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Migratory and sedentary blackcaps in sympatric non-breeding grounds: implications for the evolution of avian migration

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Summary

1. Several hypotheses have attempted to explain why sedentary populations persist in the wintering grounds of many migratory bird species. For instance, residents may overcome the flooding of their range if they are better competitors than migrants. Alternatively, each population fraction may use different resources or even different habitat types, for example because residents benefit from site tenacity while migrants benefit from resource tracking.

2. To evaluate these hypotheses, we studied the distribution of sympatric migratory and sedentary blackcaps (*Sylvia atricapilla*) in southern Spain during two winters. We distinguished two habitat types: forests, which are used by residents for breeding, and shrublands, to which blackcaps spread in winter with the arrival of migrants. Shrublands are unsheltered habitats that show more abundant but less diverse fruits than forests. We investigated (i) if blackcaps show habitat segregation with respect to migratory behaviour, sex, age and body size, (ii) what resources are used by each population fraction within each habitat type and (iii) how habitat occupancy affects the body condition of individuals.

3. Residents were almost completely restricted to forests, while migrants occupied both habitat types. Among migrants, adults predominated in forests and juveniles in shrublands, but no sexual segregation was found. Body size was larger in residents than in migrants, and these were larger in forests than in shrublands (especially juveniles). If larger birds are dominant, these results support the idea that residents may endure in forests and exclude the most subordinate migrants (juveniles and small birds) towards shrublands.

4. Within forests, migrants and residents tracked fruit abundance, but residents were also associated with the most suitable breeding sites. Migrants tracked fruits less closely in shrublands, due probably to a higher fruit abundance and a lower availability of shelter.

5. Habitat segregation did not affect muscular development of migrants. However, migrants accumulated more fat in shrublands. Therefore, differences in nutritional quality cannot explain why adult and larger blackcaps predominate in forests. Instead, other factors such as food diversity or exposure to predators might account for this distribution.

6. Our results provide a mechanism to explain the persistence of sedentary populations despite migrants overflowing their range and using the same resources. Residents may challenge the arrival of conspecifics because they are better competitors. From an evolutionary perspective, this shows that non-breeding processes may be as important as breeding benefits accrued to migrants for explaining the dynamics of migratory and sedentary populations.

Key-words: body condition, habitat segregation, resource use, *Sylvia atricapilla*, winter ecology.

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Introduction

Birds are able to exploit the most seasonally suitable habitats at each moment in their life cycle. By moving between highly productive breeding and wintering grounds, they may improve fecundity and non-breeding survival, paying a comparatively low cost of movement (Gauthreaux 1982; Alerstam 1991; Berthold 1993). Variation in migratory behaviour is widespread, not only among species but also within species, shifting from sedentary at low latitudes to completely migratory at high latitudes in temperate regions (Newton & Dale 1996; Berthold 1999). As a consequence of this gradation, the wintering area of migratory populations overlaps with the range of residents, which may be literally flooded during winter by migrant conspecifics.

The coexistence of migrant and resident conspecifics in non-breeding grounds poses a dilemma. In the absence of resource partitioning, and assuming that migrants and residents have a similar winter survival, migrants would have a higher recruitment than residents due to the higher fecundity they may achieve in their more productive breeding grounds, eventually putting an end to the resident population (Alerstam & Enckell 1979; Fretwell 1980; Ricklefs 1992; Bell 2000). Competition with migrants has long been thought to explain why residents are absent from the wintering areas of many migratory species, despite these maintaining favourable environmental conditions (Alerstam & Enckell 1979; Bell 2000). However, in many other species residents have somehow overcome the negative impact of migrants, maintaining their population despite their lower fecundity. Nowadays, we have a little knowledge of the processes that may have caused sedentary populations to have persisted in some cases but to have gone extinct in others (Bell 2000).

In two influential papers, Cox (1968, 1985) proposed that residents can outcompete migrants and hence persist in their range as long as environmental conditions allow their existence. If residents take advantage of prior occupancy, site-tenacity and familiarity with the area, they might endure in their breeding territories by expelling arriving migrants once saturation is reached. This may well explain the stable coexistence of both population fractions in non-breeding grounds. Competitive advantages would improve non-breeding survival of residents so as to counterbalance their comparatively low fecundity, while the reproductive benefits accrued to migrants would counteract their reduced non-breeding survival (Greenberg 1980).

Although Cox's hypothesis has been the basis of much subsequent theoretical work (Rappole 1995; Safriel 1995), the actual mechanisms of coexistence of migrants and residents remain poorly studied, and alternative hypotheses have been proposed. Thus, a number of studies have suggested that site-fidelity or familiarity with the area may not have that impact on the outcome of social contests, and prior occupancy by residents cannot preclude that migrants overflow their range (Alerstam & Enckell 1979; Fretwell 1980; Bell 2000). According to this view, whether or not residents may overcome competition with migrants would primarily depend on the size of the migratory population instead of the relative competitive abilities of migrants and residents (Bell 2000).

A third hypothesis for coexistence suggests that competition between migrants and residents may be attenuated through resource partitioning if they preferred different resources or habitat types. This idea originated from the observation that migratory species often occupy secondary-growth habitats in wintering areas. Alerstam & Enckell (1979) even suggested that this is a result of the lower predictability of these habitats, where residents would lose the advantage of site-tenacity and hence might compete less efficiently. However, different requirements of migrants and residents could facilitate habitat segregation without too extensive competition. Residents have reproductive interests within their range, where they could try to endure over winter to benefit from an early occupancy of the best breeding territories (Verboven & Visser 1998). Migrants, which are free of these pressures, may track resources necessary to secure self-maintenance, such as food and refuge to escape predators (Herrera 1985; Blem 1990; McNamara & Houston 1990; Watts 1991; Rey 1995).

Understanding non-breeding interactions between migrants and residents is also crucial to the theory of the evolution of migration. Based on the former models of conspecific interaction, three main hypotheses have tried to explain how migratory behaviour could appear from an otherwise sedentary population, leading to a migratory species with nonoverlapping breeding and wintering grounds (Rappole 1995). According to the first hypothesis (Cox 1985), if locals are better competitors the split between breeding and non-breeding areas of migrants could proceed by selection for leap-frogging the residents' range. Leap-frog migration could be favoured because many migrants are obliged to leave the areas already occupied by residents, and birds that move beyond could eventually reach suitable non-breeding habitats without competitors (Cox 1985). However, this cannot account for the final extinction of residents, which has to be explained by advocating other processes such as the deterioration of environmental conditions or interspecific competition (Cox 1985).

The second hypothesis is based on the assumption that residents lack advantages over migrants, so that intraspecific competition may drive sedentary populations to extinction (Alerstam & Enckell 1979; Bell 2000). In this case, the split between breeding and non-breeding areas of migrants would occur through a wave-like latitudinal expansion of their breeding range caused by a progressively increased fecundity at higher latitudes, combined with the inability of resident populations to afford flooding by migrants below some fecundity threshold at lower latitudes. Thus, breeding populations would disappear from areas in which the breeding output was too small to counterbalance mortality due to competition with more northerly migratory populations, so the persistence of sedentary populations would provide evidence that only migratory populations have not directly outcompeted them (Bell 2000).

Finally, the third hypothesis does not require competition to explain the separation of breeding and wintering grounds of migrants, and suggests that this would be triggered by selection by migrants of resources located outside the residents' geographical range (Chesser & Levey 1998). The first migrants would occupy a sort of 'ecological vacuum' in winter bird communities (Hutto 1980), which would allow them to increase their numbers in a population dominated by sedentary birds (Levey & Stiles 1992). For instance, Levey & Stiles (1992) realized that many temperate migrants are frugivorous and occupy open habitats, two strategies based on the exploitation of unpredictable environments that force birds to track resources, and proposed that wandering movements connected to these strategies would be precursors of true migrations (Levey & Stiles 1992; Chesser & Levey 1998).

To resolve which of these theories best explains the evolution of migration requires knowledge of how migrant and resident conspecifics interact in non-breeding grounds (Cox 1985; Levey & Stiles 1992; Rappole 1995; Bell 2000). This should elucidate whether they have a different habitat distribution, and how this may be affected by competition or habitat preferences. In order to enter into social contests, both migrants and residents should use the same resources within habitats (Greenberg 1986). In addition, competition should make dominant individuals predominate in the best habitat types. For example, in many species adults and males are dominant over juveniles and females, respectively, and often occupy the best habitat types in wintering grounds (Marra, Sherry & Holmes 1993; Sherry & Holmes 1996; Marra 2000). On the other hand, to be large may give subordinate individuals (e.g. females or juveniles) priority of access to the best habitats compared to the smallest subordinates, or even to the smallest dominants (Ketterson 1979; Marra 2000). Finally, the consequences to individuals of habitat occupancy should be evaluated. Social dominance can only have ecological significance if it affects adversely some fitness component of subordinates, for example survival (Greenberg 1986). Indeed, the occupation of poor, subordinate-biased habitats in wintering grounds usually translates into an increased physiological stress and an impaired body condition of birds (Sherry & Holmes 1996; Marra & Holberton 1998; Strong & Sherry 2000).

However, the difficulty of telling apart migrants from residents has precluded resolving their interactions in winter. These have been inferred by studying migratory and sedentary species with different degrees of relatedness (Fretwell 1980; Hutto 1980; Cox 1985; Levey & Stiles 1992; Ricklefs 1992; Chesser & Levey 1998), or by relying on the patterns of distribution and the relative size of migratory and sedentary populations in the whole species range (Safriel 1995; Bell 2000). However, to our knowledge very few studies have attempted to analyse winter interactions between migrant and resident conspecifics (Pérez-Tris, Carbonell & Tellería 2000a; Tellería *et al.* 2001).

We studied sympatric migratory and sedentary blackcaps, *Sylvia atricapilla* (L.), wintering at the northern side of the Strait of Gibraltar (southern Spain). In this region, sedentary blackcaps breed in forests, but avoid neighbouring shrublands for reproduction. However, both habitat types are occupied in winter, with the arrival of migratory blackcaps from north-western Europe. This gives an excellent opportunity to test the hypotheses mentioned above, because resident blackcaps can be distinguished accurately from migrants based on their morphology (Pérez-Tris, Carbonell & Tellería 1999). We studied the extent to which migrants occupy the breeding areas of residents, and the extent to which residents disperse towards neighbouring environments during winter. We also analysed habitat segregation in relation to sex, age and body-size to evaluate the role of social dominance in determining such distribution. In addition, we examined whether migrants and residents differ in habitat use by comparing how closely they track food resources and shelter within forests and shrublands, and by studying whether residents remain in their breeding territories during winter. Finally, we studied the consequences to individuals of conspecific interactions by analysing the variation in body condition of blackcaps in relation to habitat occupancy, sex, age and migratory behaviour.

Methods

STUDY AREA AND FIELD METHODS

We studied blackcaps during two winters (between 1998 and 2000) in an area of around 200 km^2 in the Campo de Gibraltar area (36°01′N, 5°36′W). In this region, montane areas between 100 and 300 masl are forested primarily by cork-oaks *Quercus suber* L., but mixed with Mirbeck's oaks *Q. canariensis* Willd., which constitute the main breeding habitats of blackcaps. The lower elevation areas are largely bare shrublands dominated by lentiscs *Pistacia lentiscus* L. and wild olives *Olea europaea sylvestris* (Miller), where blackcaps rarely breed.

We mist-netted blackcaps in forests and shrublands from mid-December to mid-January, when the species is not migrating through the area (Cramp 1992). Five sites were sampled in forests and four in shrublands, which showed similar shelter, food abundance and migrant–resident ratios as shown by Tukey's tests in an ANOVA with site as a factor and mist-netting plots as sampling units ($P > 0{\cdot}05$ in all pairwise within-habitat comparisons; see methods to measure these variables below). Because of this we did not consider between-site differences in our analyses. We made sure that blackcaps were present as breeders in all forest sites and absent from all shrubland sites by means of extensive searching in spring (Tellería & Pérez-Tris, in preparation). All sites were sampled from dawn to dusk and at least twice in the study period, first in December and later on in January (about 3 weeks later). Every day we set up four to 12 mist-nets in randomly selected locations, but avoiding spots too bare to conceal mist nets.

Mist-nets were visited hourly, and all individuals were processed within 1 h of capture. Blackcaps were sexed and aged by plumage (Svensson 1992). We distinguished between juveniles (first-winter birds) and adults (older birds whose exact age was unknown). Of 548 blackcaps captured in total, we were unable to age 26 individuals which were excluded from the analyses. We measured flattened maximum wing chord, length of the eighth primary (feathers numbered from the body to the wing tip), tail length and distance between the wing tip and the tip of each primary (from the first to the ninth, hereafter primary distances). All these measurements were taken to the nearest half mm using appropriate rulers. We also recorded the tarsus length (to the last unbroken scale before the toes), the bill length from the skull and the bill height at the culmen, using a 0·01-mm precision digital calliper (for further details, see Svensson 1992). Finally, we estimated visually the size of the subcutaneous fat deposits (according to a nine-value scale; Kaiser 1993) and weighed blackcaps with a 0·1-g precision digital balance. All the measurements were recorded by JP-T to avoid any interpersonal bias. Every blackcap was marked with a numbered aluminium ring to avoid repetition.

HABITAT CHARACTERISTICS OF FORESTS AND SHRUBLANDS

Blackcaps are forest birds, so they are likely to be more vulnerable to predators in open landscapes (Watts 1991). On the other hand, they are intensive frugivores in winter (Jordano & Herrera 1981; Herrera 1998). Although blackcaps could prefer habitats with abundant fruits, they have been found to feed upon up to nine fruit species in places where most fruits are rare and one single species is supplied almost *ad libitum*, which suggests the need of maintaining an adequate nutrient balance in the diet (Herrera 1982, 1985). According to this, the best wintering habitats for blackcaps should be sheltered environments with a high abundance and variety of fleshy fruits.

To evaluate these features, we recorded the percentage of ground covered by trees (vegetation above 2-m height), shrubs (below 2 m) and grass or bare ground in a 50-m diameter circular plot around each mist-net. We also recorded the number and specific composition of shrubs and trees holding ripe fruits in each sampling plot. We only considered the fruits that blackcaps feed upon habitually (according to studies of diet; Jordano & Herrera 1981; unpublished data). These are all fleshy fruits in the area except *Rosa* spp., *Crataegus monogyna* Jacq. and *Ruscus aculeatus* L., three species with large and very hard berries that have never been found in the diet of these blackcaps (unpublished data).

DISTRIBUTION OF SEDENTARY AND MIGRATORY BLACKCAPS

We used a morphological discriminant function to distinguish migratory from sedentary blackcaps. The technique is based on three traits: the length of the eighth primary feather, the tail length and the difference between the primary distances 1 and 9 (a simple index of wing pointedness). When applied to Iberian blackcaps, this method allows the correct classification of 91% of individuals (Pérez-Tris *et al.* 1999). North-western European blackcaps, the main components of populations wintering in our study area, have more pronounced migratory-like traits than Iberian migratory blackcaps (Pérez-Tris & Tellería 2001). Hence, they will be more easily classified by a method that differentiates so finely between Iberian migratory and sedentary populations (for further details see Pérez-Tris *et al.* 1999).

We conducted a log-linear analysis to investigate the variation in population composition between forests and shrublands in relation to migratory behaviour, sex and age. To obtain the log-linear model, we first proceeded hierarchically by fitting all interactions of order n to the corresponding null hypotheses that all of them are simultaneously zero. As soon as the reduction in n caused a lack of fit, we selected the terms of that order or lower which significantly contributed to explain the distribution of frequencies, thus generating the final model that best fitted the data (StatSoft 1999).

We used mist-nets as sampling units to analyse whether the abundance of migrant and resident blackcaps is associated with the same or different resources within habitats. As mist-nets differed in the number of days they were opened (because of different reasons including forestry or presence of cattle), we derived capture indices for each net computed as the number of individuals captured per day, excluding recaptures. Capture indices were computed for each population group; that is, individuals with the same migratory behaviour, sex and age, and were used as measures of abundance in our analyses (after log-transformation to meet normality).

Because the patterns of distribution of different population groups are non-independent, to analyse how they are associated with habitat characteristics one by one would increase the risk of detecting significant effects by chance alone. To avoid this, we conducted a principal components analysis (PCA) with the capture indices of each population fraction and the variables measured to assess habitat characteristics. By so doing, we studied (1) if there is a match between the abundance of migrants and residents within habitats and (2) which resources are associated with the distribution of each population fraction at the within-habitat scale, taking into account the possible effects of sex and age. We considered food and vegetation cover to be important resources for all blackcaps, and the distribution of breeding resources to be possible particular requirements of residents. In our study area, breeding territories show a high cover of Mirbeck's oaks and brambles (*Rubus* spp.), a thorny bush commonly chosen by blackcaps as the nest site (Carbonell & Tellería 1998).

BODY SIZE AND BODY CONDITION

We conducted a PCA with several body dimensions to extract an index of structural body size (Rising & Somers 1989). The PC1 was a good descriptor of body size, showing high positive loadings for all body measurements except wing length (eigenvalue = 1·59; factor loading for tarsus length = 0·74, bill length = 0·71, bill height = 0·44, wing length = 0·13, tail length = 0·57). Wing length showed a small loading on this component and was separated on the PC2 together with tail length (eigenvalue = 1·34; tarsus = 0·14, bill length = 0·34, bill height = 0·28, wing = −0·86, tail = −0·62). This was due probably to the strong variation in flight-related morphology in the population, which includes birds from many different breeding-site origins (Pérez-Tris *et al.* 1999; Pérez-Tris & Tellería 2001).

We used the amount of fat stored by blackcaps as a measure of their body reserves, as it has been suggested that starvation probabilities decrease exponentially with increasing fat stores (Blem 1990; McNamara & Houston 1990). Visual estimates of fat content have long been used to measure the nutritional condition of wintering birds (Brown 1996). However, the relationship between the amount of fat scored by visual indices and the actual fat content is not linear, but usually fits better a quadratic model (Rogers 1991; Kaiser 1993). Because of this, we used the logarithm of the squared fat scores as a measure of fat content, which was normally distributed and linearly related to body mass (changes in avian body mass are chiefly due to fat mobilization; Blem 1990). We controlled for daily fat accumulation in the analysis of fat content, but fat storage also depends on other factors which are less easily controlled, such as unpredictable variations in environmental conditions, predation risk or dominance hierarchies (Blem 1990; McNamara & Houston 1990; Witter & Cuthill 1993). Because of this, we also studied the muscular development of individuals, which measures long-term nutrient reserves more effectively (Brown 1996). At a given body size, changes in avian body mass are related primarily to fat accumulation, but after this they depend principally on the development of the large pectoral muscles (Blem 1990). We regressed body mass on structural size and fat content (beta values: size = 0·47, $P < 0·0001$; fat = 0·45, $P < 0·0001$) and used the residuals of this regression as indices of muscular development.

Results

HABITAT CHARACTERISTICS OF FORESTS AND SHRUBLANDS

A PCA with the arcsine-transformed proportion of ground covered by trees, shrubs and grass in each sampling plot extracted a single component which accounted for 80% of variance, whose scores increased with increasing vegetation cover (eigenvalue = 2·39; factor loading for trees = 0·81, shrubs = 0·91, grass or bare ground = −0·94). Obviously, forests are more sheltered environments than shrublands (Fig. 1; two-way ANOVA: habitat $F_{1,109} = 206·53$, $P < 0·0001$, year $F_{1,109} = 0·003$, $P = 0·95$, interaction $F_{1,109} = 3·41$, $P = 0·068$).

The average number of fruit-holding shrubs per plot was higher in shrublands than in forests in both years, and slightly increased in the second winter (ANOVA with the log-transformed abundance of fruits: habitat $F_{1,109} = 68·46$, $P < 0·0001$, year $F_{1,109} = 4·25$, $P = 0·042$, interaction $F_{1,109} = 1·83$, $P = 0·18$; Fig. 1). The lentisc and the wild olive were by far the most abundant and widely distributed species in both habitat types. However, while these were the only species found in shrubland plots (where some scattered *Smilax aspera* L. observed during fieldwork apparently made up the rest of available fruits), three other species occurred frequently in forest plots: *Myrtus communis* L., *Phillyrea latifolia* L. and *S. aspera*, the first two being common depending on year (Fig. 1). Moreover, we observed some scattered *Rhamnus alaternus* L., *Hedera helix* L. and *Viburnum tinus* L. in forests during our fieldwork. Therefore, despite the fact that fruits were less abundant in forests, they were more diverse there than in shrublands.

HABITAT SEGREGATION IN RELATION TO MIGRATORY BEHAVIOUR, SEX AND AGE

The composition of blackcap populations varied between forests and shrublands, which remained similar between study years with only slight changes with respect to sex. The best log-linear model to explain the frequency of each population group in forests and shrublands included five interactions (Table 1, Fig. 2). The first one, between habitat and population, showed that resident blackcaps were almost restricted to forests, while migrants occupied both habitats more equally although they were more abundant in shrublands. Adult blackcaps were more frequent in forests while juveniles predominated in shrublands, leading to an interaction between age and habitat type. Males were more frequent than females in forests in the first winter, but this trend disappeared in the second winter causing an interaction between sex, habitat and year. However, this was not associated with sexual segregation in the first winter, but to a higher proportion of resident juvenile males captured in forests that year, as shown by the significant change between years in the proportions of individuals of each sex and age. Finally, we captured a higher proportion

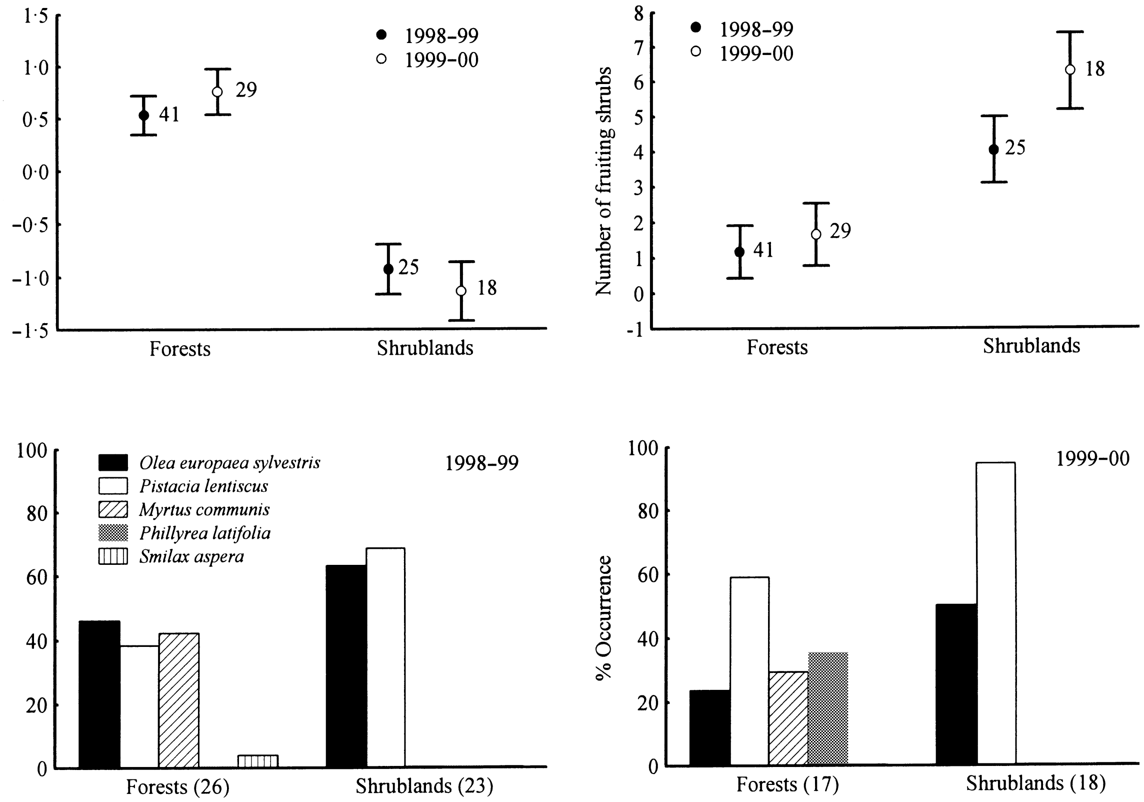

Fig. 1. Habitat characteristics of forests and shrublands. Above, variation between habitats and years in shelter (an index obtained by PCA that increases with increasing cover of trees and shrubs) and fruit abundance measured around mist-nets (means ± SE and sample sizes). Below, variation between habitats and years in the species composition of fruiting shrubs (frequency of each species in sampling plots with fruits, whose number is indicated in brackets).

Table 1. Log-linear analysis of blackcap frequencies according to population, sex, age, habitat type and year. From top downwards, the fit to the lack of interactions of the corresponding order (only the relevant orders are shown), the goodness of fit of the final model and the contributions of each interaction included in the model are shown. Partial associations are computed by evaluating the gain of fit of the model that includes the corresponding interaction with the model that excludes it. Marginal associations are computed by comparing the fit of the model including all effects of lower order than the one of interest with the model including that interaction instead (StatSoft 1999)

		Maximum likelihood chi-square			
	d.f.	χ^2	P		
Order of interactions					
No fourth-order interactions	5	2·06	0·840		
No third-order interactions	10	26·35	0·0033		
Test of fit of the final model:	14	6·65	0·948		
		Partial association		Marginal association	
Interactions in the model		χ^2	P	χ^2	P
Population × habitat	1	148·80	< 0·0001	154·62	< 0·0001
Age × habitat	1	25·11	< 0·0001	25·30	< 0·0001
Sex × habitat × year	1	8·86	0·0029	9·27	0·0023
Sex × age × year	1	7·02	0·0081	3·68	0·0549
Sex × age × population	1	7·83	0·0051	8·47	0·0036

of juveniles of the migratory population, which was especially accentuated in females leading to an interaction between sex, age and population (Table 1, Fig. 2).

The differences in population composition identified in our analyses could be influenced by different probability of capture of migrants and residents. To evaluate this possibility, we analysed 20 recaptures of blackcaps obtained during the study, of which none was recaptured more than once. In forests, residents had a slightly higher recapture rate (13 of 134 residents and

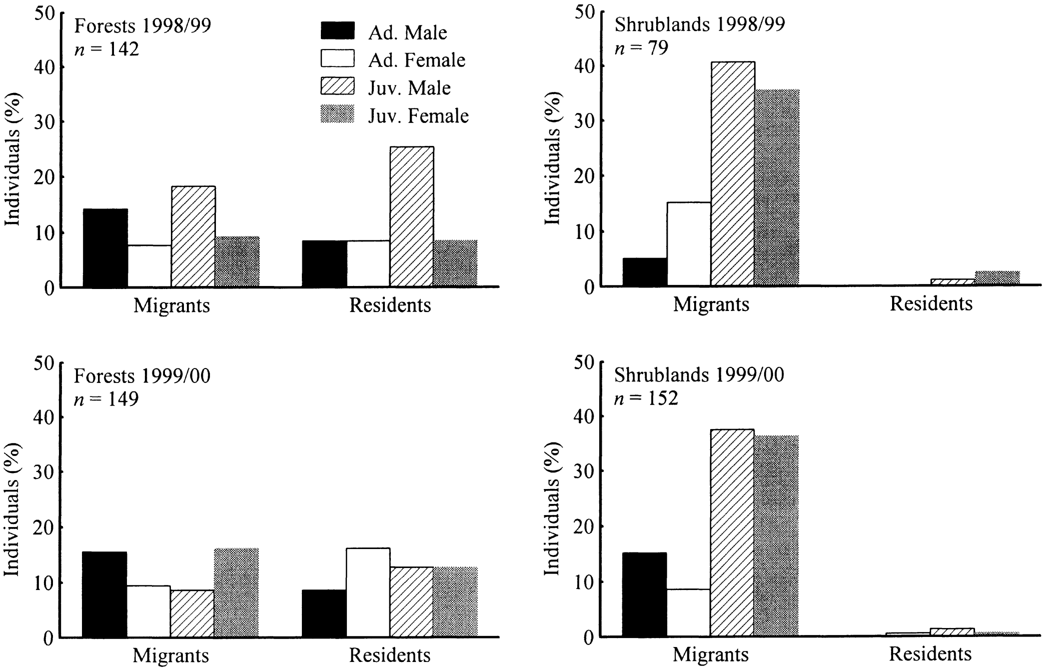

Fig. 2. Composition of the blackcap populations wintering in forests and shrublands in each study year, with respect to migratory behaviour, sex and age.

three out of 151 migrants were recaptured; Fisher's exact test: $P = 0{\cdot}02$). In shrublands, four of 224 migrants were recaptured, but none of seven residents was ever recaptured. Although the number of recaptures was too small, these data showed that residents had the same recapture probability than migrants in this habitat ($P > 0{\cdot}99$), and that migrants had the same probability of recapture in both habitat types ($P > 0{\cdot}99$). These results support the view that residents remain in their breeding territories during winter, thus being easier to recapture, while migrants track resources more intensely in wintering grounds regardless of the habitat occupied.

We tested for between-site variation in population composition by repeating the log-linear analyses within habitats, including a site factor and excluding year effects to keep a suitable within-cell sample size. In forests, changes among localities in population composition were difficult to model (maximum likelihood chi-square of goodness of fit of the final model: $\chi^2 = 14{\cdot}38$, d.f. = 10, $P = 0{\cdot}16$). The model obtained did not include interactions between site and population or age, as we obtained using habitat as a factor. However, there was a significant interaction between sex, age and site (partial association chi-square: $\chi^2 = 14{\cdot}64$, d.f. = 4, $P < 0{\cdot}01$) and an almost significant interaction between sex, population and site ($\chi^2 = 8{\cdot}95$, d.f. = 4, $P = 0{\cdot}062$). The fact that some combinations of sex and age classes were more frequent in some localities than in others could be related to the higher proportion of resident juvenile males captured during the first winter, as we captured slightly different numbers of blackcaps each winter in each site ($\chi^2 = 8{\cdot}92$, d.f. = 4, $P = 0{\cdot}063$). Nevertheless, this slight variation in population composition cannot affect our conclusions, as sexes, ages and migratory behaviours were represented in similar proportions in all forest sites. In shrublands, between-site variation was negligible, as shown by the log-linear analysis which could not discard the absence of lowest-order interactions (maximum likelihood chi-square of goodness of fit to the null hypothesis that all two-way interactions are simultaneously zero: $\chi^2 = 13{\cdot}42$, d.f. = 12, $P = 0{\cdot}34$).

DISTRIBUTION WITHIN HABITATS OF MIGRANTS AND RESIDENTS

It follows from the former results that the comparison of within-habitat distribution of migrants and residents must be restricted to forests, where both population groups occur in enough numbers. Furthermore, a PCA including forests and shrublands would give a non-realistic picture of the association between breeding resources and the abundance of residents, as both are restricted to forests. To avoid these problems, we analysed the associations between migrants, residents and habitat characteristics within forests by means of a first PCA. After this, we checked whether migrants track the same resources in both habitat types by conducting another PCA for shrublands, including only migrants and excluding the cover of Mirbeck's oaks (which are absent from shrublands).

The PCA from forest plots extracted two components (Table 2). The PC1 showed that, in general, all blackcaps track the abundance of fruits in that habitat type (Fig. 3). Moreover, because fruits are abundant in forest clearings and very scarce in the most developed areas covered by Mirbeck's oaks, this analysis allowed us to discern unequivocally the generalized preference

Table 2. Factor loadings in the PCAs evaluating the association between abundance of blackcap population fractions and the variables measured to describe habitat characteristics (cover of Mirbeck's oaks and brambles, number of fruit-holding shrubs, and an index of shelter obtained by PCA from vegetation covers) in forest and shrublands. The significance of each correlation is also shown

	Forests (n = 70)		Shrublands (n = 43)	
	PC1	PC2	PC1	PC2
Migrants				
Adult males	−0·614**	0·015	0·608**	−0·172
Adult females	−0·672**	−0·101	0·806**	−0·104
Juvenile males	−0·700**	−0·035	0·816**	−0·037
Juvenile females	−0·593**	0·270*	0·830**	−0·224
Residents				
Adult males	−0·271*	−0·067	–	–
Adult females	−0·607**	0·390**	–	–
Juvenile males	−0·587**	−0·294*	–	–
Juvenile females	−0·477**	0·520**	–	–
Habitat features				
Mirbeck's oaks	0·397	0·674**	–	–
Brambles	0·004	−0·646**	−0·102	−0·922**
Fruit abundance	−0·664**	−0·160	0·534**	0·579**
Shelter	−0·001	0·564**	−0·006	−0·267
Eigenvalue	3·283	1·813	2·670	1·349
Variance (%)	27·36	15·11	38·15	19·27

*P < 0·05; **P < 0·001.

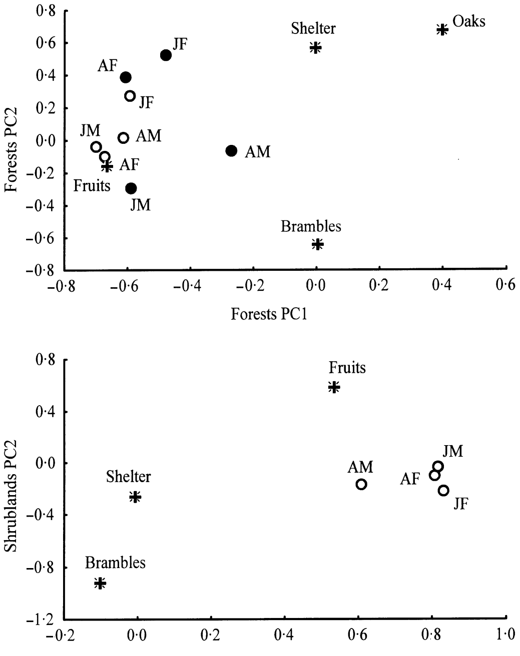

Fig. 3. Plot of loadings in the two components extracted by PCA with the capture index of each blackcap population group (open dots: migrants, filled dots: residents) and the variables measured to describe habitat characteristics (cover of Mirbeck's oaks *Quercus canariensis* and brambles *Rubus* spp., and number of fruit-holding shrubs; stars). Labels identify age classes (A: adults, J: juveniles) and sexes (M: males, F: females). Above, residents and migrants in forests; below, migrants in shrublands. Mirbeck's oaks never occurred in shrublands and hence were excluded from the second PCA. Further details on the correlations of each variable with each component are given in Table 2.

of blackcaps for fruits above shelter and breeding territories. Only resident adult males deviated towards a higher preference for these latter resources, indicating that they tend to remain in their breeding territories during winter to a greater extent than other resident population groups (Fig. 3). The PC2 defined a gradient of increasing forest development, with highest loadings for oak cover and shelter. However, the cover of brambles (the main nesting substrate of blackcaps in the area) had a very low, negative loading in this component. Interestingly, controlling for the strong effect of fruit abundance in the distribution of blackcaps, resident males tended to be better associated with brambles, while resident females tended to occur in more sheltered sites (Fig. 3). Meanwhile, migrants chiefly situated themselves in the space between, in closer correlation to the abundance of fruits than any of the resident population groups (Fig. 3).

We found sensibly different patterns for migrants when we analysed their distribution in shrublands with the second PCA (Table 2). As in forests, the PC1 showed that migrants tended to be better related to fruit abundance than to any of the other variables considered. However, fruit abundance was a poorer predictor of the abundance of migrant blackcaps in shrublands compared to forests (Fig. 3), suggesting that the distribution of birds in this habitat is affected by other factors. Indeed, all population groups were weighted similarly to vegetation cover in the PC2 (Fig. 3, Table 2), indicating that, controlling for fruit availability, shelter is important in determining the distribution of blackcaps in this habitat type.

Table 3. Results of analyses of structural size (scores of the PC1 from body dimensions), subcutaneous fat (controlling for time of day) and body condition (residuals of body mass on structural size and fat content) in migratory and sedentary blackcaps wintering in forests. Non–significant interactions have been omitted (all with $P > 0{\cdot}10$). Sample sizes are the same as in Fig. 2, with some missing values as summarized at the foot of the table

	Structural size*		Subcutaneous fat		Body condition†	
	$F_{1,274}$	P	$F_{1,274}$	P	$F_{1,273}$	P
Sex	7·95	0·0052	0·27	0·602	3·61	0·059
Age	1·85	0·175	0·50	0·480	0·04	0·847
Population	15·69	0·0001	1·63	0·203	1·02	0·312
Winter	0·49	0·486	3·47	0·064	12·73	0·0004
Time of day§	–	–	108·35	< 0·0001	–	–

*A juvenile resident male without wing length data was excluded.
†Another juvenile resident male (without body mass data) was excluded.
§The interactions between factors and the covariate were not significant.

CHANGES IN BODY SIZE AND BODY CONDITION

The absence of residents from shrublands made it difficult to test for between-habitat variation in body size and body condition. To avoid the confounding effect of an extreme imbalance when conducting ANOVA, we divided our analysis of body size and body condition into two parts. First, we tested for differences between migrants and residents in forests, and then we studied changes between forests and shrublands in migrants.

In forests, body size varied in relation to migratory behaviour and sex (Table 3). Residents were larger than migrants, and females were larger than males (Fig. 4). When studying the variation between habitats in body size of migrants, we also found females to be larger than males, although in this case the pattern was not significant (Table 4). Migrant blackcaps were larger in forests compared to shrublands and, on average, adults were larger than juveniles. Interestingly, however, we found significant interactions between age, sex and habitat. Thus, the juvenile migrant males captured in forests were larger than those captured in shrublands. By contrast, no such trend could be detected in migrant females, whose body size was larger in forests regardless of the age of individuals (Table 4, Fig. 5).

Controlling for daily fat storage, we did not find differences in fat content between residents and migrants in forests, nor did we find any significant trend with respect to sex or age (Table 3, Fig. 4). Muscular development, however, significantly increased in the second winter in all population groups. No differences were found between population groups, sexes or age classes, although there was a non-significant trend towards females to be heavier than males in both years (Table 3, Fig. 4). When studying the body condition of migrant blackcaps, we observed differences between habitats and years. Controlling for time of day, migrant blackcaps stored more fat in shrublands than in forests, and decreased fat reserves from the first to the second winter in both habitats (Table 4, Fig. 6). However, muscular development did not vary in the same way. Remarkably, differences between habitats were not significant. There was a trend to increase protein reserves in the second winter when studying migrants in both habitats, but this change was not significant. In fact,

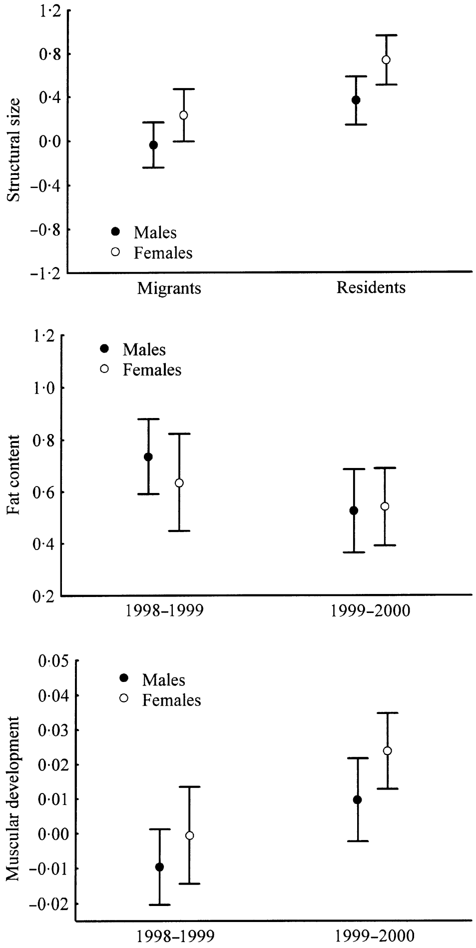

Fig. 4. Variations in structural size (scores of the PC1 from body dimensions), fat content (measured as the logarithm of the squared fat scores) and muscular development (residual body mass controlling for size and fat content) among blackcaps wintering in forests (means ± SE, adjusted by time of day in the case of fat). The relevant comparisons of means according to our results (Table 3) are shown.

Table 4. Results of analyses of structural size (scores of the PC1 from body dimensions), subcutaneous fat (controlling for time of day) and body condition (residuals of body mass on structural size) of migratory blackcaps wintering in forests and shrublands. Non–significant interactions have been omitted (all with $P > 0{\cdot}14$). Sample sizes are the same as in Fig. 2, with some missing values as summarized at the foot of the table

	Structural size*		Subcutaneous fat		Body condition†	
	$F_{1,351}$	P	$F_{1,351}$	P	$F_{1,350}$	P
(1) Sex	2·98	0·085	1·91	0·168	7·29	0·007
(2) Age	8·37	0·004	< 0·001	0·962	0·001	0·977
(3) Habitat	5·98	0·015	40·34	< 0·0001	2·37	0·125
(4) Winter	0·27	0·605	7·97	0·0050	3·44	0·064
2 × 3	7·50	0·0065				
1 × 2 × 3	4·37	0·037				
Time of day§	–	–	134·53	< 0·0001	–	–

*One juvenile female (without bill height data) was excluded.
†Another juvenile female (without body mass data) was excluded.
§The interactions between factors and the covariate were not significant.

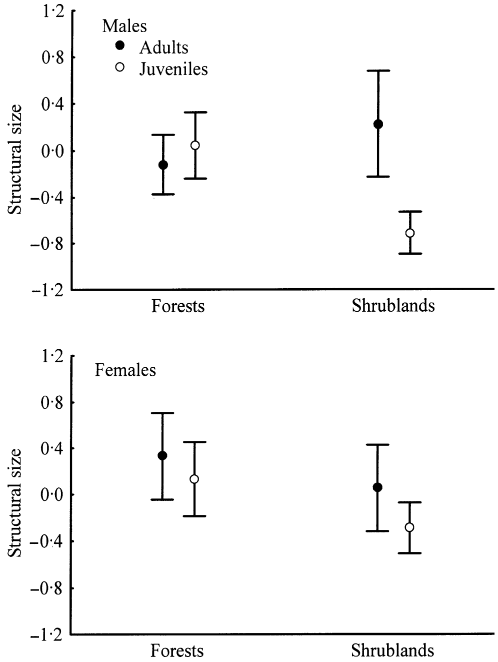

Fig. 5. Changes in structural size (scores of the PC1 from body dimensions) between habitat types in migrant blackcaps, according to sex and age (means ± SE).

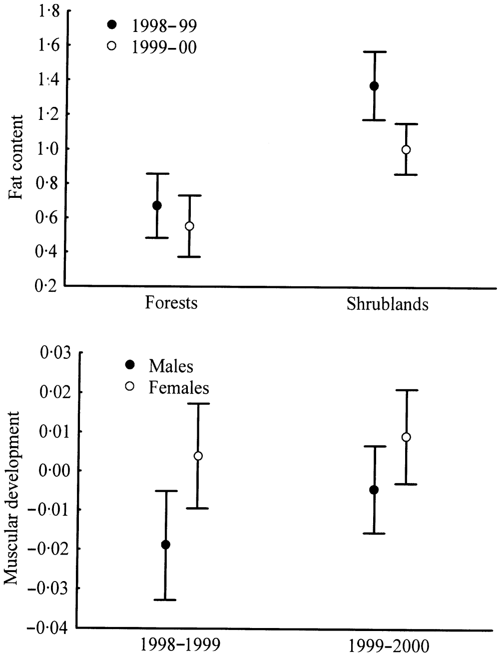

Fig. 6. Changes in fat content (measured as the logarithm of the squared fat scores) and muscular development (residual body mass controlling for size and fat content) in migrant blackcaps wintering in forests and shrublands. The relevant comparisons of means according to our results (Table 4) are shown.

only sexual differences, which were already intimated in the comparison between migrants and residents in forests, were significant in this analysis, with females being heavier than males in both habitat types and in both winters (Table 4, Fig. 6).

Discussion

DISTRIBUTION OF BLACKCAPS BETWEEN HABITATS: A ROLE FOR DOMINANCE

According to our evaluation of habitat characteristics, forests are better environments than shrublands for blackcaps wintering in our study area. In forests, blackcaps can move into sheltered sites and hence escape predators. In addition, fruits are more diverse in forests, where blackcaps can therefore maintain better nutrient balance. Apparently, the only advantage of shrublands is that they sustain larger fruit crops than forests. Due to the abundance of wild olives and lentisc berries, blackcaps might find more food in this habitat. Nevertheless, this difference may be unimportant in so far as these fruits are not exhausted in winter in either of the habitats (pers. obs.). If these fruits are supplied *ad libitum* in forests and shrublands, the higher variety of other fruiting shrubs in forests could make them more appealing for blackcaps (Herrera 1982, 1985).

In this heterogeneous landscape residents are almost restricted to forests, while migrants also occupy shrublands. However, this does not necessarily mean that one population fraction, for instance migrants or residents, is displacing the other to worse habitats. Residents could be enduring in their breeding territories, while migrants could be tracking winter resources that are more uniformly distributed between habitats. Considerable insight on this respect was gained by studying the distribution of blackcaps according to sex, age and body size. Adults were more frequent in forests than juveniles, but no sexual habitat segregation was found. In the majority of species studied, males are dominant over females and hence predominate in the preferred habitat types (e.g. Sherry & Holmes 1996). This trend also holds in partial and differential migrants, in which males make up the bulk of the sedentary fraction or migrate shorter distances than females on average (Ketterson & Nolan 1983; Adriaensen & Dhont 1990). The few studies that have failed to detect dominance of males have dealt with non-territorial birds (Myers 1981) or with species in which females are larger than males (Arnold 1991 and references therein). Remarkably, blackcaps rarely defend winter territories (Cramp 1992), and reversed sexual size dimorphism was revealed by our analysis of body size. Although the non-territorial character of blackcaps could somewhat lessen interactions, these clearly occur between adults and juveniles (see below), and we have no reason to believe that social contests are feebler between sexes than between age classes (Marra 2000; but see Greenberg 1986). In our view, it is the reversed sexual size dimorphism that most probably accounts for the lack of sexual segregation in blackcaps. In fact, although males could be behaviourally dominant, for example due to the correlation between testosterone levels and aggressive behaviour (Ketterson & Nolan 1992), the larger size of females could mitigate this effect leading to a similar distribution of the two sexes.

While the sexes did not segregate between the two habitats, the ages did. A number of studies have found the same association between age and habitat quality in other species (for a review see Sherry & Holmes 1996), and experiments involving removal of territory owners have supported dominance as the mechanism (Marra *et al*. 1993; Marra 2000). In our study, the variation in body size is consistent with dominance as the cause of spatial segregation. Thus, juvenile migrants were larger in the dominant-biased habitat (forests). Moreover, this trend held in males, the smallest-sized sex, but not in females. Similarly, in wintering American redstarts (*Setophaga ruticilla*) sexual habitat segregation is reinforced by social dominance in which males are larger and dominant over females, and females have a larger body size in the male-biased habitat type (Marra 2000). In addition, if smaller individuals are subordinates and hence suffer higher mortality rates, selection for a larger body size could explain why adults are larger than juveniles in male migrant blackcaps (Fig. 5).

Based on these results, our study provides a possible explanation for the ability of residents to remain in their breeding range when migrants arrive seasonally. Residents are larger than migrants and, interestingly, migrants are on average larger in forests than in shrublands. If larger birds are dominant, as our results suggest, residents could prevent migrants from occupying their range. Once saturation is reached in these habitats, subordinate migrants (juveniles and, among these, small birds) would make up the bulk of the fraction excluded to shrublands, leading to the differences in body size between habitats that we observed. Among the morphological correlates of migration, the reduction in body size has been interpreted as a way to decrease wing load (Winkler & Leisler 1992). Indeed, migrant blackcaps wintering in our study area are smaller but show longer and more pointed wings than residents, consistent with selective pressures related to migration (Pérez-Tris & Tellería 2001). According to our results, morphological adaptations of migratory blackcaps could improve migration performance at the expense of reduced competitive ability in the wintering grounds.

WITHIN-HABITAT DISTRIBUTION OF MIGRANTS AND RESIDENTS

Within forests, the distribution of blackcaps was associated with the distribution of fruits, independently of migratory behaviour, sex or age. The movements of blackcaps tracking fruit crops are well known, especially in migratory populations wintering in the Mediterranean (Herrera 1985; Rey 1995). Our results support this finding even in residents, which at a reduced scale compared to migrants also track the availability of fruits. Since migrant and resident blackcaps use the same resources within forests, their habitat segregation is unlikely to be caused by different habitat preferences. Instead, the use of common resources within forests could propitiate the social dominance interactions that force subordinate migrants to occupy shrublands. Consistent with this interpretation, a year-round monitoring of blackcap abundance has found that forests are saturated habitats (where blackcaps hardly increase in abundance from spring to winter), whose fruits are more intensely depleted in winter compared to shrublands (Tellería & Pérez-Tris, in preparation). In addition, singing blackcaps are more frequent in forests than in shrublands, suggesting some defence of territories in the former habitats (Tellería & Pérez-Tris, in preparation).

Although migrants and residents do not appear to partition resources within forests, their distribution was slightly different in this habitat. Resident adult males showed a weaker relationship with fruit abundance than the other population components. In addition, controlling for the effect of fruit abundance on the distribution of blackcaps, residents tended to be more abundant in areas with abundant shelter, and particularly in sites covered by brambles in the case of males. This association between the abundance of breeding resources – such as brambles – and the abundance of resident males supports the hypothesis that residents may benefit from site tenacity by increasing the probability of getting a suitable breeding site. The higher recapture rates of residents in this habitat supports this, which agrees with the view that forests make the best alternative to resident blackcaps, both from the breeding and the non-breeding perspective.

Based on the pattern of habitat segregation in relation to age and body size, migrants also prefer forests instead of shrublands. However, food abundance cannot account for the higher abundance of adults and larger birds in forests. According to differences in shelter and food diversity between habitats, the preference for forests could be related to diet quality or antipredator defence. In shrublands, migrant blackcaps were less clearly associated with fruit abundance but better associated with shelter than in forests. Shelter may be found everywhere in forests, where antipredator vigilance during foraging would lose importance and hence blackcaps may track fruit abundance more closely (McNamara & Houston 1994). In turn, this could counterbalance the lower abundance of fruits in forests emphasizing their higher quality compared to shrublands.

DOES HABITAT SEGREGATION AFFECT BODY CONDITION OF BLACKCAPS?

In forests, migrants and residents had similar body condition, based on similar amounts of fat and muscular development. However, migrant blackcaps stored more fat in shrublands than in forests. This hardly involves a higher nutritional quality of shrublands, as this would imply that adults and large birds are subordinates displaced to the worst habitats or, alternatively, that dominants prefer the worst habitats. Fat dynamics are thus probably related to factors other than nutritional restrictions. Although putting on fat will reduce the risk of starvation (Blem 1990; McNamara & Houston 1990), heavier birds incur predation-related mortality costs due to impaired flight performance (Kullberg, Fransson & Jakobsson 1996). As a consequence, birds appear to regulate their fat reserves at a level that is neither at the physiological nor at the environmental optimum (Rogers & Smith 1993; Witter & Cuthill 1993). Usually, birds store more fat when they perceive a reduced predation risk or a lower probability to secure their food (McNamara & Houston 1990; Witter & Cuthill 1993; Strong & Sherry 2000). Given that blackcaps accumulated more fat in shrublands (the less sheltered environments), predator avoidance seems not involved in this case. However, food predictability could be higher in forests than in shrublands. Because fruit production of a single plant species varies in time and space (Levey & Stiles 1992; Herrera 1998), a higher variety of fruiting species might secure a more predictable crop by overlapping fruiting periods. None the less, this could be counterbalanced by a higher fruit abundance in shrublands than in forests, which should increase food predictability in the former.

Apart from the trade-off between predation and starvation, other factors could explain why blackcaps store more fat in shrublands than in forests. For example, dominant birds usually store less fat than subordinates because they have priority of access to food (Matthysen 1990), so that blackcaps displaced to shrublands could put on more fat because they perceive a lower probability to secure their food. On the other hand, differences between habitats in diet composition could also affect fat dynamics. Lentiscs and wild olives, the unique fruits available in shrublands, are also the fat-richest in the area (Herrera 1982), so fat accumulation could be a by-product of basing the diet on these fruits. This would mean that in forests, where birds may choose among many more fruits, blackcaps might maintain better nutrient balance than in shrublands (Herrera 1982, 1985). In turn, fat accumulation probably depends on the combination of all these factors, and partialling out their contribution to the variation observed will require experimentation.

Notwithstanding these caveats, we can conclude that habitat segregation has no effect on mortality of subordinate blackcaps due to starvation, as long as fat is the first energy source to be depleted under nutritional stress (Blem 1990). Consistent with this idea, we found no change between habitats in muscular development, which better measures long-term nutritional reserves. Differences between habitats in the risk of predation might provide a mechanism for competition to depress fitness of individuals displaced out of forests without effects on body condition, since the lower availability of shelter in shrublands could increase exposure to predators. We acknowledge, however, that the reasons why blackcaps prefer forests over shrublands remains an open question, and other methods have to be applied to conclusively elucidate the consequences to individuals of habitat segregation (e.g. Marra & Holberton 1998).

NON-BREEDING COMPETITION AND EVOLUTION OF MIGRATION

This paper presents evidence to rule out the hypothesis that migrant blackcaps avoid competition with residents by selecting different resources or environments. Several studies of non-breeding bird communities have suggested resource partitioning between migrant and resident species as a way to avoid competition (e.g. Hutto 1980), and even that using resources that are underexploited by residents would make up a ‘just better than nothing’ alternative for migrants (Poulin & Lefebvre 1996; Strong 2000). Particularly in winter frugivores, migratory species usually occupy secondary-growth, fruit-rich habitats outside the range of residents, which remain in their breeding sites over the winter (Leck 1987; Levey & Stiles 1992). In blackcaps, both the concentration of residents in forests and their distribution within this habitat support this preference for breeding territories. However, habitat preferences alone cannot explain the distribution of migrant blackcaps in our study area. Secondary-growth habitats sustain a large part of the migratory population, yet migrants are also abundant in forests. Although migrant and resident blackcaps differ in morphology and behaviour (Tellería & Carbonell 1999), this variation has much less ecological significance than interspecific differences and is less likely to cause their segregation. Instead of this, direct competition in forests may cause the exclusion of subordinate migrants to shrublands.

Usually, the role of non-breeding competition in the evolution of migration has been inferred from the distribution of migrants and residents in the whole species range. For example, Bell (2000) proposed that the lack of sedentary populations in adequate areas within the wintering range of migratory species supports their extinction as a result of flooding by migrants. Thus, resident populations would remain only when their breeding success could counterbalance the negative impact of non-breeding competition. In blackcaps, however, fecundity of sedentary populations can hardly compensate winter mortality due to competition with migrants. In the Iberian Peninsula, sedentary blackcaps have a smaller clutch size than their migratory counterparts (Pérez-Tris & Tellería 2002). In addition, the lower quality for breeding of the residents' range is accentuated by the summer drought in southern Mediterranean environments, which may reduce fledgling survival, as shown in robins (*Erithacus rubecula*) breeding in the same area (Pérez-Tris, Carbonell & Tellería 2000b). However, despite sedentary populations facing these handicaps, their competitive advantages in winter could well increase their recruitment so as to allow their persistence in Mediterranean environments. Our results support the idea that residents are better competitors than migrants and hence maintain populations in their breeding habitats, which seem also to be the best wintering sites. Body size, prior occupancy or the advantages of familiarity with the area could all determine these dynamics of habitat occupation. In robins, indeed, it has been shown that the arrival of migrants is connected to a density-dependent, sequential occupation of habitats of decreasing quality in which residents are better competitors (Tellería *et al*. 2001). Therefore, despite their large population size and reproductive advantages over residents, direct behavioural interactions between migrant and residents also play an important role in maintaining sympatric populations.

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