

# DISTRIBUTION OF ROBINS *ERITHACUS RUBECULA* IN WINTERING GROUNDS: EFFECTS OF CONSPECIFIC DENSITY, MIGRATORY STATUS AND AGE

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This paper studies how population density affects the dynamics of habitat occupation by Robins in a wintering area of southern Spain (Gibraltar area), and how the between-habitat distribution is influenced by the age and migratory behaviour of birds (whether they are year-round residents or wintering migrants). We studied two different habitat types: forested sites, some of which are breeding habitats of Robins, and shrubland sites, to which Robins spread their range in autumn-winter due to the arrival of migrants. As arriving migrants increased abundance in the area, new habitat patches were sequentially colonised, forested sites being the first to be occupied and the last to be abandoned (regardless they maintained breeding populations or not). In addition, the abundance of Robins tended to decrease along the autumn-winter period in the most densely populated patches, which made the among-site distribution of Robins to be progressively more uniform. Juveniles of both local and migratory populations dominated (83% of individuals) in lowlands. Local Robins were more abundant (67%) than migratory ones in montane forests, although they also contributed to the winter colonisation of lowland habitats (47%). Together, these results support that the between-habitat distribution of Robins depends not only on population density, but also on the migratory status and age of individuals attempting to get a wintering site. Therefore, if winter habitats differed in quality, these factors could influence the mechanisms of regulation of Robin populations in the non-breeding season.

**Key words:** *Erithacus rubecula* - density-dependent habitat occupation - habitat suitability - migratory behaviour - social organisation - wintering grounds

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## INTRODUCTION

Winter is frequently regarded as the season in which populations of migratory land birds are most often limited, although the processes underlying non-breeding limitation are still poorly known (Terborgh 1989; Baillie & Peach 1992; Rappole & MacDonald 1994; Newton 1998). The occupation of habitats of different quality, for

instance, has been considered to be one of the most important such processes (Sherry & Holmes 1996; Rodenhouse *et al.* 1997). Since both direct and indirect interactions among individuals attempting to colonise a heterogeneous landscape may produce their sequential arrangement from the most suitable habitat patches to the less suitable ones (Fretwell & Lucas 1970; Pulliam & Danielson 1991), density-dependent habitat selec-

tion may well provide a mechanism for population regulation in non-breeding areas. Migrants may saturate the best patches on arriving at the wintering grounds, which will cause increasing interactions among conspecifics and, in turn, the occupation of suboptimal patches by surplus individuals. If these dynamics of habitat occupation affected survival rates, wintering populations could be regulated by the availability of suitable habitat patches (Greenberg 1986; Goss-Custard *et al.* 1994; Sutherland & Dolman 1994; Sherry & Holmes 1996; Rodenhouse *et al.* 1997).

This paper studies the effects of population density on the patterns of landscape occupation by Robins *Erithacus rubecula* wintering in the Campo de Gibraltar area, Southern Spain. This area sustains breeding populations of Robins in some montane forests, and receives in autumn a large number of migrants from northern and central Europe (Tellería 1981). The arrival of migrants is coupled with the expansion of the species' range across the area during winter, when Robins occupy shrublands located at the bottom of mountains. But despite there being a sharp difference between forests and shrublands in some features that are certainly relevant from the perspective of Robin preferences (e.g. vegetation cover; see Cuadrado 1997; Johnstone 1998), little is known on the numerical rearrangements of Robins among habitat types, or on the way year-round residents and overwintering migrants are distributed in the area. We address these topics in this paper through two complementary approaches:

(1) Patterns of habitat occupation of wintering grounds. We studied how the increase in regional abundance of Robins due to the arrival of migrants influences their dynamics of landscape occupation. If habitat selection depends on density of conspecifics, birds are expected to follow an ordered pattern of occupation of habitat patches according to among-site differences in habitat quality. In this case, it is predicted that the increase in regional abundance will cause the saturation of the most suitable sites before the less suitable ones are occupied (Fretwell & Lucas 1970; Pulliam & Danielson 1991).

(2) Distribution according to migratory status and age. The social status of birds could determine whether they will be able to remain in the best patches or, conversely, will be displaced to worse sites as soon as population density increases in the preferred habitats (Sherry & Holmes 1996). Robins are territorial in winter (Cramp 1988), and exhibit a strong wintering-site fidelity in southern Iberia (Cuadrado 1992), which could involve dominance relationships among individuals. In this case, it could be expected that year-round residents monopolised the best habitat patches by occupying them before the arrival of migrants (Tobias 1997). On the other hand, dominance relationships could also shape the distribution of Robins in relation to age, adults occupying the best patches and causing the displacement of juveniles to the worst sites (Sherry & Holmes 1996). Therefore, the composition of populations during the winter according to the migratory status and age of individuals was studied, to evaluate whether either year-round resident or adult Robins occupy the best habitat patches in the area, and to what extent their distribution affects that of overwintering migrants or juveniles, respectively.

## METHODS

### Study area

We studied the winter distribution of Robins in an area of about 200 km<sup>2</sup> located at the northern side of the Gibraltar Strait (36°01'N, 5°36'W). This area is crossed from north to south by several parallel, low-elevation mountain ranges, which are surrounded by shrublands and grasslands that extend westwards to the Atlantic Ocean and eastwards to the Mediterranean Sea. The influence of humid winds from the Atlantic, together with the north-to-south arrangement of mountains, allow the growth of well-developed forests in the moister ravines in mountains, which are covered by Cork Oaks *Quercus suber* mixed with Mirbeck's Oaks *Q. canariensis*. These forests sustain breeding populations of Robins and other forest birds, which are increased in winter due to arrival of

many overwintering migrants (Arroyo & Tellería 1983; Pérez-Tris *et al.* 1999; Tellería & Carbonell 1999). In the surroundings of mountains, however, the lowland landscape is covered by grasslands, shrublands (Lentisc or Mastic Tree *Pistacia lentiscus*, Wild Olive *Olea europaea sylvestris* and Spiny Broom *Calicotome villosa*) and some more developed riparian formations (Oleander *Nerium oleander*, brambles *Rubus* spp. and Black Poplar *Populus nigra*) associated with the rivers that cross the area. In these habitats, the environmental conditions are typical of the dry Mediterranean region, characterised by an extreme summer drought. Because of this, Robins and many other forest birds avoid these habitats for breeding. However, lowland shrublands are colonised in autumn by a large amount of Robins and many other birds that arrive at the area for wintering (Tellería 1981; Arroyo & Tellería 1983; Pérez-Tris *et al.* 1999).

### Patterns of site occupation

We studied 21 sites representative of the lowland habitats occupied by wintering birds in the study area (Appendix). Tellería (1981) described the variation in abundance of Robins in these sites throughout the autumn-winter periods of 1975-76 and 1976-77. Since Robins confer more importance to shelter than to feeding resources when selecting their winter territories (Cuadrado 1997; Johnstone 1998), we considered vegetation cover to be a reliable clue for evaluating the quality of wintering sites. Study sites were classified according to two levels of suitability for Robins (see Appendix). Sites of high suitability (HS) were represented by cleared cork-oak forests with a great cover of bushes (e.g. Wild Olives, Single-seed Hawthorn *Crataegus monogyna*, Mastic Trees, brambles, etc.), and riparian forests (European Black Alder *Alnus glutinosa*) with Oleander, Singleseed Hawthorn and Wild Olive bushes. A mixture of grasslands (with some sprinkled bushes) and shrublands of Bruc Boal *Erica arborea*, Spiny Broom and *Adenocarpus complicatus* (with some isolated patches of Mastic Trees and Wild Olives) represented sites of low suitability (LS).

Each study site was censused during one autumn-winter period, either in 1975-76 or 1976-77. The distribution of HS and LS sites was homogeneous between study years, each habitat type making up near 50% of sites censused (Fisher exact test:  $P > 0.99$ , see Appendix). The seasonal changes in Robin abundance were monitored at the study sites by repeated counting at 4-day intervals from September to mid-November, with two additional counts in January to estimate winter abundance. Counting periods were the same in both study years. Robins were censused by means of transects in which the number of Robins seen or heard was noted. Since the transect lengths changed among sites (Appendix), the abundance of Robins was finally measured in number of birds  $\text{km}^{-1}$ . It should be noted that we did not include in our analyses two open grasslands with some scattered shrubs (sites 3 and 6 in Appendix) where Robins never occurred.

The abundance of Robins in forested sites and shrubland sites was compared, taking into account the between-year variations in abundance and the seasonal changes in Robin density. To do so, we specifically tested for between-habitat differences in abundance (log-transformed) in a three-way ANOVA, in which sites were the sampling units, habitat type and year were between-subjects factors, and counts were the levels of the third (within-subjects) factor. By using this design, the amount of variance that is accounted for by within-site fluctuations in abundance throughout the study period was controlled for when testing for between-habitat differences. Since for such an effect to be properly evaluated it is required that the possible variations in abundance between years do not affect changes between habitats, we also tested for the year effect and the habitat by year interaction in the model. However, we did not test for the remaining effects and interactions, in which the changes in abundance within sites from count to count were involved. Actually, the variation accounted for by within-site fluctuations in abundance is not interesting in this study beyond its utility for computing a more appropriate error term when testing for the relevant hypothesis.

To analyse how regional abundance influenced the distribution of Robins in the study area, it was first studied to what extent the eventual increases in Robin abundance along the study period were coupled with a concomitant expansion of the species' range. In this analysis, the mean abundance in the occupied sites at each count was used to estimate the regional abundance of Robins, whose effect on the number of occupied sites was evaluated by means of regression analysis (Gaston & Lawton 1990). In order to establish whether the expansions or retreats of the range of Robins as a response to fluctuations of regional abundance were random or followed a hierarchical order, we set a matrix tallying the presence or absence of Robins in each site and count, both sorted by decreasing number of pres-

ences (Table 1). We compared the number of observed absences in this matrix to the number of expected absences generated at random by the Nestedness Calculator computer program (Atmar & Patterson 1995). This software measures the degree of nestedness (order) in the matrix by means of a metric (the so-called temperature of the system, T) proposed by Atmar & Patterson (1993), which assumes a value between 0 (a perfectly nested matrix) and 100 (a random matrix). The program allows one to contrast the observed T with a Monte Carlo-derived expected value, by means of a z-score whose associated probability estimates the likelihood of randomly producing a matrix even more nested than the observed one (Atmar & Patterson 1995). To assess the role of habitat suitability in determining the sequence of

**Table 1.** Temporal distribution of Robins across the 19 sites where the species occurred at least once in the study period. Sites have been labelled as high (HS) or low (LS) suitability sites, and those occupied in summer show an asterisk. The matrix takes into account the presence (1) or absence (0) of individuals in every site (columns) and count (rows). To facilitate the perception of the nested pattern of site occupation, both sites and count dates have been sorted by decreasing number of sightings (*n*).

Sites	9*	18*	20*	8	15	1	11	21	12	16	13	17	19	4	5	10	14	7	2	
Habitat type	HS	HS	HS	HS	HS	LS	HS	LS	HS	LS	HS	LS	HS	LS	HS	LS	LS	LS	LS	<i>n</i>
Census dates																				
November 3	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	18
November 7	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	17
January 8	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	16
January 4	1	1	1	1	1	1	1	1	1	1	1	1	0	1	0	1	1	1	0	16
November 11	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	0	0	1	16
October 30	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	0	0	16
October 26	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	16
October 22	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	0	0	1	0	15
October 18	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	0	0	0	15
October 14	1	1	1	1	1	1	1	1	1	1	0	0	1	0	1	0	0	0	0	12
October 10	1	1	1	1	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	10
October 6	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	6
September 8	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
October 2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
September 12	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
September 28	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
September 20	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
<i>n</i>	16	16	13	12	12	11	11	11	10	10	9	9	9	8	8	8	5	3	1	

occupation of sites, we compared the ranks acquired by HS and LS sites in the matrix by means of a Mann-Whitney *U*-test.

We used linear regression to model how the among-site abundance distribution in a given month determined the patterns of site occupation in the next one, an approach based in a modification of the isodar method (Morris 1987, 1990). To do so, we obtained the mean abundance in each site (*i*) around September (mean of the first five counts), October (five counts), November (five) and January (two). These data were used to perform simple regression analyses ( $x_i = a + b x_{i-1}$ ) in which the mean abundance in a given month ( $x_i$ ) was regressed on the mean abundance in the previous one ( $x_{i-1}$ ). In these relationships, the regression slopes (*b*) will reflect how the patterns of site occupation change from month to month, indicating a similar month-to-month pattern of abundance distribution among sites ( $b = 1$ ), the crowding of the most densely populated sites ( $b > 1$ ), or an increased inter-patch parity ( $b < 1$ ).

#### Distribution of Robins according to migratory status and age

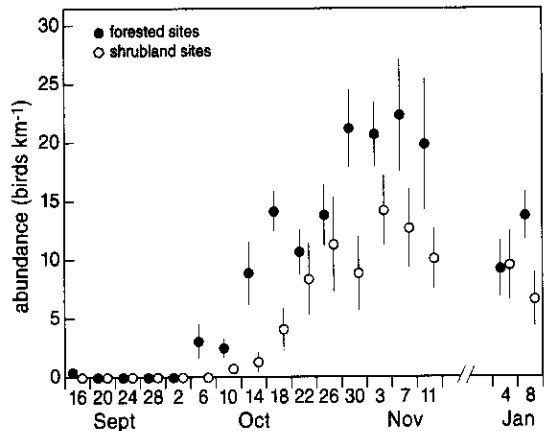
During the winters 1997-98 and 1998-99 (mid-Dec to mid-Jan), Robins were mist-netted in sites 8, 12, 13 and 15 (Appendix). Robins were captured in two other lowland localities also (in areas covered by *Pistacia*, *Calicotome* and *Olea* shrubs), and in six other forested sites in the mountains. Robins were aged according to plumage features (Svensson 1992) and measured to identify them as locals or migrants. To do so, the discriminant function analysis described by Pérez-Tris *et al.* (2000) was used. This method relies on changes in migration-related morphology (wing length and wing formula) between migratory and sedentary Robins breeding in the Iberian Peninsula, and allows one to correctly classify 80% of individuals. Because of their stronger migratory behaviour, Robins from further north in Europe have longer and more pointed wings than Iberian Robins (Cramp 1988), so they are expected to be accurately classified as migrants by this method. Since foreign Robins

make up the bulk of wintering populations in southern Iberia (Bueno 1998), the discriminant function can be so regarded as a reliable clue for differentiating between migratory and sedentary Robins during winter in this area (see Pérez-Tris *et al.* 2000 for further details). We conducted a hierarchical, three-factor log-linear analysis with these birds to compare the proportion of adults and juveniles of both local and migratory populations between montane forests and lowland shrublands.

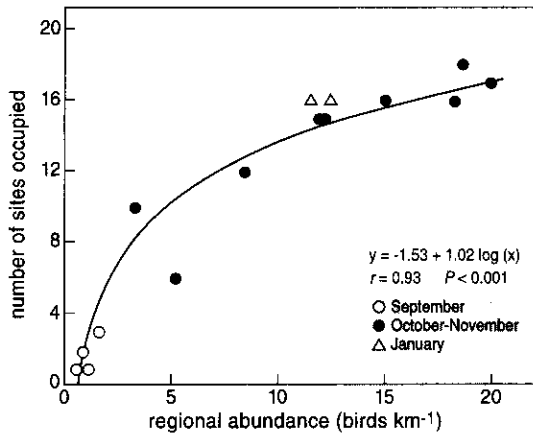
## RESULTS

### Patterns of site occupation

The abundance of Robins increased from September to November and decreased from November to January in the study area (Fig. 1). Forested sites were occupied first and consistently showed higher abundance than shrublands, despite variations in abundance both between years and throughout the autumn-winter period (specific effects in a three-way ANOVA with the count date

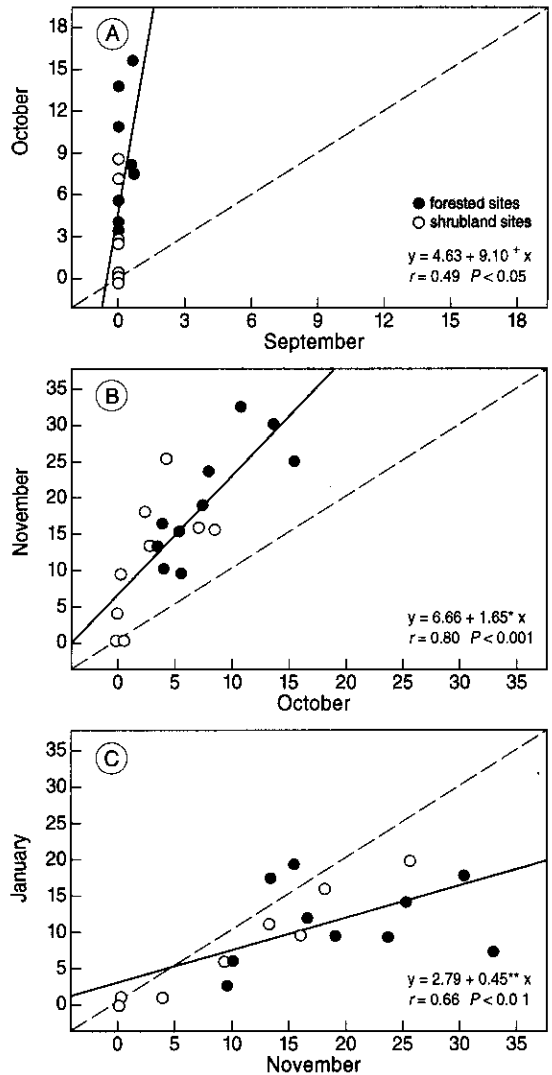


**Fig. 1.** Variation in the regional abundance (mean  $\pm$  SE) of Robins during the study period (both years pooled), in forested sites (high suitability) and shrubland sites (low suitability) of lowlands. Figures in abscissas refer to the first day of each 4-day counting period used to assess the changes in Robin abundance.



**Fig. 2.** Relationship between the regional abundance (mean abundance in the occupied sites) and the number of sites occupied by Robins through the study period. Censuses have been labelled as late summer (Sep), autumn (Oct-Nov) and winter (Jan) counts.

as a controlling factor: habitat type  $F_{1,15} = 6.07$ ,  $P < 0.05$ , year  $F_{1,15} = 5.09$ ,  $P < 0.05$ , habitat  $\times$  year  $F_{1,15} = 2.76$ ,  $P = 0.12$ ). Although Robins occupied more sites with increasing regional abundance, this relationship was not linear (Fig. 2). Thus, the number of occupied sites sharply increased with increasing abundance at the lowest interval of regional abundance (abscissa in Fig. 2), corresponding to the arrival of the first migrants to the area. By contrast, when regional abundance reached its highest level, larger increases were required for Robins to occupy more sites. This supports the view that Robins increased their abundance to saturation in some sites before colonising others. Consistent with this, the occupation of sites fitted a nested pattern (observed  $T = 5.47$ , random generated  $T$  after 1000 simulations: 57.94, SD = 5.57,  $z = -9.41$ ,  $P < 0.001$ ), supporting an ordered advance and retreat from the most frequently occupied sites to the scarcely used ones (Table 1). According to our hypothesis, this sequence of occupation of sites was related to habitat suitability, the most suitable sites being the first to be occupied and the last to be abandoned ( $U$ -test comparing the ranks attained by HS and



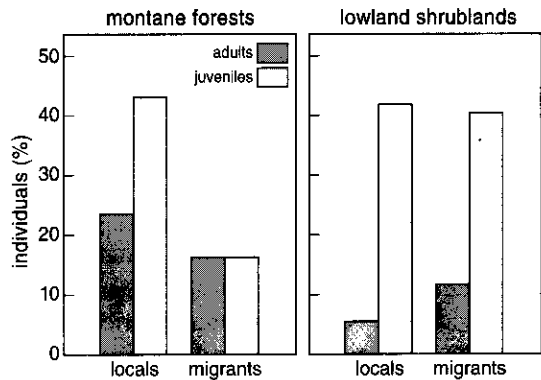
**Fig. 3.** Relationships between the abundance of Robins (birds  $\text{km}^{-1}$ ) in occupied sites each month and the abundance in the same sites the previous month. Filled dots refer to forested sites and open dots to shrubland sites. The observed slopes have been labelled to show the significance of their deviations from a slope of 1, represented by the main diagonal in the plot (\* $P = 0.05$ , \* $P < 0.05$ , \*\* $P < 0.001$ ).

LS sites in Table 1:  $z = 2.45$ ,  $n = 19$ ,  $P < 0.05$ ). This pattern remained, although not significantly so, after excluding the three sites that were already occupied in September by local Robins ( $z = 1.75$ ,  $n = 16$ ,  $P = 0.08$ ).

The month-to-month arrangement of Robin numbers among sites varied along the autumn-winter period (Fig. 3). The first Robins arriving on the wintering grounds sharply increased overall abundance in forested sites (Fig. 3A). During the peak of the autumn movements (Oct-Nov), the species tended to show a more parallel inter-patch abundance distribution (Fig. 3B), the most densely populated patches in October being also the most densely populated sites in November. However, the abundance of Robins tended to decrease more strongly in the most densely occupied sites during November (Fig. 3C), suggesting a preemptive distribution during winter following the crowding of forests in autumn. According to this, the drop in regional abundance observed in January (Fig. 1) may be interpreted as a decrease in the abundance of Robins in the most suitable sites.

#### Distribution of Robins according to migratory status and age

The best saturated log-linear model fitting the frequency of Robins in each habitat type according to migratory behaviour and age was the one including all two-way interactions (Maximum-likelihood chi-square,  $\chi^2_1 = 0.056$ ,  $P = 0.81$ ). The reduced model resulting from removing the non-significant age  $\times$  migratory status interaction (Marginal association chi-square,  $\chi^2_1 = 1.196$ ,  $P = 0.27$ ) suitably fitted the contingency table (Maximum likelihood chi-square,  $\chi^2_2 = 3.074$ ,  $P = 0.22$ ). Regardless the migratory status of Robins, adults were far more frequent in the montane forests than were in the lowland habitats, where wintering populations were almost completely composed of juveniles (Fig. 4; Age  $\times$  habitat type interaction:  $\chi^2_1 = 8.610$ ,  $P = 0.003$ ). Local individuals, especially juveniles, greatly contributed to the seasonal occupation of lowlands, where they represented almost a half of the whole population. However, migrant Robins were less fre-



**Fig. 4.** Composition of Robin populations according to migratory status and age in the two winter habitat types that have been considered in this study. The bars show the percentage of individuals belonging to each population fraction, in montane forests (above,  $n = 85$ ) and in lowland shrublands (below,  $n = 59$ ).

quent than locals in the montane forests, representing only 33% of all individuals (Fig. 4; Migratory status  $\times$  habitat type interaction:  $\chi^2_1 = 5.410$ ,  $P = 0.020$ ).

#### DISCUSSION

The arrival of migrant Robins at the Gibraltar area may be regarded as a massive occurrence of individuals, which increases both the regional abundance and the local range of the species across the area. The sequential occupation of wintering sites found in this study is similar to that observed in many bird species whose population dynamics have been monitored in the long-term, in which the species' range in a given area either spreads or retreats following fluctuations of population size (e.g. Newton 1998). Migrant Robins arrive at the Mediterranean wintering grounds at the end of the summer drought, coinciding with the beginning of the intense productive output that characterises these environments during the autumn-winter period (Herrera 1985; Fuentes 1992). At this time, the main food resources that the species exploits during winter experience a notable increase (fles-

hy fruits, cracked oak acorns, insects; Herrera 1977, 1981; Jordano 1989). This enhancement of the carrying capacity in these habitats could explain the sharp increase of Robin abundance in the study area from September to November (Fig. 1), as well as the time-lag between the increase of regional abundance and the expansion of Robins from the most preferred sites to the less preferred ones (Fig. 2). However, our results show that this enhancement does not rule out the effect of conspecific density on the numerical distribution of birds among the occupied sites. This is supported not only by the sequential occupation of habitats in relation to their suitability (a fair evidence of density-dependence; Brown 1969; Rosenzweig 1981), but also by the between-site arrangement of Robin numbers along the autumn-winter months. In turn, the outcome of these density-dependent dynamics of habitat occupation may well be the displacement of surplus individuals to marginal habitats (Bowers 1994). With the occurrence of many conspecifics in the best patches, increasing intraspecific interactions would cause the rearrangement of birds among sites (Pulliam & Danielson 1991). At the equilibrium, the outcome of these two processes is likely to be a balance between the saturation of a few sites and a homogeneous inter-patch distribution throughout the autumn-winter period. Although this pattern of settlement has been observed in many bird species during spring, little evidence has yet been gathered of this sort of landscape occupation in wintering birds (Newton 1998).

Although some information is available on the segregation mechanisms among migrant and local species in wintering areas, how local populations cope with the arrival of migrant conspecifics on their grounds is not so well known (Greenberg 1986; Sherry & Holmes 1996). This paper suggests that local Robins prevent a massive irruption of migrants in their breeding sites. Moreover, there are age-related differences in the distribution of individuals, adults tending to occupy the montane forests and juveniles being the most abundant in the lowland shrublands, regardless the migratory status of individuals. According to the distribution

of each population fraction between habitat types, a dominance hierarchy seems to rule the Robin populations studied here, in which the social rank of birds would decrease from adult locals to juvenile migrants. It is likely that adults and locals have priority of access to territories compared to juveniles and migrants, respectively (Tobias 1997). If the latter were more prone to fail when attempting to acquire a winter territory and endured as floaters in the best patches, they could be easily displaced from these habitats to the less suitable ones once circumstances become more difficult for territory owners. It has been suggested that individuals that abandon the breeding habitats in partially migrant populations of Robins are making 'the best of a bad job' (Adriaensen & Dhondt 1990). In our study area, if differences in habitat suitability were related to differential rates of mortality during winter, juveniles and migrants would actually be the population fractions which would suffer the highest mortality (Bowers 1994). In summary, our results put forward that interactions between locals and migrants could be a major determinant of the regulation of Robin populations in wintering areas, where both population fractions are sympatric during almost half of the annual cycle (Sep-Mar). This supports the view that a full understanding of the mechanisms underlying population regulation of birds will require the control of both breeding and wintering processes.

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### SAMENVATTING

Vanuit het oogpunt van de vogel zijn er grote verschillen tussen de biotopen waar de winter kan worden doorgebracht en overleefd moet worden. Het is daarom interessant om te zien hoe de verspreiding van de vogels over biotopen verandert naarmate het aantal concurrenten toeneemt. Daarnaast is het interessant om te zien welke dieren uiteindelijk erin slagen zich te vestigen in de beste biotopen. Dit onderzoek gaat over Roodborstjes *Erithacus rubecula* die overwinteren in een bosachtig gebied in Zuid-Spanje nabij de straat van Gibraltar. Een klein aantal broedvogels wordt er elke winter aangevuld met een groot aantal migranten uit noordelijker streken - een enorme verandering van de populatiegrootte. Op basis van de literatuur over overwinterende Roodborsten concluderen de auteurs dat bescherming tegen predatie en niet zozeer voedselaanbod de belangrijkste factor is die de kwaliteit van het winterbiotoop bepaalt. Op basis hiervan verdelen ze hun 21 studiegebieden (Appendix) in gebieden van hoge kwaliteit en lage kwaliteit. Goed ontwikkelde bossen van Kurkeiken *Quercus suber* en Afrikaanse eiken *Q. canariensis* worden geassocieerd als biotopen van hoge kwaliteit.

De graslanden en gebieden met lage bosjes in het laagland worden geassocieerd als biotopen van lage kwaliteit. Roodborsten broeden alleen in de biotopen van hoge kwaliteit. Het aantal Roodborsten neemt jaarlijks toe in de periode sep-nov (na de zomerdroogte) en neemt daarna weer af. Het aantal gebieden dat bezet is door Roodborsten, neemt eerst snel toe met het aantal Roodborsten, maar de curve vertoont een duidelijke afvlakking. Het lijkt erop dat eerst de beste gebieden maximaal worden bezet voordat de Roodborsten zich vestigen in de minder goede gebieden. De aantalsafname in de tweede helft van de winter is het sterkst in de best bezette gebieden, zodat in die periode de Roodborsten steeds uniformer over het hele gebied verdeeld raken. De uit noordelijker gebieden afkomstige migrerende Roodborsten hebben langere en spitsere vleugels dan de lokale (Spaanse) dieren, omdat ze daarmee beter in staat zijn de trektochten te maken. Aan de hand van mistnetvangsten kan dus de samenstelling van de Roodborstpopulatie worden vastgesteld. In de biotopen van slechte kwaliteit komen vooral migrerende Roodborsten voor en ook het aandeel juveniele dieren is er groter. De suggestie uit onderzoek aan noordelijk broedende populaties waar een deel van de vogels 's winters wegtrekt, is dat de vertrekkende dieren kiezen uit de minste van twee kwaden. Aangekomen in het zuiden trekken ze ook daar waarschijnlijk aan het kortste einde. (BJE)

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**Appendix.** Brief description and location (UTM) of study sites. Length of transects (m), classification of sites (type) according to its suitability (HS = high, LS = low suitability), and type of occurrence of Robins at each site (S = summer presence, W= winter occupancy only, N = no occurrence) are shown. Sites 1 to 15 were censused in 1976-77, and the remaining in 1977-78. See Tellería (1981) for further details.

No	Name of site	UTM co-ord.	Site description	L (m)	type	W/S
1	Matorral-Playa	30STE594943	Shrubland	1895	LS	W
2	Pastizal-Playa	30STE627923	Sandy grassland, some scattered shrubs	900	LS	W
3	Valle del Santuario 1	30STE636935	Grassland, scattered shrubs	590	LS	N
4	Valle del Santuario 2	30STE638994	Shrubland	630	LS	W
5	Valle del Santuario 3	30STF606036	Forest	200	HS	W
6	Punta Paloma 1	30STE587956	Grassland, scattered shrubs	390	LS	N
7	Punta Paloma 2	30STE568948	Sandy grassl., some scattered small trees	590	LS	W
8	Punta Paloma 3	30STE576965	Riparian forest	420	HS	W
9	El Rayo	30STE768984	Forest	1800	HS	S
10	Punta Carnero 1	30STE804965	Shrubland	590	LS	W
11	Punta Carnero 2	30STE811948	Riparian forest	540	HS	W
12	Campamento de Anillamiento 1	30STE637974	Riparian forest	540	HS	W
13	Campamento de Anillamiento 2	30STE637981	Riparian forest	400	HS	W
14	Casa del Cable	30STE645902	Grassland, scattered bushes	554	LS	W
15	El Maestral	30STE633941	Riparian forest	2050	HS	W
16	Molino del Maestral	30STE625937	Grassland	830	LS	W
17	La Peña	30STE606943	Grassland interspersed with shrubland	360	LS	W
18	La Hoya	30STE738937	Forest	1900	HS	S
19	Rio Pícaro	30STE796978	Grassland interspersed with shrubland	600	HS	W
20	Arroyo Lobo	30STE797971	Riparian forest	600	HS	S
21	Arroyo Marchenilla	30STE790974	Grassland interspersed with shrubland	415	LS	W