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Habitat distribution of migratory and sedentary blackcaps *Sylvia atricapilla* wintering in southern Iberia: a morphological and biogeochemical approach

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In migratory species, the way in which conspecifics from different breeding populations are distributed during the non-breeding period is important from and ecological, evolutionary and conservation perspective, but such knowledge is still limited for most species. Migratory and sedentary blackcaps *Sylvia atricapilla* wintering in southern Spain can occupy two habitat types: forests and shrublands. According to earlier studies, blackcaps prefer forests over shrublands, and residents remain nearly restricted to forests. However, whether migrants with different breeding origin occupy the two habitats differently is unknown. We used morphological and biogeochemical data (hydrogen isotope ratios measured on feathers: δ^2H_f), which show variation along the breeding range of the species, to answer this question. Isotope analyses supported the reliability of morphology as a method for distinguishing between migratory and sedentary blackcaps in sympatry, showing that sedentary individuals are rare in shrublands while migratory ones are abundant in both habitat types. However, migratory blackcaps scored similar δ^2H_f values in forests and shrublands, and neither did vary in structural size or flight morphology between habitats. Our study suggests that migrants from a wide range of breeding origins end up mixing between forests and shrublands, which may explain the patterns of variation in space and time in the abundance of blackcaps in this area, and supports the view that inequalities may arise among migrants with the same origin but wintering in different habitats. Such inequalities might carry over into other stages of blackcaps' life cycle contributing to the regulation of its migratory populations.

In migratory birds, individuals from different breeding populations often meet for wintering in the same areas (Bell 2000), where they usually find an array of possible habitat choices. Alternative habitats may differ in predation risk, food abundance, or other components of environmental quality (Smith et al. 2010), which may cause variation in survival chances of individuals that settle in different habitats (Newton 1998). However, individuals with different breeding origins may differ in time of arrival on wintering grounds, competitive ability, or innate habitat preferences, which could promote certain degree of spatial segregation between populations during the non-breeding period (Webster and Marra 2005). If different breeding populations do not share the same habitat types during winter, the occupation of habitats of variable quality may reduce within-population inequalities, which could even lead to local adaptation and population differentiation (Bearhop et al. 2005). In contrast, if individuals from the same population end up occupying habitats of different quality, fitness differences among birds within such population will be expected. Thus, birds settling in poor habitats will suffer greater mortality or carry over the penalties of their habitat choice into the breeding season (Marra et al. 1998).

The populations of blackcaps *Sylvia atricapilla*, wintering in the Campo de Gibraltar region (southern Spain) provide an excellent opportunity for the analysis of the factors that determine the distribution of different populations in sympatric non-breeding grounds. Blackcaps have sedentary populations in this region, which share their home range during winter with large numbers of migratory conspecifics arrived from higher latitudes (Pérez-Tris and Tellería 2002). Conveniently, sedentary blackcaps can be distinguished from migratory blackcaps by morphology (Pérez-Tris et al. 1999, de la Hera et al. 2007). Previous studies have shown that sedentary blackcaps seldom abandon during winter the forests where they breed, while migratory blackcaps are abundant in the same forests and in the surrounding shrublands alike (Pérez-Tris and Tellería 2002).

There is evidence that blackcaps may prefer wintering in forests, a pattern which might be common to other species that use the same habitat types (such as robins *Erithacus rubecula*; Tellería et al. 2001, Tellería and Pérez-Tris 2004). The main food resource for blackcaps during winter (fleshy fruits; Jordano and Herrera 1981) is more abundant in shrublands than in forests (Pérez-Tris and Tellería 2002). However, the abundance of frugivorous birds (and particularly of blackcaps) closely matches fruit abundance, which may make per individual food supply level out among habitat patches, thereby making habitat quality more dependent on habitat characteristics other than total fruit abundance (Tellería and Pérez-Tris 2003, Tellería et al. 2005). Important components of habitat quality for blackcaps may be the diversity of fruits or the availability of shelter to escape from predators, both of which would render forests better habitats than shrublands (Pérez-Tris and Tellería 2002). Supporting this view, an earlier study found that 1) among migratory blackcaps adults are more frequently found in forests, while juveniles occur more frequently in shrublands, and 2) juvenile migrants wintering in forests are larger than those wintering in shrublands (Pérez-Tris and Tellería 2002). In addition, sedentary blackcaps are larger than migratory blackcaps, which might help them to remain in forests in spite of the massive arrival of migrants (Pérez-Tris and Tellería 2002).

Given the contrasting distribution of migratory and sedentary blackcaps between forests and shrublands, the question remains as to whether migratory blackcaps with different breeding origins may also settle for wintering nonrandomly with respect to habitat type, which would bring about opportunities for the evolution of different wintering strategies among different breeding populations. For example, migratory blackcaps may behave either as transients or resident birds during winter (Belda et al. 2007), and the ability of blackcaps to track variation in fruit abundance in space and time supports the idea that similar strategies could have been favoured in shrublands and forests, respectively (Tellería and Pérez-Tris 2003). In fact, previous results suggest that sedentary blackcaps behave as residents in forests during winter (Pérez-Tris and Tellería 2002), and a similar strategy could be favoured among migratory blackcaps occupying the same habitat. Evolutionary divergence of wintering strategies would be faster if birds wintering in the same habitat mated assortatively because they migrate back to the same breeding areas (Bearhop et al. 2005, Rolshausen et al. 2009). As an alternative hypothesis, the distribution of migratory blackcaps between the two habitat types could be independent of breeding origin, resulting from local social interactions instead.

Blackcaps wintering in the Iberian Peninsula come from central Europe on the western side of the species' migratory divide located at approximately 10–12°E (Cantos 1995). They have longer and more pointed wings at higher latitude (Cramp 1992, Fiedler 2005), which allows for using flight-related morphology as a proxy of latitudinal origin of migrants (Pérez-Tris and Tellería 2001, Arizaga and Barba 2011). In addition, the ratio deuterium/protium ($^2H/^1H$) in rainfall decreases with latitude across Europe (Hobson et al. 2004), and isotope differences are transferred to birds' feathers during their production (in breeding grounds in the case of blackcaps). Therefore, the analysis of morphology and isotope values may help to identify the patterns of between-habitat distribution of blackcaps wintering in our study area (Rubenstein and Hobson 2004, Inger and Bearhop 2008).

Variation between forests and shrublands in the body size of juvenile migrants may be evidence of habitat segregation by population origin. Or it may be the result of the settlement of the most competitive individuals (large birds regardless of their origin) in preferred habitats. It might be even an artefact if sedentary blackcaps (which are large; Tellería and Carbonell 1999) are often incorrectly classified as migratory based on flight-related morphology alone. This third alternative highlights the importance of validating different methods to infer the origin of birds. We used morphological and biogeochemical measurements ($^2H/^1H$ ratios in feathers) to test which of these alternative scenarios is best supported by the data. We 1) used $^2H/^1H$ ratios of feathers to assess the reliability of a morphology-based method designed previously to distinguish between migratory and sedentary blackcaps in wintering areas, 2) examined whether morphological variation among wintering blackcaps reveals their latitudinal breeding origin (estimated from $^2H/^1H$ ratios), and 3) tested for morphological and isotope differences between migratory blackcaps wintering in forests and shrublands. With these analyses, we aimed to shed light on the patterns of distribution between habitats in blackcaps wintering in southern Iberia.

Methods

Fieldwork and bird measurements

From mid November 2006 to mid February 2007, we made four field expeditions (5–7 d each) to capture blackcaps wintering in the Campo de Gibraltar region, southern Spain. In each expedition, 20 mist-nets were set in each habitat type (forests and shrublands), in exactly the same locations. We captured 384 individual blackcaps (excluding recaptures), which were aged and sexed by plumage (Svensson 1992, Jenni and Winkler 1994). We distinguished between adults (birds hatched before 2006, $n = 124$) and juveniles (birds hatched in 2006, $n = 256$; four individuals could not be aged). We measured tarsus length and bill length using a digital calliper (0.01 mm). We used 0.5 mm resolution rulers to measure tail length, wing length, and the length of the eighth primary feather (counting from the body; Jenni and Winkler 1994). In addition, we recorded the distances from the tips of primary 1 and 9 to the wing tip (hereafter primary distances PD1 and PD9, respectively), measured with the wing folded (for a detailed description of all measurements; see Svensson 1992). The difference PD1-PD9 increases as the wing becomes more pointed, and therefore it may be used as an index of wing pointedness. Finally, we collected one tail feather (one of the two fifth rectrices) for isotope analyses.

In order to characterize morphologically and isotopically the local sedentary population, we used a sample of blackcaps captured during a 3-d visit to the study area during early August 2006, when migrants still had not arrived in southern Iberia. Taking into account the fact that sedentary blackcaps do not show between-habitat morphological differences and they are uncommon breeders in shrublands (Tellería and Carbonell 1999), mist-netting was carried out in forests alone, in the same locations that were sampled in winter. We captured 40 sedentary blackcaps in total, which were aged (36 juveniles and 4 adults) and sexed by plumage. For 19 juveniles that had not started partial post-juvenile moult yet when caught, molecular techniques were applied on blood samples to assign their sex (Griffiths et al. 1998). We took morphological measurements and feather samples from each blackcap using the same methods described above (note that juveniles keep their flight feathers over winter, which allows for direct morphological and isotope comparisons with wintering birds). Unfortunately, adults were moulting when caught, and therefore it was not possible to obtain reliable measurements or to collect newly grown feathers from them.

Classifying wintering blackcaps as sedentary or migratory

We determined whether wintering blackcaps were local sedentary individuals or overwintering migrants using a discriminant function analysis (DFA) based on the morphology of Iberian breeding blackcaps of known migratory behaviour. The method, which has been published elsewhere (de la Hera et al. 2007), relies on three flight-related morphological traits: the length of the eighth primary feather, tail length and the index of wing pointedness PD1-PD9. Blackcaps of unknown origin are classified as migratory or sedentary according to posterior classification probabilities (Pc) estimated by DFA. The probability of a bird being migratory (Pc_m) equals 1 minus its probability of being sedentary (Pc_s), and the bird is assigned to the group for which it has $Pc > 0.5$. The method correctly classifies around 90% of birds when it is applied to Iberian breeding blackcaps (the populations used to generate the DFA), and it classifies equally well both migratory and sedentary individuals. Opportunely, when the method is applied to wintering birds of unknown origin, it improves classifying migratory blackcaps because most of these come from northern latitudes, where blackcaps have more exaggerated migratory-like morphology than Iberian migrants. Consequently, migratory blackcaps will seldom be incorrectly classified as sedentary in winter, while the error rate for sedentary individuals will remain unchanged from summer to winter (~10% of birds are expected to be incorrectly classified; de la Hera et al. 2007).

Hydrogen isotope measurements

Hydrogen isotope variation in precipitation across Europe is incorporated into birds' plumage through the diet at the time of feather growth. Once feathers stop growing, they remain metabolically inert, and their isotope composition provides information about the area where they were produced (Rubenstein and Hobson 2004). Blackcaps produce flight feathers (including the tail feathers collected in this study) in breeding grounds during summer (Jenni and Winkler 1994), and therefore their hydrogen isotope ratio can be used as a marker of birds' breeding origin (or hatching location in the case of juveniles; Hobson et al. 2004). However, hydrogen isotope values measured on juvenile and adult feathers may not equally indicate the geographic origin of the population (Langin et al. 2007). In order to minimise within-population variation in isotope ratios we analysed juvenile feathers alone, making this choice because of two reasons. Firstly, our sample contained many more juveniles than adults (we particularly missed feathers from adult sedentary birds in summer, because they were moulting). Secondly, and more importantly, juveniles are more informative for our study because they face their first wintering season, and consequently their choice of habitat cannot be conditioned by previous experience (Piper 2011). Therefore, the distribution of juveniles will best inform about whether or not populations with different breeding origin show innate habitat occupancy patterns. Because mass spectrometry is expensive, we restricted our isotope analyses to 25 randomly selected juvenile blackcaps out of 36 individuals captured in summer, and to 167 juveniles out of 251 individuals captured during winter with a complete set of morphological measurements. This winter subsample included all individuals classified as sedentary by DFA (16 wintering blackcaps with $Pc_m < 0.5$), plus a random sample of 151 juveniles classified as migratory (with $Pc_m > 0.5$).

For hydrogen isotope analysis, approximately the distal two thirds of each feather were sent to Iso-Analytical Limited (<www.iso-analytical.co.uk/>). There, each feather was washed in 0.25M sodium hydroxide solution and, afterwards, washed again twice in purified water. Washed feathers were placed in clean screw top vials and oven-dried at 50°C for one night. After this period feathers were clipped into small sections using surgical scissors, and 1 mg of sample weighted into silver capsules (5 × 8 mm). Filled capsules were left open for a period of not less than 4 d to allow the exchangeable hydrogen of feather keratin to fully equilibrate with the moisture in the laboratory air (Wassenaar and Hobson 2003). The capsules containing feather samples were only sealed just prior to analysis. Hydrogen isotope analyses were carried out in duplicate (except for two individuals with insufficient quantity of feather material) using the technique EA-IRMS. Hydrogen isotope values of feathers were expressed in delta notation (δ^2H_f) in units per mil (‰), and normalized according to the VSMOW-SLAP scale using the values obtained for a keratin standard (i.e. BWB-II whale baleen: expected non-exchangeable δ^2Hv-smow = −108‰), which allowed applying a correction for exchangeable hydrogen to the δ^2H_f data. We also used IA-R002 (mineral oil: expected δ^2Hv-smow = −111.2‰), IAEA-CH-7 (polyethylene foil: expected δ^2Hv-smow = −100.3‰) and RSPB (egg shell membrane standard: expected non-exchangeable δ^2Hv-smow = −99‰) as additional quality control check samples. In our analyses, observed values of all the standards were similar to the values conventionally accepted (observed mean ± SE for BWB-II = −108.05 ± 0.26‰; IA-R002 = −110.79 ± 0.1‰; IAEA-CH-7 = −100.98 ± 0.12‰; and RSPB = −101.44 ± 0.27‰). We used the mean value of the two isotope measurements from each feather in the statistical analyses (within individual repeatability of δ^2H_f: $r_i = 0.97$, $F_{189,190} = 58.6$, $p < 0.001$). More negative values of δ^2H_f represent a lower $^2H/^1H$ ratio in the feather, which indicates a more northern breeding origin of individuals (Hobson et al. 2004).

Statistical analyses

We conducted a principal component analyses (PCA) with morphological measurements of all juvenile blackcaps with morphological data (251 wintering birds plus 36 birds captured in summer). The analysis produced two morphological components (Table 1). The PC1 indicated the development

Table 1. Coefficients of correlation (factor loadings) and significance values ($* = p < 0.05$, $*** = p < 0.001$) between body measurements and principal components derived from the PCA. Eigenvalues and the percentage of variance explained by each component are also shown.

	PC1	PC2
Tarsus length	−0.12*	0.69***
Bill length	0.00	0.76***
Wing length	0.96***	0.01
8th primary length	0.97***	−0.08
Tail length	0.60***	0.48***
PD1-PD9	0.72***	−0.40***
Eigenvalue	2.74	1.44
Variance explained (%)	45.7	24.1

of flight-related morphology, as its scores were positively correlated with wing length, wing pointedness and tail length. The PC2 was interpreted as an index of structural size of birds, because its scores were positively correlated with tarsus, bill and tail length.

We used general linear models (GLM) to test for differences in δ^2H_f and morphology (PC1 and PC2) among three different groups of blackcaps, namely local birds captured in summer, wintering blackcaps classified as sedentary, and wintering blackcaps classified as migratory. The validity of DFA for distinguishing local sedentary birds from migrants during winter would be supported by two observations: 1) the absence of differences in morphology and δ^2H_f between local birds captured in summer and wintering birds classified as sedentary, and 2) the existence of differences in morphology and δ^2H_f between these two groups and wintering blackcaps classified as migratory.

We also explored the relationships between morphology (PC1 and PC2) of blackcaps and their geographic origin, as inferred from stable isotopes. In a first approach, we analysed morphology–isotope relationships using all wintering blackcaps with isotope data, including migratory and sedentary individuals. Then we restricted the analyses to wintering blackcaps classified as migratory. In addition, we tested for differences in morphology and δ^2H_f of migratory blackcaps wintering in forests and shrublands. We also analysed variation between habitats in the morphology of all migratory blackcaps captured ($n = 235$, including birds without isotope data) to test the same patterns with more statistical power. All analyses included the sex of birds as a factor.

We expect around 10% of sedentary blackcaps to be incorrectly classified as migratory with the classification threshold set at $Pc_m = 0.5$. Errors might affect our results because incorrectly classified birds are expected to concentrate in forests (where most residents are found; Pérez-Tris and Tellería 2002). Therefore, we repeated our analyses of between-habitat variation in morphology and δ^2H_f of migrants considering individuals classified as migratory with higher Pc_m. Although the higher the Pc_m threshold used to assign migrants, the lower will be the probability of incorrectly classifying sedentary blackcaps as migratory, it is important to note that using restrictive Pc_m values will also increase the chances of incorrectly classifying true migratory blackcaps as sedentary.

Results

Out of 251 juvenile blackcaps measured in winter, 235 were classified as migratory by DFA (123 in forests and 112 in shrublands) and 16 were classified as sedentary. The latter were more frequent in forests (15 birds) than in shrublands (1 bird; $\chi^2_1 = 9.71$, $p = 0.002$). Supporting the validity of DFA for distinguishing between migratory and sedentary blackcaps, these 16 birds did not differ significantly in δ^2H_f ($F_{1,37} = 0.2$, $p = 0.654$; Fig. 3) or flight morphology (PC1: $F_{1,37} = 0.82$, $p = 0.37$) from the 25 summer blackcaps with isotope measurements (known to be local sedentary birds), although the two samples differed marginally in structural size (sedentary blackcaps captured in summer had slightly larger PC2 values: $F_{1,37} = 4.46$, $p = 0.041$).

Wintering blackcaps classified as migratory showed a broad range of δ^2H_f values, which overlapped the range of birds known to be sedentary (Fig. 1). Nevertheless, they showed more negative values of δ^2H_f on average ($F_{1,172} = 31.52$, $p < 0.001$, Fig. 3), more exaggerated flight-related morphology (PC1: $F_{1,172} = 37.39$, $p < 0.001$), and smaller structural body size (PC2: $F_{1,172} = 28.84$, $p < 0.001$) than summer blackcaps. They also differed in the same direction from wintering blackcaps classified as sedentary (test statistic for δ^2H_f: $F_{1,163} = 44.31$, $p < 0.001$, Fig. 3; PC1: $F_{1,163} = 58.36$, $p < 0.001$; PC2: $F_{1,163} = 11.56$, $p < 0.001$). These results did not change qualitatively when blackcaps without isotope data were included in the analysis of morphology.

Based on Pc_m obtained for summer blackcaps (known to be sedentary) and variation in δ^2H_f values (Fig. 1), we set new Pc thresholds for classifying blackcaps as migratory to $Pc_m > 0.6$ and $Pc_m > 0.7$. Only four out of 36 summer blackcaps showed $Pc_m > 0.5$, which sets the percentage of incorrect classification of sedentary individuals at 10% (as shown previously; de la Hera et al. 2007). However, these four individuals (two of which had isotope data and are plotted on

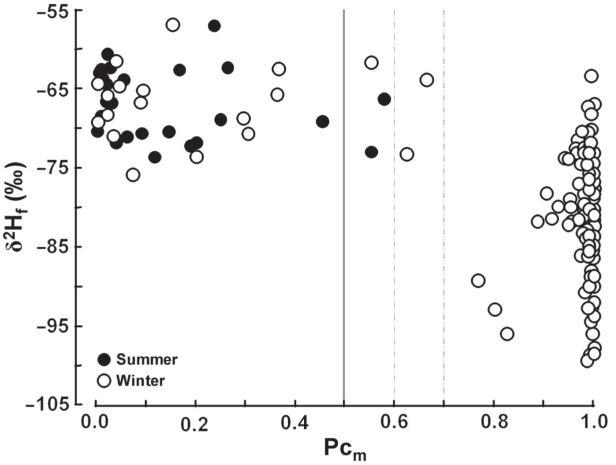

Figure 1. Variation in hydrogen isotope values (δ^2H_f) in relation to the posterior classification probability of being migratory (Pc_m) obtained from DFA in blackcaps captured in summer (known to be sedentary, black dots) or in winter (open circles). The continuous grey line separates birds classified as sedentary (to the left) or migratory (to the right). Broken lines show more conservative classification thresholds for migratory blackcaps ($Pc_m > 0.6$ or 0.7).

Table 2. Results of GLM analysing variation in flight-related morphology (PC1) and structural body size (PC2) in relation to δ^2H_f, and sex in wintering blackcaps (migratory and sedentary birds together), and in migrants classified with different classification thresholds ($Pc_m > 0.5$, 0.6 and 0.7, respectively).

	All wintering blackcaps			Migrants with $Pc_m > 0.5$			Migrants with $Pc_m > 0.6$			Migrants with $Pc_m > 0.7$		
	$F_{1,164}$	p	β	$F_{1,148}$	p	β	$F_{1,147}$	p	β	$F_{1,145}$	p	β
PC1												
δ^2H_f	35.63	< 0.001	−0.423	4.82	0.030	−0.177	4.19	0.042	−0.166	3.05	0.083	−0.143
Sex	0.09	0.762		0.98	0.325		1.04	0.310		0.90	0.343	
PC2												
δ^2H_f	0.00	0.987	−0.001	1.37	0.243	−0.093	3.41	0.067	−0.147	6.23	0.014	−0.197
Sex	6.07	0.015		8.65	0.004		7.18	0.008		8.80	0.004	

Fig. 1) had Pc_m ranging between 0.54 and 0.58, supporting the idea that sedentary blackcaps that may be incorrectly classified as migratory will usually score $Pc_m < 0.6$. However, two birds with Pc_m between 0.6 and 0.7 had isotope values well within the range of sedentary individuals. Although these individuals might be short-distance migratory blackcaps (from Iberian breeding areas), we decided to repeat our analyses with migratory blackcaps classified with a still more conservative threshold: $Pc_m > 0.7$.

Using 167 wintering blackcaps with isotope data, we found that blackcaps arrived from further to the north (those with more negative δ^2H_f scores) had more exaggerated flight-related morphology (higher values of PC1; Table 2, Fig. 2A). We found the same result when we restricted the analysis to blackcaps classified as migratory, although the correlation between δ^2H_f and PC1 was less significant in that case. The correlation maintained its effect size but progressively lost statistical significance as we raised the classification threshold of migratory blackcaps to $Pc_m > 0.6$ and $Pc_m > 0.7$ (Table 2), in spite of the fact that only three blackcaps were classified as migratory with $Pc_m < 0.7$ (Fig. 2A).

We did not find any correlation between δ^2H_f and structural size of birds when migratory and sedentary blackcaps were analysed together. However, when the analysis was restricted to wintering migrants, such correlation turned progressively more significant as we increased the classification threshold of migratory blackcaps (Table 2), with migratory blackcaps with a more northern breeding origin (according to δ^2H_f scores) showing larger structural body size (Fig. 2B).

Finally, δ^2H_f and morphology did not differ between migratory blackcaps occupying forests and shrublands (Table 3, Fig. 3). Neither the variance of these variables differed between habitat types ($p > 0.05$ in Levene's test for all variables). These results did not change qualitatively when we raised the classification threshold of migratory blackcaps, nor did they change when we considered all wintering migrants (including birds without isotope data). The only significant effect in these analyses was sex (Table 3), with blackcap females (PC2 mean [± SE] = 0.077 ± 0.111) being larger than males (PC2 = −0.369 ± 0.097).

Discussion

The advent of new techniques for inferring the geographic origin of migratory birds, such as stable isotope analyses, has greatly contributed to our understanding of the annual movements of their populations between breeding and non-breeding areas (Hobson 2008, Robinson et al. 2010). New methods have rapidly overcome more classical approaches, such as the analysis of morphology (Webster et al. 2002, Lopes et al. 2006). Most species show too little morphological

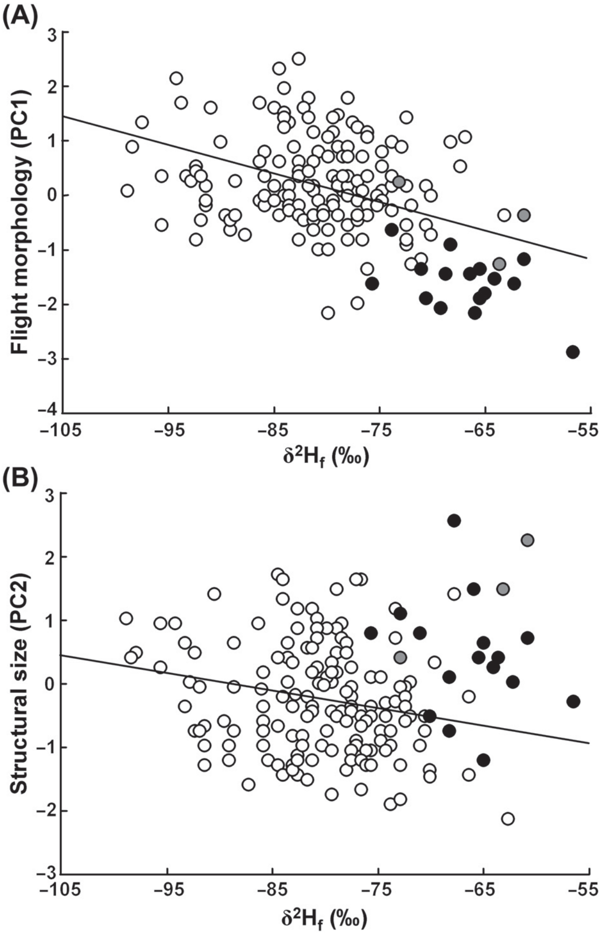

Figure 2. Relationships between hydrogen isotope signal (δ^2H_f) and (A) flight-related morphology (PC1), and (B) structural size (PC2) in wintering blackcaps. The colours represent blackcaps classified as migratory or sedentary with variable certainty, distinguishing among birds reliably classified as migratory ($Pc_m > 0.7$, open circles), blackcaps of uncertain origin ($0.5 > Pc_m > 0.7$, grey dots), and putative sedentary birds ($Pc_m < 0.5$, black dots). In (A) the regression line was drawn considering all points in the graph, but in (B) it was drawn considering putative migrants only (the open circles, see Table 2 for details on significant effects in each case).

Table 3. Results of GLM analysing variation in isotope values (δ^2H_f), flight-related morphology (PC1), and structural body size (PC2), in relation to habitat type (forests or shrublands) and sex in migratory blackcaps. The table show results obtained using migratory blackcaps that were classified with $Pc_m > 0.5$ and had isotope data (the same results were found with other possible datasets, see text for details).

	δ^2H_f		PC1		PC2	
	$F_{1,147}$	p	$F_{1,147}$	p	$F_{1,147}$	p
Habitat	0.01	0.929	2.34	0.128	0.22	0.640
Sex	0.49	0.486	0.66	0.419	9.12	0.003
Habitat × sex	1.17	0.281	0.04	0.833	0.01	0.917

variation among populations to allow for using morphology to infer the population origin of individuals. Our study system is especially advantageous because morphology can be used to accurately distinguish between migratory and sedentary blackcaps wintering in sympatry (de la Hera et al. 2007), which was confirmed by our analysis of hydrogen isotopes. Thus, mean δ^2H_f values of wintering blackcaps classified as sedentary by DFA were similar to the values obtained in the feathers of known sedentary blackcaps, while wintering blackcaps classified as migratory showed lower values of δ^2H_f than both groups of sedentary blackcaps. However, it is important to note that many migratory blackcaps, most likely those coming from the Iberian Peninsula, had isotope values of southern origin which overlapped the range of values of residents. These birds could only be distinguished as migratory based on their distinct morphology, which shows that a combination of methods may increase resolution when the population origin of birds needs to be inferred.

Unambiguous relationships between morphology (such as PC1 and PC2 in our study) and isotope values could increase the power to distinguish among breeding populations. However, our results showed that such relationships may depend on which populations are analysed. When sedentary and migratory blackcaps were analysed together, the correlation between δ^2H_f and flight morphology (PC1) was significant. Low values of δ^2H_f (indicative of northern origin) were then associated with longer and more pointed wings (higher PC1 scores), which in blackcaps are linked with long-distance migration (Fiedler 2005). Given that all blackcaps in our study share wintering grounds, birds with lower values of δ^2H_f migrate longer distances, and their morphology may be adaptive (Piersma et al. 2005, Baldwin et al. 2010). However, although our results confirm this widely accepted pattern of geographic variation in flight-related morphology for blackcaps (Cramp 1992, Fiedler 2005), the relationship between morphology and isotopes was strongly influenced by sedentary blackcaps. Thus, the correlation between δ^2H_f and PC1 became weaker when it was tested using migratory blackcaps alone. This happened because the range of variation in morphology was reduced when sedentary birds were removed from the analysis, while many migratory blackcaps (possibly of Iberian origin) had isotope ratios well within the range of sedentary populations (Fig. 1). The effect was eventually lost when three individuals classified as migrants with $Pc_m < 0.7$ (which could well be sedentary given their δ^2H_f values; Fig. 1) were also removed from the analysis. Such results suggest that migratory blackcaps wintering in the Gibraltar area span a somewhat narrow range of breeding origins, which might only be coarsely resolved using hydrogen isotope analyses (Cantos 1995, Hobson et al. 2004).

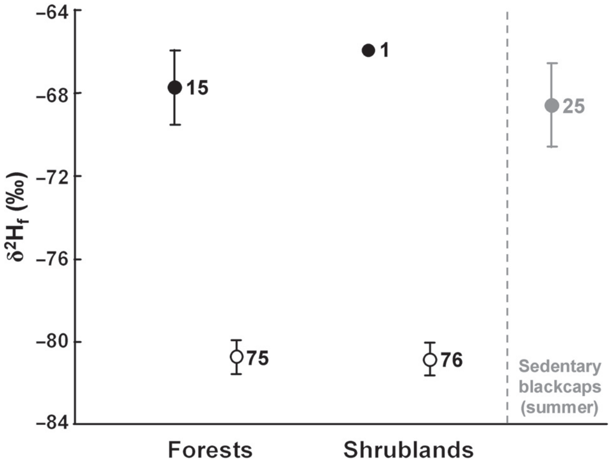

Figure 3. Variation in hydrogen isotope values (δ^2H_f) between habitats (forests and shrublands) and between wintering blackcaps classified as migratory ($Pc_m > 0.5$; represented as open circles) or sedentary ($Pc_m < 0.5$; black dots). The graph shows means with standard errors and sample sizes. Average isotope values of sedentary blackcaps captured during summer are also shown for reference (in grey).

We did not find any significant relationship between structural body size and geographic origin of blackcaps when migratory and sedentary birds were analysed together. However, this result may be confounded by the fact that the largest birds in our sample score extreme values for δ^2H_f (Fig. 2B). Thus, sedentary blackcaps are large and have δ^2H_f values of southern origin, while the largest migratory blackcaps in our sample are those coming from the northernmost part of the range of breeding origins, as shown by our analyses excluding sedentary blackcaps (see also Fiedler 2005).

Body size and timing of arrival on wintering grounds are known to influence hierarchical relationships among individual birds (Mönkkönen 1990, Snell-Rood and Cristol 2005). In fact, these two factors could play an important role in the distribution of blackcaps wintering in southern Spain, as can be interpreted from the larger structural size and earlier settlement of local sedentary blackcaps in preferred habitats, which may allow them to outcompete migrants (Pérez-Tris and Tellería 2002). In addition, previous studies suggested the existence of competition among migrants too, because migratory blackcaps were larger in forests than in shrublands (Pérez-Tris and Tellería 2002). However, we failed to replicate this result in our study, although we confirmed that body size varied geographically, which could promote variation in the competitive abilities of migratory blackcaps with different origins. Similar body size between migratory blackcaps occupying forests and shrublands suggests that the range of their breeding origins is the same, a conclusion which is also supported by the lack of variation in flight morphology and isotope values (both regarding the mean and the variance of δ^2H_f values) between habitats.

According to our results, European blackcap populations migrating to southern Spain are not spatially segregated in relation to the occupation of habitats of different quality.

Assuming that one habitat is better than the other, the ability of young blackcaps to return to breeding grounds may well depend on the outcome of winter social interactions, but will hardly be influenced by their origin. As a consequence, wintering in poor habitats may greatly contribute to the regulation of all migratory populations wintering in this area (Newton 1998), and inequalities among individuals of the same breeding population will arise in favour of the ones that settle in the best habitats (Marra et al. 1998). Interestingly, sedentary blackcaps seem to be highly capable to evade the struggle for preferred habitats and remain in forests during winter (Pérez-Tris and Tellería 2002). These populations are putative descendants of blackcap populations that may have existed in this region during the Holocene, from which migrants probably evolved after the last glaciation (Pérez-Tris et al. 2004). The long-term persistence of such relics in the face of competition with large numbers of migrants may have depended on their chances to occupy good wintering habitats (Bell 2000).

It has not escaped our notice that sedentary blackcaps may prefer forests not only because of the benefits of settling in good wintering habitats, but also because they protect their reproductive interests by keeping breeding territories year around. However, migratory blackcaps have no reproductive interests in the area and consequently will hardly benefit from winter site-tenacity. They may prefer habitats that help them to maintain their energetic balance during winter (Marra et al. 1998, Norris et al. 2004). But fruits have an unpredictable distribution among habitat patches and years in wintering grounds (Tellería et al. 2005), which can favour winter vagrancy to track the availability of food resources (Tellería and Pérez-Tris 2003). Opposing selective pressures could then favour winter residency among sedentary birds, but vagrancy among migrants. In fact, these two behaviours have been observed in other wintering populations (Cramp 1992, Belda et al. 2007), and the question remains as to whether residency is exclusive to local sedentary birds in these areas. Interestingly, large structural body size of sedentary blackcaps and similar flight-related morphology of migrants across habitat types could be interpreted as consequences of natural selection favouring winter residency in sedentary blackcaps, as opposed to vagrancy in migratory blackcaps (Senar et al. 1994).

Recent research highlights the importance of understanding the extent to which individuals from the same breeding populations migrate to the same non-breeding area and vice versa, a concept defined as migratory connectivity (Webster et al. 2002, Hobson et al. 2009, 2010, Ryder et al. 2011). However, local environmental heterogeneity could also promote structured patterns of distribution among populations within a single wintering location (e.g. among different habitat types), and not only among geographically-separated areas, although the existence of such small-scale patterns have been normally overlooked. Our results show that the process of occupancy of different wintering habitats may have complex outcomes, which also have important conservation implications. Thus, among the various blackcap populations wintering in our study area, the local resident population is clearly dependent on a single habitat type (the forest). This choice of habitat seems to be independent of the distribution of overwintering migrant conspecifics (Pérez-Tris and Tellería 2002), and creates a clear association between the breeding origin of birds (whether it is local or foreign) and wintering habitat. On the other hand, migratory blackcaps with different breeding origins in Europe end up mixing between forests and shrublands. Interestingly, such differences in the occupancy of wintering habitats with variable quality within a reduced geographic area might have similar ecological and evolutionary consequences to the connectivity patterns observed at larger scales (Studds and Marra 2005, Webster and Marra 2005), and therefore they deserve further investigation.

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