Seasonal distribution of a migratory bird: effects of local and regional resource tracking

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Abstract

Aim We studied how local and regional abundance of a migratory passerine (the blackcap *Sylvia atricapilla*) track resource availability in breeding and wintering grounds, in an attempt to understand the processes underlying the distribution and regulation of migratory bird populations in summer and in winter.

Location Our study was conducted in Spain. In summer, we sampled five localities representing the diversity of environmental conditions met by breeding Spanish blackcaps. In winter, we sampled eight localities in the wintering range of the species including different habitat types (forests and shrublands).

Methods Our approach was based on the matching rule, a model that predicts that any local variation in resource abundance between two adjacent habitat patches should be tracked by animals through a similar variation in population abundance. Eventually, this local process should conform to abundance distributions at regional scales. We sampled two habitat patches in each locality, each one including three to five line transects, 500-m long and 50-m wide, where we counted blackcaps and measured vegetation structure and fruit abundance.

Results During the breeding season, the abundance of blackcaps was strongly correlated with the ground cover of brambles (*Rubus* spp.), a bush which grows in moist sectors in Mediterranean forests and is the commonest nesting substrate of Spanish blackcaps. Both local and regional changes in bramble cover were tracked by variations in blackcap abundance. However, the rate of increase in blackcap abundance with increasing bramble cover along the Spanish gradient was lower than the one predicted under resource matching. In winter, abundance of fruiting shrubs was the best predictor of blackcap abundance, although local abundance of blackcaps not always fitted local abundance of fruits. Notwithstanding this effect, the regional pattern of abundance tracked changes in fruit availability according to the matching rule.

Main conclusions Our results support the strong effect of habitat quality on the abundance distribution of blackcaps and the tracking of different key resources along the year. Together with the different degrees of resource tracking by blackcaps at local and regional scales, these results also support the view that both breeding and wintering processes have to be studied, and studies have to be conducted at the appropriate spatial scales, if we are to understand the processes underlying the abundance distribution of migratory birds.

Keywords
Abundance distribution, Spain, matching rule, resource tracking, *Sylvia atricapilla*.

INTRODUCTION

Abundance distribution depends on processes operating at different spatial scales and varying among both taxa and geographical regions, yet the abundance distribution of a species seems to be largely influenced by the spatio-temporal distribution of some key environmental resources (Brown *et al.*, 1996). As a consequence, there is an increasing awareness of the importance of examining factors affecting abundance distribution at the spatial and temporal scales relevant to both the organisms and the processes studied (Wiens, 1989a). In migratory birds, for instance, different processes acting in breeding and wintering grounds determine both the patterns of habitat occupancy and the effects of the consequent distribution of individuals on population dynamics (Holmes *et al.*, 1996; Sherry & Holmes, 1996). Understanding these processes is decisive for the future of migratory bird species, whose conservation should ideally be programmed in all the different areas they occupy during the annual cycle (Terborgh, 1989; Baillie & Peach, 1992).

During the last decade, there has been a growing interest in applying behavioural models to the study of distribution of migratory birds (Berstein *et al.*, 1991; Sherry & Holmes, 1996; Rodenhouse *et al.*, 1997; Marra, 2000; Shochat *et al.*, 2002). Among these models, the ideal free distribution, originally proposed by Fretwell & Lucas (1970), enjoys an outstanding popularity (Weber, 1998). This model deals with a question of paramount importance in ecology: how should organisms occupy habitat patches of different quality? Or more explicitly, can abundance distribution be predicted if the distribution of resources is known? (Kennedy & Gray, 1993). A basic model to predict the distribution of organisms based on the distribution of resources assumes that, at equilibrium, the proportion of organisms and resources will be equal in all habitat patches, a relationship termed habitat matching (Pulliam & Caraco, 1984; Morris, 1995). In this way, all individuals will access a similar rate of resources whatever the habitat patch they occupy according to the algorithm

$$\log\left(\frac{D_{1i}}{D_{2i}}\right) = a + b \cdot \log\left(\frac{R_{1i}}{R_{2i}}\right) \qquad (1)$$

where D_{1i} and D_{2i} are the densities of organisms in a couple of habitat patches in the locality i, and R_{1i} and R_{2i} are abundance of resources in the same patches. Thus, b will equal 1 if population density tracks resource distribution according to the habitat matching rule, but it will be lower and higher than 1 if density undermatches or overmatches changes in resource availability, respectively (Kennedy & Gray, 1993). This approach assumes that individuals know the local and regional availability of resources, do not deplete them, move freely among habitat patches and areas, and have similar competitive abilities (Kennedy & Gray, 1993). Although the matching rule has been used to predict the effects on populations of habitat loss at regional scales (e.g. Fagen, 1988), little effort has been devoted to analyse how resource tracking affects habitat distribution at larger spatial scales. This could be because of the difficulty of defining key resources at these scales, or to the fact that the matching rule is only applicable when animals occupy all the habitat patches studied (Sutherland, 1983; Pulliam & Caraco, 1984). For example, this last assumption has limited the use of the matching rule in studies of presence or absence of species in habitat patches under extinction-colonization metapopulation dynamics (Hanski & Gilpin, 1991; Morris, 1995; Brown *et al.*, 1996).

The association between abundance of resources and distribution of individuals is particularly interesting in migratory birds. Migratory behaviour allows birds to exploit seasonal productive outputs moving across latitudinal and altitudinal gradients (Alerstam, 1990). This means that migratory populations track twice a year resource availability when settling in breeding and wintering grounds. However, the shape of the relationship between resources and individuals could vary from summer to winter because of seasonal changes in social behaviour. Most birds are territorial breeders, which probably prevent newcoming conspecifics from settling for breeding once a given density threshold is passed (Fretwell & Lucas, 1970; Pulliam & Danielson, 1991). As a consequence, territorial contests could lead to resource undermatching by breeding migratory bird populations, that is, a lower increase in bird abundance than the one predicted per unit increase in resource availability (Shochat *et al.*, 2002). However, social behaviours are much more varied in winter. Many birds maintain territorial behaviour over winter (e.g. Marra, 2000; Tellería *et al.*, 2001), but many others become wanderers which track resources across habitat patches (Levey & Stiles, 1992). This behavioural change in winter could lead to an abundance patterning consistent with the matching rule (Bautista *et al.*, 1995), but wintering-site fidelity, misinformation about the spatial distribution of resources, or conspecific interactions (if some sites are better preferred than others) could all produce resource undermatching by vagrant birds. However, the benefits of gregariousness or conspecific attraction could produce resource overmatching (i.e. a higher increase in bird abundance than the one predicted per unit increase in resource availability; see Bautista *et al.*, 1995). In turn, the rules governing resource tracking by populations should change with changing social behaviour of birds from summer to winter.

The blackcap as a model species

We studied how local and regional abundance of a migratory passerine, the blackcap *Sylvia atricapilla* (L.), tracks resources in breeding and wintering grounds of Spain. The blackcap is a forest passerine widely distributed across the Western Palearctic (Cramp, 1992). In Spain, blackcaps are abundant breeders in the North but become restricted to mountains and coastal sectors southwards, as they near their range edge (Hagemeijer & Blair, 1997). Spanish blackcaps are migratory in the northern highlands and mountains, but are sedentary in the south (Tellería & Carbonell, 1999; Pérez-Tris & Tellería, 2002a). In winter, Spain receives many blackcaps from central and northern Europe, which occupy the warmer Mediterranean sectors (Tellería *et al.*, 1999).

During the breeding season the blackcap is a typical forest bird which requires shrubby undergrowth for nesting (Cramp, 1992). Particularly, blackcaps show a strong preference for the bramble (*Rubus* spp.), to the point that its ground cover accounts for 17% of variance in blackcap abundance (Carbonell & Tellería, 1998a). This preference has been related to the suitability of this shrub for nesting, combined with the fact that brambles growth in moist forest patches maintaining a suitable production during the strong Mediterranean summer drought (Carbonell *et al.*, 2003). Indeed, the intensity of the summer drought imposes a major constraint to the distribution of blackcaps and many other common forest songbirds in Spain (Tellería & Santos, 1993, 1994).

In winter, blackcaps shift from insectivory to intensive frugivory, lose territorial behaviour and wander in search for fleshy fruits (Jordano & Herrera, 1981; Herrera, 1984, 1998; Rey, 1995). Indeed, fruit availability is one of the best predictors of the abundance of blackcaps wintering in Mediterranean environments. For example, fruit abundance may account for as much as 36% of variance in abundance of blackcaps in southern Spain (Rey, 1995). It may be postulated that forest cover, more specifically bramble cover, and fruit availability should all be key resources for blackcap populations during the annual cycle. Using the matching rule model, we analysed how closely the abundance of blackcaps breeding and wintering in Spain tracks local and regional variation in the availability of these resources.

METHODS

Study area

In June 1995, we sampled five localities representing a wide range of environmental conditions in the Spanish breeding range of blackcaps (Fig. 1; for a detailed description of the study areas see Carbonell & Tellería, 1998a; Carbonell *et al.*, 2003). The northern highlands were represented by three localities: (a) Álava (42°55′ N 2°29′ W), which is covered by mixed oak and maple forests (*Quercus faginea* L., *Q. robur* L. and *Acer campestre* L.), (b) Sierra de Guadarrama (40°54′ N 3°53′ W), covered by *Q. pyrenaica* Willd. and *Pinus sylvestris* L. forests, and (c) Madrid (40°30′ N 3°4′ W), a set of riparian forests with *Populus nigra* L., *Tamarix gallica* L. and *Salix* spp. Southern lowlands were represented by two localities: (d) Sierra de Ojén (36°01′ N 5°36′ W), covered by mixed *Q. suber* L. and *Q. canariensis* Willd. forests, and (e) Tarifa (36°01′ N 5°36′ W), a set of river banks covered with *Alnus glutinosa* (L.) Gaertn. and *P. nigra*.

Because blackcaps leave Spanish highlands in autumn and move towards southern Mediterranean areas, we restricted our winter study to a broad region located around Sierra de Ojén and Tarifa (Fig. 1). In this area, where a huge number of migratory blackcaps join local populations for wintering (Pérez-Tris & Tellería, 2002b), we delimited eight study sectors during the winter 1998–99. Four sectors were located in mixed *Q. suber* and *Q. canariensis* forests (Pista, San Carlos, Alcornocal and Ojén), and the other four in shrublands of the hill slopes and valleys (Almodóvar, Tornos,
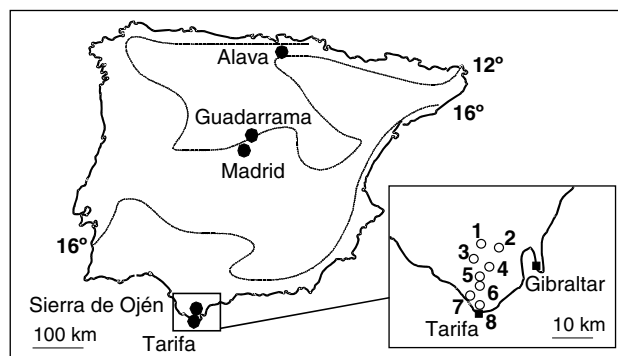

Figure 1 Location of the study sites in the Iberian Peninsula. In winter, blackcaps abandon the Iberian mountains and plateaux (an area roughly limited by the 12° isotherm), and are mainly found in warm Mediterranean sectors (delimited by the 16° isotherm). Breeding blackcaps were studied in five localities distributed across a belt from Northeast to Southwest in the Iberian Peninsula (main map), and wintering blackcaps were studied in eight localities in the Gibraltar area, which have been represented with numbered white dots in an enlarged map. Forests sites were Pista (1), San Carlos (2), Alcornocal (3) and Ojén (4), and shrubland sites were Almodóvar (5), Tornos (6), Betis (7) and Río Valle (8).

Betis and Río Valle; Fig. 1). All these sectors have abundant fruiting shrubs [*Pistacia lentiscus* L., *Olea europaea sylvestris* (Mill.) Lehr and other less common species; Pérez-Tris & Tellería, 2002b] on which blackcaps feed in winter.

Counting birds and resources

In order to obtain two different estimates of blackcap density (D_{1i} and D_{2i} in equation 1) and availability of resources (R_{1i} and R_{2i}) for each study site i, we worked on two habitat patches in each locality (five localities in summer and eight in winter; Fig. 1). Each habitat patch included three to five line transects, 500-m long and 50-m wide (25 m at either side of the progression line). During the bird counting, we measured cover of brambles, cover of other shrubs (vegetation below 2-m height), cover of trees and density of trees (number of stems above 10 cm dbh). We measured these habitat variables in 25-m radius circles distributed at 200-m intervals along the line transects (Larsen & Bock, 1986). These habitat features could affect the distribution of blackcaps within habitat patches, because moving into highly sheltered sites decreases exposure to predators, and vegetation sprouting favours the presence of foliage invertebrates and increases availability of nesting and singing places (e.g. Watts, 1991). We also measured fruit abundance by counting shrubs holding ripe fruits in a 10-m wide belt, 5 m at either side of the progression line of the transects.

Cover of brambles, abundance of fruits and availability of shelter (tree and shrub covers) might all influence habitat suitability for blackcaps. We used Principal Components Analysis to evaluate the existence of multivariate gradients of habitat suitability before accepting any individual resource as a key factor affecting the abundance distribution of blackcaps (Capen, 1981; Morrison *et al.*, 1998).

RESULTS

Fruit abundance and vegetation variables

Consistent with the typical fruiting phenology of Mediterranean plants (Herrera, 1985; Fuentes, 1992), the abundance of fleshy fruits showed strong seasonal changes in our study areas. In summer, only scattered *Viburnum lantana* L. and *Ramnus alaternus* L., always holding very little amounts of ripe fruits, were found in Álava and Sierra de Ojén, and no fruits were observed in Guadarrama, Madrid or Tarifa. Therefore, we could not consider fruits to be an available resource for breeding blackcaps, which in fact base their diet on invertebrates (Cramp, 1992). Because of this, we excluded fruits from our analysis of distribution of breeding blackcaps. However, fruits were found everywhere in wintering areas. The most abundant fruiting species were *P. lentiscus* and *Olea europaea sylvestris*, which were very common in all sites. In forest sites (see Fig. 1) we also found *Phillyrea latifolia* L., *Myrtus communis* L., *Smilax aspera* L., *Rhamnus alaternus*, *Hedera helix* L. and *V. tinus* L. All these fruits are intensely consumed by blackcaps (Jordano & Herrera, 1981; J.L. Tellería, J. Pérez-Tris, unpubl. data). Other fruiting shrubs found in the area were *Rosa* spp., *Ruscus aculeatus* L. and *Crataegus monogyna* Jacq., but these were excluded from the counts as they produce too large and hard berries that we have never found in the diet of blackcaps (J.L. Tellería, J. Pérez-Tris, unpubl. data).

The PCA on habitat variables allowed us to identify gradients of habitat suitability for blackcaps (Table 1). In summer, all cover variables were weighed with negative loading on the PC1, whose scores therefore defined a gradient of increasing exposure, which we considered to be inversely related to suitability for forest birds (the lower the PC1 scores, the more sheltered the habitat patches). Nevertheless, the PC2 arranged forest tracks in a gradient from highly covered by trees (high PC2 scores) to more shrubby (low PC2 scores). In winter, all vegetation variables were weighed with positive loading on PC1, while fruits had a negative loading on this component, consistent with the fact that forests are more sheltered but show less abundant fruits than shrublands (Pérez-Tris & Tellería, 2002b). A similar association between the abundance of fruits and the cover of shrubs came at sight in the PC2 (Table 1).

Resource tracking in summer and winter

In summer, bramble cover and PC1 scores were the best predictors of blackcap abundance along the Spanish gradient (Table 2, appendix). However, variation in PC1 scores was unable to predict changes in abundance of blackcaps at local scales according to equation 1 ($y = 0.01 + 0.06x$, $r = 0.11$

Table 1 Results of Principal Components Analyses with variables measured to evaluate habitat suitability for blackcaps in summer and winter

	Summer		Winter	
	PC 1	PC 2	PC 1	PC 2
Tree density	−0.525	0.778	0.851	−0.153
Tree cover	−0.810	0.444	0.940	0.105
Shrub cover	−0.827	−0.413	0.243	0.896
Bramble cover	−0.572	−0.745	0.725	0.197
Fruit abundance	–	–	−0.575	0.616
Eigenvalue	1.944	1.528	2.522	1.255
Variance explained (%)	48.58	38.21	50.44	25.10

Average values for each locality have been used (five sites in summer and eight in winter, see Fig. 1), and only components with eigenvalue above 1 have been considered. We did not consider fruit abundance in summer, when fruits were almost never found.

Table 2 Effects of regional variation in environmental features on the abundance of breeding and wintering blackcaps

	Summer					Winter				
	d.f.	F	R^2	β	P-value	d.f.	F	R^2	β	P-value
Tree density	1,4	2.193	0.354	0.595	0.213	1,7	0.829	0.106	0.326	0.393
Tree cover	1,4	1.658	0.050	0.224	0.318	1,7	1.529	0.384	0.492	0.294
Shrub cover	1,4	0.077	0.019	0.137	0.796	1,7	0.579	0.076	0.278	0.471
Bramble cover	1,4	4.940	0.558	0.743	0.090	1,7	0.695	0.022	−0.147	0.679
Fruit abundance	–	–	–	–	–	1,7	24.299	0.776	0.881	0.002
PC1	1,4	5.414	0.575	−0.758	0.081	1,7	0.015	0.002	−0.046	0.907
PC2	1,4	0.228	0.054	−0.232	0.658	1,7	2.445	0.259	0.509	0.162

All effects have been estimated by using average values for each locality and have been used as covariates of an ANCOVA in which localities (5 in spring and 8 in winter) have been used as factors. PC1 and PC2 are the principal components obtained from habitat variables (Table 1). The size of effects (R^2) and the beta weights are also given.
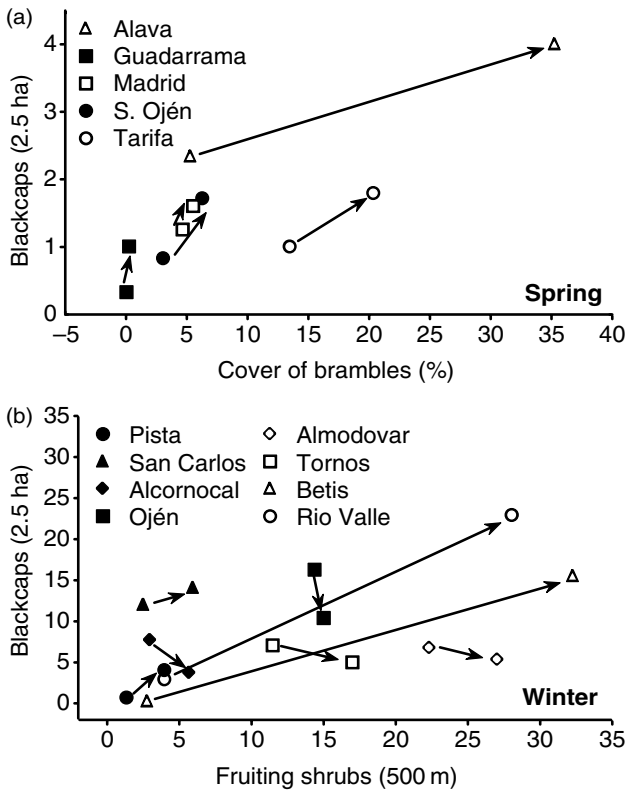
Figure 2 Relationships between the abundance of resources important for blackcaps and the abundance of the species. The cover of brambles was the main summer resource (a) and the abundance of fruits was the main winter resource (b). Each locality has been labelled with a unique symbol (two habitat patches per locality, see methods and Appendix for further details). The arrows illustrate the local trends of blackcap abundance as a response to the increase in abundance of the relevant resources.

Figure 3 Relationships between the inter-patch variation in the abundance of resources relevant to blackcaps and the inter-patch variation in blackcap density (D), illustrating the extent to which abundance variation matches resource variation (see equation 1). Stippled lines mean perfect matching. Inter-patch changes in the corresponding variables were evaluated using two sets of transects per locality (Appendix). The cover of brambles was the main summer resource (a) and the abundance of fruits was the main winter resource (b). Localities have been labelled as in Fig. 2.

$P = 0.86$). The variation in abundance of blackcaps at both local and regional scales was closely associated to changes in the cover of brambles (Fig. 2a). However, the abundance of breeding blackcaps undermatched the change in cover of brambles along the Spanish gradient ($b < 1$ in equation 1; $t = 9.25$, $P < 0.001$, $n = 5$; Fig. 3a).

In winter, the abundance of fruiting shrubs was the best predictor of blackcap abundance (Table 2, Appendix). However, the variation in abundance of blackcaps at the local scale did not fit local variation in fruit resources. In four of the eight study localities, the increase of fruit resources did not involve a concomitant increase in abundance of blackcaps, but it was associated with moderate to large decreases in population density (Fig. 2b). However, the regional pattern of abundance distribution was strongly correlated to local changes in fruit availability (Fig. 3b). Given that the slope b did not differ from 1 ($t = 0.74$, $P = 0.76$, $n = 8$, see equation 1), we could conclude that blackcaps tracked fruit resources at the regional scale adjusting the predictions of a resource-matching model.
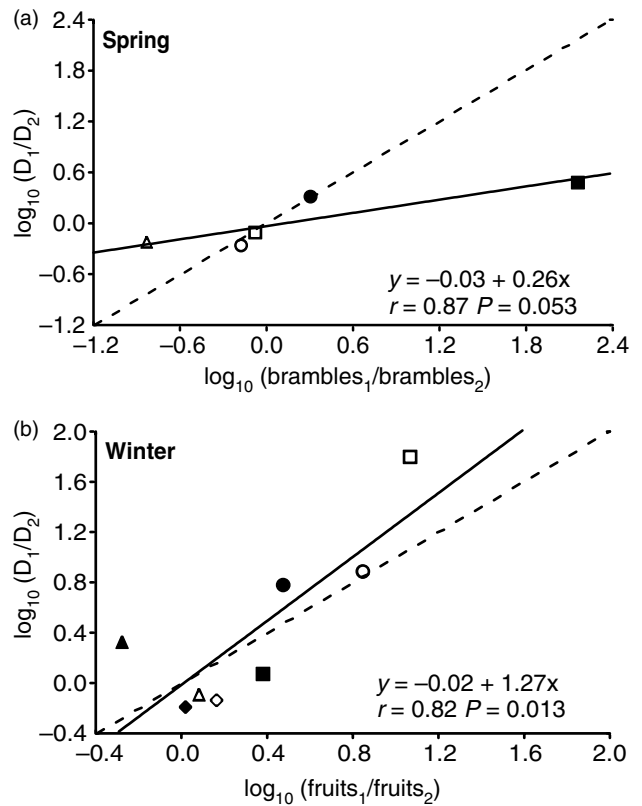
DISCUSSION

The role of resources in determining abundance distribution of blackcaps

The availability of some key resources was a good predictor of the abundance patterning of blackcaps across the habitats occupied in Spain. In addition to the implicit value of the resources chosen for this study (it is easy to establish the functional relationships between availability of nesting places or food resources and the abundance of blackcaps in summer and winter), it is worthy to note their usefulness to predict blackcap abundance at the rather large scale of our approach. This is particularly remarkable if we consider that, at large spatial scales, many processes overlapping resource tracking could erase the relationships between bird abundance and resource availability. For example, site tenacity of birds could delay the reaction of local populations facing an eventual change in habitat suitability, crashes of local populations could disrupt the predicted relationships at

the scale of Spain, and population bottlenecks could produce a weak relationship between resource availability and bird abundance (for a review see Wiens, 1989b). However, our results support the idea that habitat quality strongly influences the abundance of blackcaps and, as a consequence, their populations could be regulated by availability of suitable habitats both in breeding and wintering grounds (Dolman & Sutherland, 1994; Sutherland & Dolman, 1994). Our results also support the view that information about more than just resource distribution is required to accurately predict the distribution of animals (Morris, 1994). In turn, these studies could help us understand changes in abundance at the scale of the species range by analysing how spatial and temporal variations in limiting niche parameters affect population dynamics (Brown et al., 1996).

Seasonal changes in resource-tracking dynamics

Blackcap populations showed different models of resource tracking in summer and winter, consistent with alternating opposite social behaviours. During the breeding season, blackcaps compete for breeding territories. In Spain, these are characterized by a high cover of brambles (Carbonell & Tellería, 1998a; Carbonell et al., 2003), so the availability of this plant could limit blackcap populations, particularly in dry environments. However, local changes in blackcap abundance as a response to changing bramble cover were less pronounced than the changes predicted under resource matching. This could be explained because, once population density passes a given threshold, territorial interactions would prevent newly arriving individuals from occupying habitat patches that may otherwise have abundant resources, leading to lower-than-expected densities in such patches (Fretwell & Lucas, 1970; Lomincki, 1980; Newton, 1992). In addition, resource undermatching would be intensified by subordinates obliged to settle in suboptimal habitat patches, thus giving a mechanism of population regulation during the breeding season (Dolman & Sutherland, 1994; Rodenhouse et al., 1997).

The possibility that density-dependent resource undermatching plays a role in regulating bird populations deserves further investigation, yet some studies have produced results consistent with this view. Blackcaps breeding in dry Spanish forest are in a worse body condition than those breeding in moister areas (Carbonell & Tellería, 1998b, 1999; Carbonell et al., 2003). Remarkably, these studies refer to the same sites used in this study. Although we do not know whether birds face a lower survival or breeding success in these dry environments (see however an example in Holmes et al., 1996), a poor body condition should have a negative impact on fitness (Brown, 1996). This is important because population density may be a weak indicator of habitat suitability (Van Horne, 1983). For example, blackcaps breeding in moist central European forests (which are considered to be the core area for many forest birds; Mönkkönen, 1994), may have similar breeding rates at very different population densities (Weidinger, 2000). By contrast, at the border of the species range in the Iberian Peninsula, habitat suitability for forest passerines steeply decreases with increasing forest

dryness (Pérez-Tris et al., 2000), causing a decrease in abundance (Tellería & Santos, 1994), fecundity (Pérez-Tris & Tellería, 2002a) and body condition (Carbonell et al., 2003) of blackcaps.

While habitat structure was the best predictor of blackcap abundance during the breeding season, food was the key resource for wintering populations, consistent with the need of wintering birds to accumulate body reserves to secure self-maintenance (Blem, 1990). Blackcaps arrive in the Mediterranean at the start of the autumn–winter productive output, when fruit availability rises considerably increasing the carrying capacity for frugivorous birds (Herrera, 1985; Fuentes, 1992). This could explain the outstanding densities reached by blackcaps in wintering habitats of southern Spain, several times higher than the ones recorded in breeding grounds (Fig. 2). However, the distribution of fruits in winter is less predictable than the distribution of insects in summer. In fact, fruit production may abruptly change from site to site, which has probably triggered the evolution of vagrant behaviour in many frugivorous birds (Levey & Stiles, 1992; Rey, 1995; Herrera, 1998).

Seasonally changing behaviour, from territorial in summer to vagrant in winter, could explain the different efficacy of local tracking of resources by breeding and wintering blackcap populations. Local variation in breeding densities was closely related to changes in bramble cover (Fig. 2a), but wintering blackcaps sometimes reached lower densities than expected from fruit abundance (Fig. 2b). This result suggests that, while the local distribution of breeding blackcaps would be largely constrained by the distribution of key resources (i.e. nesting places), the local distribution of wintering blackcaps would be less restricted by food abundance, which would be essential for explaining blackcap distribution but only in conjunction with other factors like the need of sheltered sites to avoid predators, daily movements back and forth from roosts, and so on (Newton, 1981). In our study area, another likely relevant factor is the presence of sedentary birds remaining in their breeding sites, characterized by a high cover of brambles but a low availability of fruits (Pérez-Tris & Tellería, 2002b). This can contribute to mismatches between the abundance of fruits and blackcaps at the local scale, and eventually lead to a worse fit of abundance to fruit resources in forests compared with shrublands, which are rarely occupied by residents (Fig. 3). However, mismatches are equally frequent in both habitat types, so other factors, similar to the kind of the aforementioned, should also cause local resource mismatching in our study area.

The abundance of wintering blackcaps better tracked the abundance of resources at the regional scale, suggesting that individuals would have a similar access to food resources in all sites. This is consistent with the absence of differences in body condition of blackcaps wintering in different habitat types (Pérez-Tris & Tellería, 2002b), but it could still be an oversimplified view, and other factors may finely tune blackcap distribution in winter. For example, the fruit-richest habitats (shrublands) remain vacant before the arrival of migrants increases regional abundance, suggesting habitat preferences independent of fruit abundance (Tellería &

Pérez-Tris, unpubl. data). In addition, habitat segregation in relation to age and body size clearly suggests that social interactions may determine which individuals remain in forests and which ones occupy shrublands (Pérez-Tris & Tellería, 2002b).

Shifting tracking rules and the future of migratory populations

It has long been accepted that habitat loss or degradation is a major cause of decline of many threatened birds, yet the components of habitat quality affecting bird distribution have rarely been identified. Our results show that both the relevant resources for defining habitat suitability and the way these resources are tracked by birds may change seasonally, emphasizing the importance of considering both breeding and wintering processes when facing the conservation of migratory bird populations (Baillie & Peach, 1992). In breeding areas, any habitat alteration affecting local availability of key resources may produce a concomitant decrease in regional population size. The identification of local processes afecting regional population dynamics is in the basis of many current management strategies (Verner et al., 1986; Morrison et al., 1998).

However, in species like the blackcap, conservation strategies based on local management of resources would be less efficient in non-breeding areas. Abundance of wintering blackcaps often failed to adjust local changes in abundance of fruits (see also Herrera, 1998). But, if blackcaps can reduce starvation risk by moving among sites, we should be particularly concerned with the conservation of the regional pool of habitat patches, responsible of the long-term sustenance of wintering populations. This would imply monitoring these populations at an adequate geographical scale, and evaluating habitat suitability without paying too much attention to local abundance patterns (Berstein et al., 1991). In summary, blackcaps provide a good example of how important selecting the adequate spatial scales may be when trying to identify which resources are relevant for year-round population regulation of migratory birds.

ACKNOWLEDGMENTS

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BIOSKETCHES

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Appendix Distribution of key resources (bramble cover and abundance of fruiting shrubs) and blackcap abundance in two adjacent habitat patches within each study site (referred to as patch 1 and patch 2 in equation 1 and in Figs 2 & 3). This numeration of patches depends on census order (patch 1 was the first to be sampled), so that we studied the response of birds to sampled variation rather than to increase or decrease in resource availability. Nevertheless, using any other patch order did not change our results

	Bramble cover (%)		Blackcaps/2.5 ha	
Summer sites	Patch 1	Patch 2	Patch 1	Patch 2
Álava	5.33	35.33	2.33	4.00
Guadarrama	0.29	0.002	1.00	0.33
Madrid	4.65	5.52	1.25	1.60
Sierra de Ojén	6.29	3.09	1.71	0.83
Tarifa	13.50	20.40	1.00	1.80
	Fruiting shrubs/ 500 m		Blackcaps/2.5 ha	
Winter sites	Patch 1	Patch 2	Patch 1	Patch 2
Pista	4.00	1.33	4.00	0.67
San Carlos	3.00	5.67	7.67	3.67
Alcornocal	6.00	2.50	14.00	12.00
Ojén	15.00	14.33	10.33	16.33
Almodóvar	27.00	22.33	5.33	6.67
Tornos	17.00	11.50	5.00	7.00
Betis	32.25	2.75	15.50	0.25
Río Valle	28.00	4.00	23.00	3.00