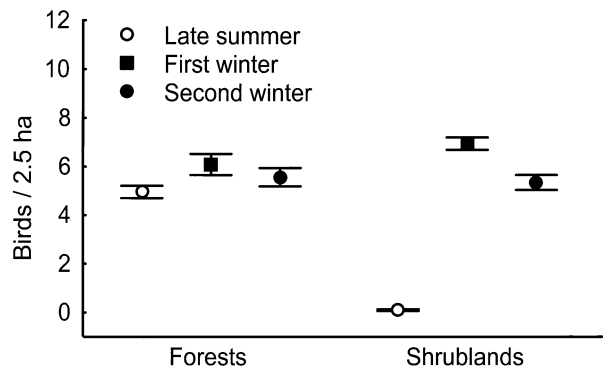


**Figure 2.** Variation in Robin abundance between forests and shrublands in both winters and in late summer (September 1999). Means and standard errors are shown.

in forests, where we found sparse fruiting plants of *Phyllirea latifolia*, *Myrtus communis*, *Rhamnus alaternus*, *Hedera helix* and other less common species. By contrast, apart from Lentisc and wild Olive, only some isolated *Smilax aspera* were found in shrubland transects.

## Between-habitat distribution of Robins

In September, before the arrival of migrants, Robins were almost completely restricted to forests, despite the availability of ripe fruits being much greater in shrublands. In fact, the abundance of fruits did not affect the distribution of resident Robins in late summer, which depended only on shrub cover controlling for habitat type (Table 2, Fig. 2). After the arrival of migrants, Robins occupied shrublands in abundance (Fig. 2). However, population density in forests remained similar from late summer to winter (separate analyses comparing each winter with September 1999: first winter $F_{1,44} = 0.19$, $P = 0.66$; second winter $F_{1,44} = 0.01$, $P = 0.92$), suggesting that forests were already saturated before the arrival of migrants. Controlling for habitat effects, we found

no between-year difference in the regional abundance of wintering Robins (two-way ANOVA: $F_{1,86}$ = 1.25, $P$ = 0.27). In winter, regional distribution of Robins was associated strongly with fruit abundance and, once this factor was controlled for, Robins showed a similar density in both habitat types, regardless of tree and shrub cover (Table 2, Fig. 2). The expansion of Robins to shrublands after the arrival of migrants was paralleled by a change in the distribution of residents (Fig. 3), some of which moved to this habitat (recall that they only occurred in forests in September, before migrants arrived). Nevertheless, residents predominated in forests and migrants in shrublands during winter, as shown by log-linear analyses of the distribution of birds in relation to habitat type, population and age (Table 3). There was also segregation in relation to age, with juveniles being found more frequently in shrublands and adults predominating in forests, although this effect was absent in the second winter (Table 3) owing to a lesser movement of juvenile residents towards shrublands (Fig. 3).

## Between-habitat variation in body condition

Robins accumulated fat through the day, and stored similar amounts of fat in both habitat types. Fat accumulation was not affected by age or migratory status of birds (Table 4). However, Robins wintering in forests were heavier than birds occupying shrublands,
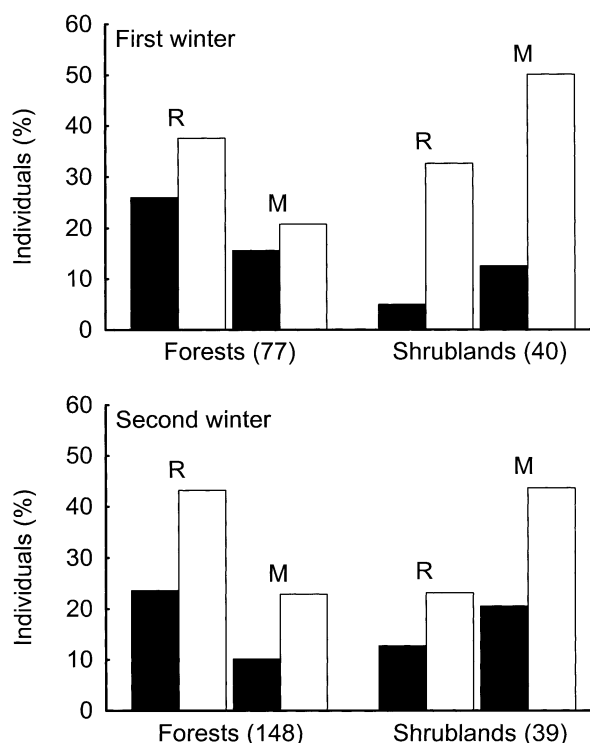


**Figure 3.** Composition of Robin populations wintering in forests and shrublands in both study years, as shown by the percentage of individuals of each population group (R, residents; M, migrants) and age (black bars, adults; white bars, juveniles) captured in mist-nets. Sample sizes are shown in parentheses.

**Table 3.** Log-linear analyses of the distribution of Robins in relation to habitat type, population and age during the two winters. The analysis hierarchically tests the fit of interactions of order $n$ (from $n$ = 3 to 1) to the null hypothesis that all of them are simultaneously zero. When a lack of fit is obtained, significant terms of that order or lower are selected, based on partial associations (which test the gain in fit of the model that includes the interaction compared with the model that excludes it) and marginal associations (which test the gain in fit of the model including all effects of lower order than the one of interest compared with the model including that interaction instead). Only the relevant effects are shown.

| | First winter | | | Second winter | | |
|---|---|---|---|---|---|---|
| | df | $\chi^2$ | P | df | $\chi^2$ | P |
| No third-order interactions | 1 | 0.09 | 0.766 | 1 | 0.001 | 0.972 |
| No second-order interactions | 3 | 13.87 | 0.003 | 3 | 12.33 | 0.006 |
| Test of fit of the model | 2 | 0.23 | 0.889 | 3 | 0.37 | 0.946 |

| | | First winter | | | | Second winter | | | |
|---|---|---|---|---|---|---|---|---|---|
| | | Partial | | Marginal | | Partial | | Marginal | |
| Interaction | df | $\chi^2$ | P | $\chi^2$ | P | $\chi^2$ | P | $\chi^2$ | P |
| Habitat × population | 1 | 7.14 | 0.008 | 7.05 | 0.008 | 11.99 | 0.001 | 11.96 | 0.001 |
| Habitat × age | 1 | 6.76 | 0.009 | 6.68 | 0.010 | 0.03 | 0.865 | < 0.01 | 0.986 |
| Age | 1 | – | – | – | – | 19.83 | < 0.001 | 19.83 | < 0.001 |

**Table 4.** Results of analyses of fat storage, body mass and body mass variance (absolute value of residuals in the analysis of body mass). The effects of age, habitat type (forests vs. shrublands), population (migrants vs. residents) and year are shown, but all non-significant interactions have been omitted from the table. Time of capture and structural body size of Robins have been included as covariates, except in the analysis of body mass variance.

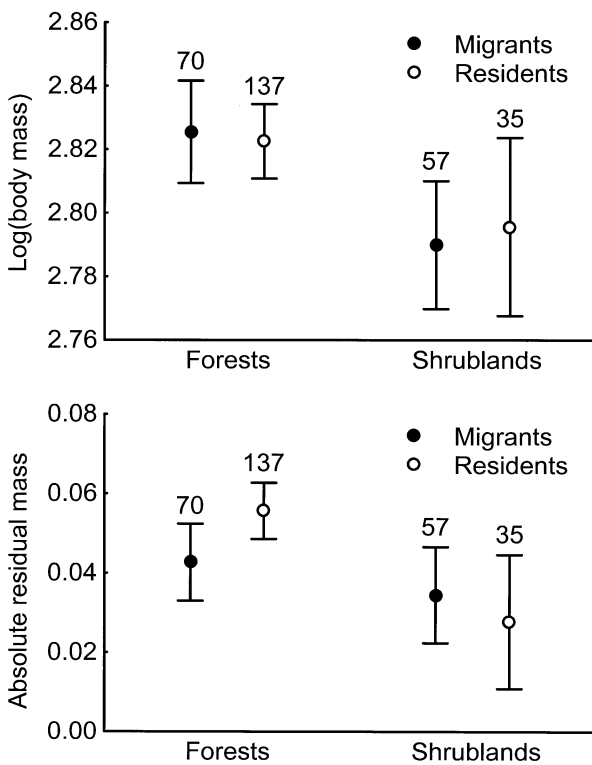| | Amount of fat stored | | | Body mass | | | Body mass variance | |
|---|---|---|---|---|---|---|---|---|
| | $F_{1,281}$ | $P$ | $\beta$ | $F_{1,281}$ | $P$ | $\beta$ | $F_{1,283}$ | $P$ |
| Age | 2.71 | 0.101 | – | 0.45 | 0.502 | – | 0.33 | 0.564 |
| Habitat type | 0.003 | 0.959 | – | 9.88 | 0.002 | – | 8.57 | 0.004 |
| Population | 0.90 | 0.343 | – | 0.02 | 0.900 | – | 0.03 | 0.855 |
| Winter | 1.34 | 0.248 | – | 2.44 | 0.120 | – | 2.71 | 0.101 |
| Time of day | 35.67 | < 0.0001 | 0.33 | 39.33 | < 0.0001 | 0.33 | – | – |
| Body size | 0.68 | 0.411 | 0.05 | 41.30 | < 0.0001 | 0.34 | – | – |



**Figure 4.** Differences in body mass and body mass variation in migrant and resident Robins captured in forests and shrublands. Means adjusted by covariates (see Table 4), standard errors and sample sizes are shown.

once body size and daily mass increase as a result of fat accumulation were controlled for. This effect was independent of age and migratory status of birds, and remained similar in both study years (Fig. 4, Table 4). The variance of body mass relative to body size was greater in forests (Fig. 4, Table 4), supporting the idea that environmental constraints on energy management were higher in shrublands than in forests.

## DISCUSSION

### Evidence for competition underlying habitat segregation

The arrival of migratory Robins in the Gibraltar area increased the regional abundance of the species, leading to a dense occupation of the previously vacant shrublands (see also Tellería *et al*. 2001a). However, the density of Robins in forests hardly increased from late summer to winter, supporting the idea that forests were already saturated before the arrival of migrants. Forest saturation in winter was mainly due to the presence of residents, which before the arrival of migrants settled in this habitat only, and still predominated there after migrants arrived. An early occupancy of forest territories could confer a competitive advantage on residents (Tobias 1997), allowing them to challenge the arrival of migrants and to persist in the preferred sites. However, not all residents seemed to benefit from early occupancy, as some of them (around 35% of birds) moved from forests to shrublands after migrants arrived, being substituted by these (cf. Fig. 3 and Table 3). The change in Robin distribution from late summer to winter, together with the composition of populations wintering in each habitat type, support the idea that the arrival of migratory conspecifics causes the displacement of a part of the resident population from forests to shrublands. First-year birds, which are likely to be worse competitors in territorial contests, made up the bulk of the resident population displaced to shrublands. Several studies have found an age-biased distribution of birds wintering in habitats of differing quality (for a review, see Sherry & Holmes 1996); and experiments involving the removal of territory owners have supported social dominance as the cause (Marra *et al*.

1993, Marra 2000). Therefore, our results are consistent with the effect of dominance hierarchies on the between-habitat distribution of Robins (see also Tellería *et al.* 2001a, Pérez-Tris & Tellería 2002a).

The apparent competitive superiority of residents compared with migrants could be mediated by sexual dominance, which we did not control for in this study. In many territorial species, males are dominant over females during the non-breeding season (Sherry & Holmes 1996). This is in fact the case in the Robin, which moreover shows differential migration in relation to sex (females make up the bulk of the migratory fraction in partially migratory populations; Adriaensen & Dhondt 1990). Consequently, females (i.e. subordinate Robins) could be over-represented in the migratory population occurring in our study area, thus explaining a higher abundance of migrants in the worst habitat type. Whether sexual dominance totally or partially underlies habitat segregation between migrants and residents requires further investigation, yet this uncertainty does not affect our main conclusion that residents can successfully challenge the arrival of migrant conspecifics, whatever their sex is, taking over the best habitat patches in wintering grounds.

## Habitat quality and the distribution of Robins

A large body of research supports the idea that starvation and predation are the principal causes of mortality in wintering passerines, and that their impacts are inversely related to the availability of suitable food and appropriate refuges against predators (e.g. McNamara & Houston 1990, Watts 1990, 1991, Rogers & Smith 1993, Witter & Cuthill 1993, Walther & Gosler 2001). In our study area, forests are more sheltered habitats for forest passerines, as they show a greater tree cover, but shrublands have more abundant fruiting shrubs. This variation in habitat features provides a good scenario for understanding the relative importance of these two components of habitat quality in determining the distribution of Robins. In late summer, many fruiting plants have already produced their crops (Herrera 1985, Fuentes 1992), providing extremely abundant food to the small resident populations inhabiting the area before the arrival of migrants. In these circumstances, even intensive frugivores such as Robins may base their choice of habitats on factors other than fruit abundance. For instance, they may decide to settle in the safest places available or where fruit

diversity and invertebrate availability make the habitats better for winter survival. In fact, this could explain why resident Robins only occupied forests before the arrival of migrants, although shrublands maintained a much greater fruit abundance, which was largely ignored. Once migrants arrived and populations spread over the area, the most productive sectors in both habitat types maintained the highest densities of Robins whereas any correlation between the availability of cover and the abundance of Robins was lost (Table 2).

It may be argued that reproductive benefits accrued to residents through breeding-site fidelity all the year round are sufficient to explain the distribution of Robins in late summer (Pérez-Tris & Tellería 2002b). However, there are two reasons to believe that residents not only limit themselves to remain in their breeding sites, but actively select these habitats in winter. First, reproductive benefits obtained from breeding-site fidelity in winter may be counterbalanced by survival benefits obtained by tracking the most fruit-rich habitats (e.g. Levey & Stiles 1992, Pérez-Tris & Tellería 2002b), yet shrublands were completely neglected before the arrival of migrants. Secondly, once migrants arrived, population density increased in shrublands but not in forests. This is consistent with the idea that forests were saturated by residents from late summer. Later in the season, habitat segregation in relation to age supported the idea that social interactions induced a rearrangement of populations, so that the most dominant individuals prevailed in the most preferred sites regardless of their migratory behaviour (Tellería *et al.* 2001a, Pérez-Tris & Tellería 2002a). However, birds could be attracted to forests for other reasons. For example, owing to innate habitat preferences, migrant birds could just select sites similar to their breeding habitats (Hildén 1965, Hutto 1985), or they could be attracted by the decoy effect of conspecifics already settled there (Stamps 1988, Jenni-Eiermann & Jenni 1999). Further studies are thus required to understand completely which factors determine the habitat preferences of wintering Robins.

## Consequences for individuals

Variation in the body condition of Robins was consistent with the pre-emptive distribution typical of territorial species (Brown 1969, Fretwell & Lucas 1970). Robins wintering in shrublands showed a lower body mass than birds occupying forests. However, this variation in body mass is unlikely to be

related to a different nutritional profitability of forests and shrublands, even though fruit diversity could be important in relation to this (Herrera 1985). First, food was much more abundant in shrublands than in forests. Secondly, Robins stored similar amounts of fat in both habitats, so that variation in body mass was not related to short-term energy management (i.e. fat storage as a response to immediate environmental pressures), but was probably related to long-term body condition (muscular development, a better index of health status; Brown 1996). According to the view that food is not limiting in this highly productive area, and hence starvation risk is less important than exposure to predators or food quality, a plausible explanation for differences in body condition of Robins is that heavier birds are dominant over lighter ones, and hence they occupy the best habitats and displace lighter birds to worse sites.

Robins not only showed a greater body mass relative to body size in forests, but also showed a greater variation in body mass. This suggests that, in addition to the possible effect of dominance hierarchies underlying differences in body mass between habitats, body condition could be affected by habitat quality, in particular by food predictability and predation risk. Food predictability may be lower in shrublands than in forests if the latter supply a more constant fruit crop as a result of overlapping fruiting periods of their more diverse plant species (Herrera 1982). In addition, the low density of protective cover in shrublands should contribute to increased predation risk even though predator abundance may be similar in both habitat types. Consistent with these environmental constraints, the narrower scatter of body mass relative to body size found in Robins wintering in shrublands suggested a somehow restrictive management of body reserves in this habitat type. Compared with in forests, Robins that were either relatively light or heavy were scarce in shrublands, suggesting that birds may try to optimize their condition in relation to their anti-predator behaviour (Adriaensen *et al.* 1998, Tellería *et al.* 2001b). Therefore, the variation in body condition provides additional insight into how Robins may perceive habitat suitability: unsheltered shrublands appear to be more restrictive than forests.

## Consequences for populations

Competition for the best sites is expected when the availability of suitable habitats limits wintering bird populations. Under these circumstances, aggressive interactions are manifested as territoriality and habitat saturation, with some individuals being prevented from settling in the preferred habitats, and with effects of habitat occupancy on fitness components (Sherry & Holmes 1996). This study shows that wintering Robins adjust such a model of distribution, and also sheds light on how conspecific interactions may affect both overwintering migrants and resident locals. Forests are successfully colonized by adults and heavier birds despite these habitats already being saturated by resident conspecifics, showing that individual competitive abilities (adults and heavier Robins are likely to be dominant) may allow birds to occupy their preferred habitats. However, our results also suggest that prior occupancy may play an important role in territory defence. Thus, although competition for forests seemed to be high, residents finally predominated in this habitat, forcing more migrants than expected by chance to settle in shrublands.

Given that forests are likely to offer less exposure to predators, more diverse food resources and less restriction on energy management, the ability of residents to remain in forests could allow them to survive better than migrants during winter, which would counterbalance their comparatively low fecundity (Pérez-Tris & Tellería 2002b). The ability to remain in the best habitat types could be a major mechanism for sedentary Robins to challenge the annual arrival of migrant conspecifics in their range, and might also impose an extra cost of migration on populations breeding at higher latitudes.

## REFERENCES

**Adriaensen, F. & Dhondt, A.A.** 1990. Population dynamics and partial migration of the European robin (*Erithacus rubecula*) in different habitats. *J. Anim. Ecol.* **59**: 1077–1090.

**Adriaensen, F., Dhondt, A.A., Van Dongen, S., Lens, L. & Matthysen, E.** 1998. Stabilizing selection on Blue Tit fledgling mass in the presence of sparrowhawks. *Proc. R. Soc. Lond. B* **265**: 1011–1016.

**Bell, C.P.** 2000. Process in the evolution of bird migration and pattern in avian ecogeography. *J. Avian Biol.* **31**: 258–265.

**Blem, C.R.** 1990. Avian energy storage. *Current Ornithol.* **7**: 59–113.

**Brown, J.L.** 1969. Territorial behavior and population regulation in birds. *Wilson Bull.* **81**: 293–329.

**Brown, M.E.** 1996. Assessing body condition in birds. *Current Ornithol.* **13**: 67–135.

**Bueno, J.M.** 1998. Migración e invernada de pequeños turdinos en la península Ibérica. V. Petirrojo (*Erithacus rubecula*). *Ardeola* **45**: 193–200.

**Cox, G.W.** 1968. The role of competition in the evolution of migration. *Evolution* **22**: 180–192.

**Cox, G.W.** 1985. The evolution of avian migration systems between temperate and tropical regions of the new world. *Am. Nat.* **126**: 451–474.

**Cuadrado, M.** 1997. Why are migrant Robins (*Erithacus rubecula*) territorial in winter?: the importance of the anti-predatory behaviour. *Ethol. Ecol. Evol.* **9**: 77–88.

**Fretwell, S.D.** 1980. Evolution of migration in relation to factors regulating bird numbers. In Keast, A. & Morton, E.S. (eds) *Migrant Birds in the Neotropics*: 517–527. Washington, DC: Smithsonian Institution Press.

**Fretwell, S. & Lucas, H.L.** 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.* **19**: 16–36.

**Fuentes, M.** 1992. Latitudinal and elevational variation in fruit phenology among Western European bird-dispersed plants. *Ecography* **15**: 177–183.

**Gosler, A.G., Greenwood, J.J.D. & Perrins, C.** 1995. Predation risk and the cost of being fat. *Nature* **377**: 621–623.

**Greenberg, R.** 1986. Competition in migrant birds in the non-breeding season. *Current Ornithol.* **3**: 281–307.

**Herrera, C.M.** 1981. Fruit food of Robins wintering in Southern Spanish Mediterranean scrubland. *Bird Study* **28**: 115–122.

**Herrera, C.M.** 1982. Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian dispersers. *Ecology* **63**: 773–785.

**Herrera, C.M.** 1984. A study of avian frugivores, bird-dispersed plants, and their interaction in Mediterranean scrublands. *Ecol. Monogr.* **54**: 1–23.

**Herrera, C.M.** 1985. Habitat–consumer interaction in frugivorous birds. In Cody, M.L. (ed.) *Habitat Selection in Birds*: 341–365. Orlando, FL: Academic Press.

**Herrera, C.M.** 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-year study. *Ecol. Monogr.* **68**: 511–538.

**Hildén, O.** 1965. Habitat selection in birds: a review. *Ann. Zool. Fenn.* **2**: 53–75.

**Hutto, R.T.** 1985. Habitat selection by non-breeding migratory landbirds. In Cody, M.L. (ed.) *Habitat Selection in Birds*: 455–476. Orlando, FL: Academic Press.

**Jenni-Eiermann, S. & Jenni, L.** 1999. Habitat utilisation and energy storage in passerine birds during migratory stopover. *Proc. Int. Ornithol. Congr.* **22**: 803–818.

**Johnstone, Y.** 1998. Territory structure of the Robin *Erithacus rubecula* outside the breeding season. *Ibis* **140**: 244–251.

**Jordano, P.** 1989. Variación de la dieta frugívora otoño-invernal del Petirrojo (*Erithacus rubecula*): efectos sobre la condición corporal. *Ardeola* **36**: 161–183.

**Larsen, D.L. & Bock, C.E.** 1986. Determining avian habitat preferences by bird-centered vegetation sampling. In Verner, J., Morrison, M.L. & Ralph, C.J. (eds) *Wildlife 2000: Modelling Habitat Relationships of Terrestrial Vertebrates*: 37–43. Madison, WI: University of Wisconsin Press.

**Levey, D.G. & Stiles, F.G.** 1992. Evolutionary precursors of long-distance migration: resource availability and movement patterns in Neotropical landbirds. *Am. Nat.* **140**: 447–476.

**Lind, J., Fransson, T., Jakobsson, S. & Kullberg, C.** 1999. Reduced take-off ability in robins (*Erithacus rubecula*) due to migratory fuel load. *Behav. Ecol. Sociobiol.* **46**: 65–70.

**Marra, P.P.** 2000. The role of behavioural dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. *Behav. Ecol.* **11**: 299–308.

**Marra, P.P., Sherry, T.W. & Holmes, R.T.** 1993. Territorial exclusion by a long-distance migrant warbler in Jamaica: a removal experiment with American Redstarts (*Setophaga ruticilla*). *Auk* **110**: 565–572.

**McNamara, J.M. & Houston, J.A.** 1990. The value of fat reserves and the trade-off between starvation and predation. *Acta Biotheor.* **38**: 37–61.

**Metcalfe, N.B. & Ure, S.E.** 1995. Diurnal variation in flight performance and hence potential predation risk in small birds. *Proc. R. Soc. Lond. B* **261**: 395–400.

**Pérez-Tris, J., Carbonell, R. & Tellería, J.L.** 2000a. Abundance distribution, morphological variation, and juvenile condition of robins *Erithacus rubecula* (L.) in their Mediterranean range boundary. *J. Biogeogr.* **27**: 879–888.

**Pérez-Tris, J., Carbonell, R. & Tellería, J.L.** 2000b. Identificación e importancia poblacional de los Petirrojos *Erithacus rubecula* locales durante la invernada en el sur de España. *Ardeola* **47**: 9–18.

**Pérez-Tris, J. & Tellería, J.L.** 2002a. Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration. *J. Anim. Ecol.* **71**: 211–224.

**Pérez-Tris, J. & Tellería, J.L.** 2002b. Regional variation in seasonality affects migratory behaviour and life-history traits of two Mediterranean passerines. *Acta Oecol.* **23**: 13–21.

**Pulliam, H.R. & Danielson, B.J.** 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *Am. Nat.* **137**: S50–S66.

**Rey, P.J.** 1995. Spatio-temporal variation in fruit and frugivorous bird abundance in olive orchards. *Ecology* **76**: 1625–1635.

**Rising, J.D. & Somers, K.M.** 1989. The measurement of overall body size in birds. *Auk* **106**: 666–674.

**Rodenhouse, N.L., Sherry, T.W. & Holmes, R.T.** 1997. Site-dependent regulation of population size: a new synthesis. *Ecology* **78**: 2025–2042.

**Rogers, C.M. & Smith, J.N.M.** 1993. Life-history theory in the non-breeding period: trade-offs in avian fat reserves? *Ecology* **74**: 419–426.

**Sherry, T.W. & Holmes, R.T.** 1996. Winter habitat quality, population limitation, and conservation of Neotropical–Nearctic migrant birds. *Ecology* **77**: 36–48.

**Stamps, J.A.** 1988. Conspecific attraction and aggregation in territorial species. *Am. Nat.* **131**: 329–347.

**Svensson, L.** 1992. *Identification Guide to European Passerines*, 4th edn. Stockholm: L. Svensson.

**Tellería, J.L.** 1981. *La Migración de las aves por el estrecho de Gibraltar, Vol. II. No planeadoras*. Madrid: Editorial de la Universidad Complutense.

**Tellería, J.L., Pérez-Tris, J., Ramírez, A., Fernández-Juricic, E. & Carbonell, R.** 2001a. Distribution of Robins (*Erithacus rubecula*) in wintering grounds: effects of conspecific density, migratory status and age. *Ardea* **89**: 363–373.

**Tellería, J.L., Virgós, E., Carbonell, R., Pérez-Tris, J. &**

**Santos, T.** 2001b. Behavioural responses to changing landscapes: flock structure and anti-predator strategies of tits wintering in fragmented forests. *Oikos* **95**: 253–264.

**Tobias, J.** 1997. Asymmetric territorial contests in the European robin: the role of settlement costs. *Anim. Behav.* **54**: 9–21.

**Walther, B. & Gosler, A.G.** 2001. The effects of food availability and distance to protective cover on the winter foraging behaviour of tits (Aves: *Parus*). *Oecologia* **129**: 312–320.

**Watts, B.D.** 1990. Cover use and predator-related mortality in song and savannah sparrows. *Auk* **107**: 775–778.

**Watts, B.D.** 1991. Effects of predation risk on distribution within and between habitats in savannah sparrows. *Ecology* **72**: 1515–1519.

**Witter, M.S. & Cuthill, I.C.** 1993. The ecological cost of avian fat storage. *Phil. Trans. R. Soc. Lond. B* **340**: 73–92.