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Running head: *Feeding ecology of wintering Blackcaps*

Migratory and resident Blackcaps *Sylvia atricapilla* wintering in southern Spain show no resource partitioning

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When different populations of the same bird species share non-breeding habitats, competition for food may promote resource partitioning. We studied food choice by resident and migratory Blackcaps *Sylvia atricapilla* in sympatric wintering grounds in southern Spain. Resident Blackcaps may know the distribution of food better than migrants, and have a larger bill that may allow them to feed on a broader range of fruit sizes. Based on fruit and bird counts, we transformed both fruit crop and bird abundance to a common energy currency. During two winters with low and high fruit production, available energy from fruit in mid-January was estimated to be 80 and 1300 times the daily requirements of Blackcaps, respectively. Furthermore, Blackcap numbers did not track between-winter changes in fruit abundance during ten consecutive years of monitoring, further suggesting that fruit food is not limiting. Analysis of food items from 760 samples of 717 individuals showed that migrants and residents fed primarily on fruits of Wild Olive *Olea europaea sylvestris*, the most energetic fruit resource. In addition, there was no evidence that the larger bills of resident Blackcaps provided any foraging benefit. Migratory Blackcaps fed on Wild Olives and invertebrates, two resources with high energetic and structural value, more frequently than residents. This food choice could be more important for migratory Blackcaps because they have lower

body mass to reduce wing load. Our results suggest that the wintering grounds of Blackcaps in Iberia provide abundant food, which is used by sympatric migrants and residents without resource partitioning. Slight differences in food choice suggest that migrants might benefit from feeding on more nutritive food than residents to counteract the energetic constraints associated with a smaller body size.

Keywords: body condition, food selection, foraging ecology, frugivory, migration, morphology, sympatry

In many bird species, migratory populations often attain higher reproductive success than their non-migratory counterparts because their breeding habitats are more productive. If the range of migratory and resident conspecifics overlaps during the non-breeding period and both groups show similar competitive abilities in the exploitation of shared resources, the higher growth rate of migratory populations might be sufficient to drive resident populations to extinction (Bell 2000). However, residency may have several counteracting advantages that could favour the persistence of non-migratory populations over time, including freedom from the physiological stress and mortality risk associated with migratory journeys (Sillet & Holmes 2002), increased ability to settle in the most suitable non-breeding habitats, and the ability to obtain the most rewarding food resources (Cox 1985, Greenberg 1986, Bell 2000). Therefore, assessing whether or not non-breeding behaviour differs between migratory and resident birds is important in understanding the evolution and maintenance of divergent migratory strategies, yet our knowledge of the mechanisms allowing the coexistence of resident and migratory conspecifics in the non-breeding grounds remains limited (Pérez-Tris & Tellería 2002a).

The Blackcap *Sylvia atricapilla* is a common passerine in the Western Palearctic (Cramp 1992). It is a summer visitor to most of its west European range, but resident populations exist within its main wintering area in southern Spain (Pérez-Tris *et al.* 2004). Most migrants overwinter in Mediterranean scrublands, which hold fruit resources in winter but are unsuitable for breeding (Carbonell & Tellería 1998). However, many migratory individuals also enter forests where non-migratory conspecifics occur all year (Pérez-Tris & Tellería 2002a). This offers an opportunity to study how migratory and resident conspecifics interact during winter. Previous studies

have shown that, in forests, many resident Blackcaps (particularly males) prefer sites that produce few fruits but are highly suitable for breeding (Carbonell & Tellería 1998), while migrants move in search of fruit-producing patches (Pérez-Tris & Tellería 2002a). This could result in a different exploitation of food resources, and might be correlated with observed differences in morphology between migratory and resident Blackcaps (Tellería & Carbonell 1999).

Food is a major determinant of bird biology during winter, when self-maintenance is greatly influenced by the energetic cost of thermoregulation (Calder & King 1974, Blem 1990, Gosler 2002, Krams *et al.* 2010). For Blackcaps wintering in southern Spain, fruits are the main source of energy (Jordano & Herrera 1981), and Blackcaps actively track these resources during winter (Rey 1995, Tellería *et al.* 2008). Some studies have suggested that frugivorous birds become satiated by the immense fruit production of Mediterranean habitats (Herrera 1984, García *et al.* 2001, Hampe 2008), but there is also great heterogeneity in the distribution of this food between habitats. For example, in our study area fruit production is huge in the scrublands where most migratory Blackcaps spend the winter, but considerably lower in forests (Tellería & Pérez-Tris 2007). This raises the question of whether food is a limiting factor in forests where migratory and resident birds coexist, leading to competition or resource partitioning in forest habitats but not in scrublands.

We assessed whether food may limit Blackcap populations in a forest in southern Spain where both migratory and resident individuals occur during winter, and whether any limitation is linked to variation in food choice and body condition between migratory and resident birds. We first examined whether between-winter changes in fruit abundance are related to changes in Blackcap abundance. Such an association is necessary to conclude that fruit food regulates bird numbers, but not sufficient because the same pattern may result from the ability of Blackcaps to track the most productive fruit patches, with no population effects being caused by food scarcity. Second, we assessed whether the energy available from fruit is enough to satisfy the energy demands of the birds (Peer *et al.* 2003, Tellería *et al.* 2011). On the basis of our assessment of food abundance, we set out to test the null hypotheses that resident and migratory Blackcaps feed on similar food resources, leading to fitness differences between the two classes of birds if food is limiting. The alternative is that resident and migratory Blackcaps express different food choices reflecting resource partitioning if food is limiting. Within this alternative, we recognise that is plausible either that

resident Blackcaps may take the more energetically rewarding food, as a consequence of larger bill size and familiarity with the local environment (Wheelwright 1985, Tellería & Carbonell 1999), or that migratory Blackcaps may do so because of the energetic needs imposed by smaller body size and migratory behaviour (Blem 1990, Winkler & Leisler 1992, Tellería & Carbonell 1999). Specifically, we tested whether the larger gape of resident Blackcaps allows them to swallow larger fruits of Wild Olives *Olea europaea sylvestris*. Olives are one of fruits most frequently consumed by Blackcaps (Jordano & Herrera 1981, Herrera 1987), but are at the upper limit of fruit sizes that Blackcaps can swallow.

METHODS

Study area and monitoring scheme

San Carlos del Tiradero forest is located in southern Spain near the Strait of Gibraltar (36° 10' N, 5° 34' W) in a wooded, hilly landscape. The forest is dominated by Cork Oak *Quercus suber* and Algerian Oak *Q. canariensis*, with clearings covered by fruit-bearing shrubs. The most abundant shrubs are Wild Olives and Mastics *Pistacia lentiscus*, but also Broad-leaved Phillyrea *Phillyrea latifolia*, Common Myrtle *Myrtus communis* and other species.

From 1999 to 2009, we monitored the abundance of birds and fruiting shrubs in San Carlos forest in mid-January. We counted all birds and shrubs with fruits along seven 500-m long transects (with no detection limit distance) at elevations from 110 to 265 m. These general counts provided abundance indices of birds and fruit-bearing shrubs (number/transect) that allowed us to gain a general long-term perspective of the way they varied from winter to winter. Between-winter changes in fruit and bird estimates were analysed using repeated measures ANOVA, in which transect identity was used as a within-subject factor (StatSoft 2007). Residuals were found to support use of models assuming a Gaussian error distribution.

Food availability and bird requirements

In January 2008 and 2009, two winters with contrasting fruit abundance (Fig. 1), we recorded additional data from the seven 500-m long transects, in order to obtain estimates of bird and fruit density. We identified the birds that were detected within 25

m of the transect line, and counted the fruits of each shrub species found within 5 m. This allowed us to estimate for each transect the number of birds per 2.5 ha and the number of fruits per 0.5 ha, both of which were then extrapolated to an arbitrary area of 10 ha. The crop (g/10 ha) of each fruiting shrub species was transformed to metabolisable energy (kJ/10 ha) available to birds during the day of mid-January in which we estimated fruit density. The energetic content of each fruit species was determined according to their average mass (g) and lipid, protein and carbohydrate composition of dry pulp following Herrera (1987). From these data, we estimated the metabolisable energy (kJ) of individual fruits according to the Atwater system (FAO 2003). We used the sum of the energy provided by all fruit species to estimate the total energy available in the entire standing crop of fruiting shrubs. To compare the availability of fruit energy in 2008 and 2009 with the energy demanded by Blackcaps and other frugivorous birds, we calculated the field metabolic rate (FMR; kJ/day) of each species as $FMR = 10.5 M^{0.681}$ (Nagy 2005), where M is the species' average body mass in grams (Dunning 1993). This equation estimates the energy (kJ) one bird needs to live during one day. We multiplied the daily FMR of each individual species by its population density in 2008 and 2009 to estimate the daily energetic demands of that species' population (Peer *et al.* 2003, Tellería *et al.* 2011), then summed this across frugivorous species and multiplied this by the number of days remaining to the beginning and mid of March (45-60 days), when wintering season comes to its end. Differences between 2008 and 2009 in bird and fruit density were also analysed by repeated measures ANOVA (see above).

Body condition and migratory status of Blackcaps

In each winter from 1999 to 2007, Blackcaps were captured using mist-nets set close to the transects ($n = 769$ captures of 717 individuals), individually ringed, and sex and age (first-year or adult) determined by plumage examination (Svensson 1992). We measured the length of the eighth primary feather, tail length and the distance from the wing tip to the tips of the first and ninth primary feathers (descendant numbering of primaries; Svensson 1992). These measurements were used to distinguish between migratory and resident individuals by means of a discriminant function analysis developed from Blackcaps with known migratory behaviour (de la Hera *et al.* 2007), which showed that migratory birds have longer and more pointed wings, but a shorter tail, than resident birds (Pérez-Tris *et al.* 1999, de la Hera *et al.* 2007). This

classification method has proved highly reliable (more than 90% of correct assignments) when its validity was tested using hydrogen isotope data from feathers (de la Hera *et al.* 2012). We also measured wing length, tarsus length, and the length, depth and width of the bill. We combined wing, tail, bill and tarsus lengths in a principal components analysis (PCA) to obtain an index of structural body size of Blackcaps. All four body dimensions had high positive loading on PC1 (eigenvalue = 1.56, variance explained = 38.9%; factor loadings: bill = 0.509, tarsus = 0.624, wing = 0.531, tail = 0.790), which we therefore regarded as a good index of structural size (Rising & Somers 1989). We scored development of pectoral muscle using a four-point scale (0-3: concave, straight, convex or bulging; Pinilla 2000). We used General Linear Models (GLMs) to test for differences in body mass and muscle scores between resident and migratory Blackcaps, controlling for effects of year, age and sex and structural size as a covariate, thereby testing for variation in body condition (body mass relative to body size; Brown 1996).

Fruit choice

All Blackcaps captured were retained for 30 - 60 minutes in cloth bags containing a filter paper bag in which seeds and other food remains ejected by birds were collected. From a total of 717 individual Blackcaps we obtained 760 diet samples, which were labelled and stored in a refrigerator (-18°C) until analysis. For 39 individuals we collected more than one sample (35 with two, and four with three samples). In the laboratory, we placed the content of paper bags in a Petri dish with water to separate fruit seeds and other food remains, which were inspected using a binocular microscope ($\times 20$). Fruit species consumed were determined based on the seeds present in each sample, using a reference collection obtained from fruits collected at the study site. We counted the number of seeds of each species in each food sample, and summed these to obtain the total number of seeds in the sample. Recognisable invertebrate remains were composed of cuticle fragments, ant legs and heads, beetle elytra and snail shells. However, most invertebrate remains were difficult to classify, and counting individuals of identified taxa proved unreliable, so we scored only presence or absence of invertebrates in the sample. We assumed that migratory and resident Blackcaps had the same opportunities to choose any fruit species available in the forest during the study period. We used a logistic model with binomial errors (StatSoft 2007) to test whether the probability of occurrence of animal remains or individual fruit species in diet

samples varied with population type (migratory or resident), sex and age of birds, all expressed as categorical fixed effects. **Because of an excessive fragmentation of the multifactorial contingency table, we pooled the data across years for analyses.**

Correlates of variation in consumption of Wild Olives

We analysed variation in seed size of Wild Olives from 285 Blackcap diet samples in which this fruit appeared. We used general linear mixed models (GLMMs) to test whether seed diameter or size differed between resident and migrant Blackcaps, controlling for effects of sex and age and total number of seeds in the sample, and including year as a random effect. We used data only from first captures of individual Blackcaps to eliminate pseudoreplication.

An important assumption of the analysis is that seed size correctly predicts fruit size and amount of fruit pulp, which is what ultimately determines fruit nutrient content. To validate this assumption, we sampled fruits from 20 randomly selected Wild Olive trees. Within each tree, we collected ripe fruits spanning the range of available fruit sizes, and kept them refrigerated until their analysis, within three days of collection. In all, we measured 613 ripe fruits. We first weighed the fresh fruit, and measured its total length and four diameters obtained by turning the seed by 45° between measurements. The mean diameter was computed from the four measurements. We then placed the fruits in an oven at 100°C to measure their dry mass before separating the pulp from the seed, and weighing and measuring the seed following the same procedure as described for the fresh fruit. The dry mass of the pulp was obtained by subtracting seed mass from the overall dry mass of the fruit. We confirmed that seed dimensions were strongly associated with fruit pulp dry mass (seed diameter: $r = 0.76$, $P < 0.001$; seed length: $r = 0.71$, $P < 0.001$), and that seed diameter was strongly correlated with fruit diameter ($r = 0.91$, $P < 0.001$). This validates our assumption that seed size reflects fruit size in Wild Olives.

Because olive seed diameter and length were correlated (Pearson's correlation coefficient for fruits sampled in the field: $r = 0.75$, $P < 0.001$, $n = 613$; seeds found in diet samples: $r = 0.68$, $P < 0.001$, $n = 285$), we obtained a composite index of seed size by means of PCA. Both variables had a high positive loading (0.92) in the resultant principal component. This measure best represented nutrient content of fruits, while seed diameter may best represent manageability of fruits to a foraging Blackcap,

because birds with the smallest mouth gapes may find it more difficult to swallow wide fruits, regardless of length. Using eight diet samples with olive seeds from recaptured birds, we found seed attributes (especially seed diameter) to be repeatable among individual Blackcaps (intra-class correlation coefficients, olive seed size: $r_1 = 0.62$, $F_{3,4} = 4.27$, $P = 0.097$; olive seed diameter: $r_1 = 0.85$, $F_{3,4} = 12.14$, $P = 0.018$). Although statistical power was low, these analyses supported the view that observed food items in diet samples represented individuals' fruit-size choices.

We repeated all analyses using both mean and maximum seed size in each sample because the latter might better capture the upper limit of fruit sizes manageable by each individual. However, results were the same in each case and the two measurements of seed size were highly correlated ($r = 0.95$, $P < 0.001$, $n = 285$), so we report results only for mean seed size.

RESULTS

Food availability in wintering grounds

The abundance of shrubs that were in fruit varied among winters ($F_{9,54} = 2.86$, $P = 0.008$; Fig. 1), a pattern which was primarily related to annual changes in the abundance of Wild Olives ($F_{9,54} = 4.09$, $P < 0.001$), the most common fruiting shrub in our study area (Fig. 1). The abundance of all frugivorous birds wintering in the forest did not show significant variation among years during the study period ($F_{9,54} = 1.13$, $P = 0.357$; Fig. 1), and it did not correlate with the annual abundance of shrubs with fruits ($r = 0.258$, $P = 0.469$, $n = 10$ winters). Blackcap abundance showed marginally significant variation among winters ($F_{9,54} = 2.07$, $P = 0.049$), but this was not correlated with the abundance of fruiting shrubs ($r = 0.113$, $P = 0.736$, $n = 10$).

According to our long-term monitoring of fruiting shrubs (Fig. 1), the winters of 2008 and 2009 represented situations of low and high, but not extreme, fruit availability. However, they did not reach the extreme situations of 2002 and 2007 (Fig. 1), when fruiting shrubs were very scarce and abundant respectively. In January 2008 and 2009, frugivorous birds accounted for the 35.3% and 35.4% of the wintering bird community, with European Robins *Erithacus rubecula* and Blackcaps most abundant. Tits (Paridae) were the second most abundant group (24.1% and 32.3% of the total number of birds; Table 1). The abundance of fruiting shrubs differed between these two

winters, particularly for Wild Olives (Table 1). Accordingly, available fruit energy differed between years ($F_{1,6} = 12.91$, $P = 0.011$; Fig. 2), and in mid-January ranged between 19 (2008) and 187 (2009) times the energy required by all frugivorous birds (winter 2008: $F_{1,6} = 13.67$, $P = 0.009$; winter 2009: $F_{1,6} = 202.55$, $P < 0.001$), and between 87 times (winter 2008; $F_{1,6} = 11.74$, $P = 0.013$) and 1317 times (winter 2009: $F_{1,6} = 7.77$, $P = 0.029$) the energy requirements of Blackcaps (Fig. 2).

Food choice of Blackcaps

Of 760 diet samples collected, 454 contained identifiable food remains. The number of seeds per sample varied between zero and nine (mean \pm SE = 2.05 ± 0.07 seeds and 1.16 ± 0.02 species per sample). Four fruit species dominated the samples, with Wild Olive as the most consumed species (Table 2). Rarely consumed fruits (Common Myrtle, Wild Madder *Rubia peregrina* and Black Bryony *Tamus communis*) were excluded from further analyses, although their seeds contributed to total seed count. Fruit choice was roughly related with the availability of different fruiting shrub species (Fig. 3). However, this was not the only determinant of food choice since all Blackcaps selected fruits with the highest energetic content (Wild Olive, Mastic and Common Ivy *Hedera helix*) among those available below a certain size (Herrera 1987). Blackcaps did not consume the large fruits of Common Hawthorn *Crataegus monogyna* and Wild Roses *Rosa* spp. although these species have high energetic content, probably because they were too large to swallow (Herrera 1987).

There was no effect of year on either Wild Olive seed number ($F_{8,0.63} = 3.56$, $P = 0.494$) or seed size ($F_{8,1.84} = 3.37$, $P = 0.266$), so data were pooled across years for subsequent analyses. Diet samples obtained from resident birds contained more seeds on average than the samples of migrants, but there was no effect of age or sex (migratory status: $F_{1,406} = 5.78$, $P = 0.016$; sex: $F_{1,406} = 0.160$, $P = 0.689$; age: $F_{1,406} = 0.170$, $P = 0.678$; interactions not significant). However, there was no effect of migratory status on the mean number of fruit species consumed ($F_{1,406} = 1.01$, $P = 0.316$), controlling for the effects of sex ($F_{1,406} < 0.01$, $P = 0.993$) and age ($F_{1,406} = 0.47$, $P = 0.491$; interactions not significant).

Diet samples of migratory Blackcaps more often contained animal remains and olive seeds than those of resident Blackcaps (Table 3). In addition, female Blackcaps showed evidence of preference for fruits other than olives (Mastic, Broad-leaved Phillyrea), although there was no age effect (Table 3).

Resident Blackcaps had larger mouth gapes (as measured by bill width) than migratory Blackcaps, with females and adults having larger mouth gapes than males and juveniles, respectively (Table 4). However, there was no difference in the diameter or overall size of olives consumed by migratory and resident Blackcaps (Fig. 4), whether a negative relationship between the number and diameter (and size) of olive seeds in diet samples was controlled for or not (Table 4). We found a general trend towards migrants and juveniles consuming larger olives than adults, although there was an interaction between age and migratory behaviour (resident adult Blackcaps fed on smaller olives than all other groups, creating the main effect described). When the number of seeds was excluded from the analysis, the same results were obtained, except for the fact that the main effect of age was no longer statistically significant ($F_{1,255} = 3.58$, $P = 0.059$).

Body condition of Blackcaps

Structural body size of Blackcaps (PC1 of body measurements) was positively correlated with body mass ($r = 0.36$, $P < 0.001$, $n = 703$). Resident Blackcaps had higher pectoral muscle scores, and showed better body condition (body mass relative to body size), than migratory Blackcaps (Table 5). Adult Blackcaps wintering in the forest were larger and heavier than juveniles, although the two age classes showed similar body condition (Table 5). Females were heavier than males, but the two sexes did not differ in size, muscle score or body condition (Table 5).

DISCUSSION

Food availability and bird requirements

Fruit availability changed between winters in San Carlos forest, but this was not correlated with changes in bird abundance. This is atypical for frugivorous birds, which usually track the changing spatio-temporal distribution of fruit resources (Levey & Stiles 1992, Burns 2004, García & Ortiz-Pulido 2004). In San Carlos forest region, fruit tracking by Blackcaps does occur, but it is associated with scrublands occupied by migrants, rather than oak forests occupied by both migratory and resident individuals (Tellería & Pérez-Tris 2007, Tellería *et al.* 2008). Scrublands also host more juvenile individuals, and those of a smaller size, than forests, suggesting that habitat segregation is related to site tenacity of resident birds (which rarely leave their breeding territories) and competitive interactions in which young and small migrants seem to be at a

disadvantage in settling in forest habitats (Pérez-Tris & Tellería 2002a). This pattern may extend to other bird species wintering in the area (Tellería & Pérez-Tris 2004), and is similar to habitat segregation found in other regions (Sherry & Holmes 1996, Marra 2000). Such distribution suggests a regional scenario in which forests (such as our study area) are less suitable than scrublands for efficient tracking of fruit resources by Blackcap populations (Tellería & Pérez-Tris 2007).

Between-winter decoupling of bird and fruit abundance in San Carlos forest suggests that fruit availability does not limit bird numbers. This conclusion is supported by the fact that available fruit energy was 90-1300 times the daily requirements of Blackcaps, and 20-200 times the requirements of all frugivorous birds (Fig. 2). Our methods are only approximate. For example, the energy demanded by birds was calculated following Nagy (2005), which is a model derived from a wide range of bird species, but has unknown applicability to this specific study. In addition, there may be error in line transect estimation of bird densities (Bibby *et al.* 1992), and the energetic value of fruits was obtained using standard laboratory protocols, which do not consider the digestive ability of birds (Fisher 1972). Finally, we did not consider depletion by other fruit consumers such as small mammals (Rey & Alcántara 2000) on the availability of food for frugivorous birds. In addition, it is important to note that energetic requirements of birds refer to just one day in mid-January. If all migrants remain in San Carlos until the end of the wintering period (mid-March), fruit resources in mid-January may not be enough to maintain birds through the whole wintering season in some winters, especially in years of poor fruit production (e.g. 2002 in Fig. 1) or high number of frugivorous birds (e.g. 1999 and 2000; Tellería & Pérez-Tris 2007). In any case, the ability of migratory Blackcaps to track the extant availability of fruit resources in other habitat patches (e.g. scrublands) will probably contribute to buffer any extreme situation (Tellería *et al.* 2008).

Overall, it seems reasonable to conclude that fruit provides a huge energy surplus to Blackcaps during most of the winter, and will not be limiting in most years. At times of fruit limitation, Blackcaps will also feed upon invertebrates (e.g. small arthropods, snails; Cramp 1992, Schaefer & Schmidt 2002).

Food choice by migratory and resident Blackcaps

High food availability in San Carlos forest during the winter does not suggest that there is a food constraint that is likely to cause competition and resource partitioning between

migratory and resident Blackcaps. Rather, our results suggest that food choice depends on preferences of migratory and resident Blackcaps. Both migratory and resident birds selected the most energy-rich fruits, suggesting a similar response to the high metabolic demands of winter survival (Calder & King 1974). Although winter conditions are mild in coastal areas of southern Spain, low night temperatures and episodic frosts are frequent, being 3-8°C the minimum range of temperatures in January (Hijmans *et al.* 2005). In winter, small passerine birds are strongly constrained by the metabolic cost of thermoregulation in areas where temperature drops under the thermo-neutral zone (around 19 °C for small passerines; Calder & King 1974, Kendeigh *et al.* 1977). In this context, olives, the fruit most consumed by Blackcaps, represents a key resource because of their local abundance, high energetic content and large size (Herrera 1987).

Migratory and resident Blackcaps selected olives of similar size, despite clear differences in mouth gape size (Fig. 3 and 4). The larger bill and mouth gape of resident Blackcaps have been interpreted as adaptations to an omnivorous diet in a habitat where fruiting plants are present all around the year. Alternatively, the slender bill of migratory Blackcaps may be an adaptation to exploit invertebrates in northern breeding grounds (Tellería & Carbonell 1999). Nonetheless, the bill morphology of migratory Blackcaps does not constrain their ability to feed on the same range of fruit sizes as resident Blackcaps. In fact, the birds that consumed small olives in our sample were also the ones with a large gape (adult resident individuals). This rules out any benefit of a larger gape for resident Blackcaps that is associated with exploitation of large fruits. A possible explanation for this lack of differences arises from the observed negative correlation between seed number and seed size in diet samples, supporting the existence of a trade-off between eating many fruits and eating large fruits (Table 4). Mechanical constraints probably limit the amount of fruit material (including seeds) that a Blackcap may carry in its digestive system. Under these circumstances, eating large, energy-rich fruits may be beneficial if it increases nutrient intake at a given total fruit volume, which is feasible because many small fruits reduce the pulp-to-seed ratio compared to a few large fruits. By consuming more and, at least in the case of adults, smaller fruits, resident Blackcaps may end up feeding on less rewarding food sources than migratory Blackcaps. This possibility is supported by previous studies which found that adult resident Blackcaps occupy habitat patches with scarce fruits but abundant brambles *Rubus* spp., the preferred nesting substrate of Blackcaps; while juveniles and migratory Blackcaps were more frequent in fruit-rich patches (Perez-Tris & Tellería 2002a). Thus,

resident birds may value holding breeding territories during winter over food availability, which is possible when food is not limiting.

Finally, we detected other differences in food choice between migratory and resident Blackcaps. Migratory birds fed more frequently on olives and invertebrates than resident birds (Herrera 1987). This suggests that migratory individuals may benefit from more energetic fruits (olives) than residents. Such benefit may be attained through bird ranging in search of rewarding fruits, a strategy unavailable to territory-defending resident birds. However, resident birds may compensate reduced access to olives by exploiting alternative fruit sources, on which the long-term persistence of resident populations may therefore depend (Tellería *et al.* 2005). Migratory Blackcaps also fed more often upon invertebrates, a rarer behaviour among resident individuals despite the fact that the latter faced stronger constraints on fruit choice, and might have benefitted more from alternative food sources. However, this may reflect greater protein need to fuel higher muscular power demands in migratory Blackcaps (Jenni & Jenni-Eiermann 1998, Bauchinger & Biebach 2001). Migratory Blackcaps are lighter for their size than residents, perhaps to reduce wing load during migration (Winker & Leisler 1992, Tellería & Carbonell 1999), but reduced body mass can force them to seek more energetic food during winter, a demand that may be increased if winter body condition determines migration and breeding success in spring (Norris *et al.* 2004, Robb *et al.* 2008). Such challenges to maintaining energy balance may impair body condition and deplete protein reserves stored in pectoral muscles of migratory Blackcaps, thus prompting exploitation of invertebrates even in habitats rich in fruits, where a fruit-based diet is sufficient to sustain resident birds. In contrast, resident Blackcaps, remaining in their breeding territories and without the challenges of wider ranging behaviour and preparation for migration, may more easily maintain better body condition than migrants.

Conclusions

Our results illustrate two ideas that are fundamental for our understanding of the feeding ecology of migratory and resident Blackcaps in sympatric wintering habitats. The first is that the habitat where the populations coexist offers superabundant food resources. This results from seasonal processes which set the basis of migratory movements of many species (Alerstam & Enckell 1979). In lowland Mediterranean areas, winter is a productive season, when many fruiting shrubs have their ripening period, producing

crops that are large enough to satiate avian frugivores (Hampe 2008). The second is that in a context of food abundance and similar use of resources by migrants and residents, reduced body mass relative to body size or smaller muscle scores of migrants is unlikely to result from asymmetric competition with resident conspecifics. As an alternative explanation, we conclude that migratory and resident Blackcaps follow different behavioural strategies during winter (nomadism and territoriality, respectively), which may be favoured by divergent morphology associated with migration or residency (Tellería & Carbonell 1999). These strategies may involve different constraints, such as increased energy or protein demands for migratory Blackcaps or restrictions on fruit choice for resident Blackcaps, each counterbalanced by corresponding benefits (increased accessibility of food sources or release from the energetic and social costs of movement, respectively). Within this framework, reduced body mass related to migration would be the cause, not the consequence, of the preference by migratory Blackcaps for food of high energetic and structural value. At most, this scenario suggests stronger pressures acting on migrants related to self-maintenance during winter, which may account for shorter life-time expectancy of migratory Blackcaps (Pérez-Tris & Tellería 2002b). Whether this contributes to explaining the persistence of resident populations in the face of coexistence with overwintering migrants remains to be investigated, but our results support this idea as feasible.

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Table 1. Mean number (\pm SE) of frugivorous birds and fruits per 10 ha recorded along 7 transects in San Carlos del Tiradero forest during two winters of low (2008) and high (2009) fruit crop.

	January 2008 (number/10ha)	January 2009 (number/10ha)
Frugivorous birds		
<i>Sylvia atricapilla</i>	8.6 \pm 3.3	7.4 \pm 2.8
<i>Erithacus rubecula</i>	9.1 \pm 3.5	9.1 \pm 1.7
<i>Turdus philomelos</i>	2.9 \pm 1.9	6.3 \pm 2.9
<i>Turdus merula</i>	2.9 \pm 1.1	2.9 \pm 1.4
Other bird species	42.9 \pm 11.1	46.9 \pm 9.6
Fruits		
<i>Pistacia lentiscus</i>	7,037.1 \pm 6,062.3	3,522.9 \pm 1,719.1
<i>Olea sylvestris</i>	12,502.9 \pm 7,179.0	327,197.1 \pm 140,748.9
<i>Phillyrea latifolia</i>	22,857.1 \pm 22857.1	0.0 \pm 0.0
<i>Crataegus monogyna</i>	154.3 \pm 141.4	571.4 \pm 428.6
<i>Rosa</i> spp.	1,165.7 \pm 975.1	271.4 \pm 225.4
<i>Smilax aspera</i>	185.7 \pm 142.1	0.0 \pm 0.0
<i>Myrtus communis</i>	2,314.3 \pm 2281.1	0.0 \pm 0.0
<i>Daphne gnidium</i>	17.1 \pm 17.1	0.0 \pm 0.0
<i>Ruscus hipophyllum</i>	8.6 \pm 8.6	0.0 \pm 0.0

Table 2. Frequency distribution by sex, migratory status and age of fruit seeds and animal remains recorded in food samples of Blackcaps wintering in San Carlos del Tiradero forest.

Sex-Migratory status-age	Sample size (<i>n</i>)	Fruit vs. animal food		Fruit species (total no. seeds)			
		Fruit presence	Animal presence	<i>Olea europaea</i>	<i>Pistacia lentiscus</i>	<i>Hedera helix</i>	<i>Phillyrea latifolia</i>
Male-migratory-adult	119	58	68	58	13	37	12
Male-migratory-young	173	108	106	110	24	37	13
Male-resident-adult	41	25	18	18	9	9	8
Male-resident-young	83	45	31	43	22	20	11
Female-migratory-adult	72	46	32	41	16	12	3
Female-migratory-young	99	63	56	63	20	15	14
Female-resident-adult	51	31	22	25	14	10	24
Female-resident-young	56	39	23	24	8	17	25

Table 3. Log-linear analyses of fruit frequency distribution in relation to age, migratory status and sex of Blackcaps. Each line represents one log-linear model, describing the occurrence of the corresponding type of food (the dependent variable, measured as presence or absence of that food type in food remains) among different types of birds. The table shows the goodness of fit of the final model and the contribution of relevant effects included in the model (any significant interactions between independent variables or non-significant effects are not shown). For each interaction in the model, 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.

	Goodness of fit of the model			Interactions in the model				Food selection trends
	ML χ^2	<i>df</i>	<i>P</i>	Effect [§]	<i>df</i>	Partial χ^2	Marginal χ^2	
Animals	11.75	9	0.228	3x4	1	14.68**	15.44**	Migrants feed more on animals
Fruits	12.07	9	0.209	1x4	1	4.29*	3.98*	Females feed more on fruits
<i>Olea europaea</i>	9.58	9	0.385	3x4	1	4.06*	4.18*	Migrants feed more on <i>Olea</i>
<i>Pistacia lentiscus</i>	12.40	9	0.192	1x4	1	4.16*	4.60*	Females feed more on <i>Pistacia</i>
<i>Phillyrea latifolia</i>	10.26	8	0.247	1x4	1	7.33**	8.59**	Females feed more on <i>Phillyrea</i>
				3x4	1	6.48*	7.83**	Residents feed more on <i>Phillyrea</i>
<i>Hedera helix</i>	14.49	11	0.207	-	-	-	-	No trends detected

[§]Variables included in each model are 1: sex. 2: age, 3: migratory status, 4: occurrence of the corresponding food type (dependent variable)

P* < 0.05, *P* < 0.01

Table 4. Results of GLM for variation in bill morphology and size of olive seeds consumed by Blackcaps wintering in San Carlos forest, in relation to migratory status, sex and age.

	Bill morphology [§]						Olive seed morphology [§]			
	length		height		width		size		diameter	
	$F_{1,684}$	P	$F_{1,684}$	P	$F_{1,685}$	P	$F_{1,254}$	P	$F_{1,254}$	P
Sex	15.3	< 0.001	13.5	< 0.001	4.7	0.030	2.80	0.095	0.69	0.408
Age	3.2	0.075	5.9	0.015	8.4	0.003	4.19	0.041	3.49	0.062
Migration	48.6	< 0.001	64.9	< 0.001	31.8	< 0.001	3.91	0.049	1.75	0.187
Sex x age	0.3	0.603	0.2	0.625	0.1	0.798	0.03	0.862	0.82	0.366
Sex x migration	1.1	0.285	2.8	0.092	0.0	0.919	1.01	0.316	2.30	0.131
Age x migration	0.2	0.650	3.1	0.077	2.2	0.134	6.23	0.013	2.70	0.102
3-way interaction	0.0	0.919	1.6	0.209	0.0	0.937	2.58	0.109	3.41	0.066
Number of seeds*	-	-	-	-	-	-	13.03 [†]	< 0.001	9.04 [‡]	0.003

* Effects of number of seeds: [†] $\beta = -0.212$; [‡] $\beta = -0.181$

[§] All main effects in these models remained unchanged when non-significant interactions were removed.

Table 5. Results of GLM for on variation in body mass and pectoral muscle development of Blackcaps wintering in San Carlos forest, in relation to migratory status, sex and age. Structural body size has been included as a covariate of body mass to analyse variation in body condition.

	Structural size [§]		Body mass [§]		Muscle [§]		Body condition [§]	
	<i>F</i> _{1,669}	<i>P</i>	<i>F</i> _{1,676}	<i>P</i>	<i>F</i> _{1,651}	<i>P</i>	<i>F</i> _{1,666}	<i>P</i>
1.Sex	2.8	0.093	4.0	0.046	2.8	0.097	2.3	0.130
2.Age	24.3	< 0.001	7.1	0.008	2.6	0.107	0.5	0.466
3.Migratory status	4.9	0.027	3.1	0.078	31.5	< 0.001	7.5	0.006
1 x 2	0.2	0.666	0.03	0.872	0.0	0.868	0.2	0.673
1 x 3	3.2	0.073	0.4	0.542	1.2	0.267	0.0	0.989
2 x 3	4.3	0.039	0.7	0.390	0.0	0.856	0.0	0.890
1 x 2 x 3	0.0	0.900	0.3	0.583	0.5	0.481	0.8	0.388
Structural size (covariate)	-	-	-	-	-	-	115.3	< 0.001
Year (random factor)	4.6	< 0.001	8.3	< 0.001	6.0	< 0.001	11.1	< 0.001

[§] All main effects in these models remained unchanged when non-significant interactions were removed.

Figure legends

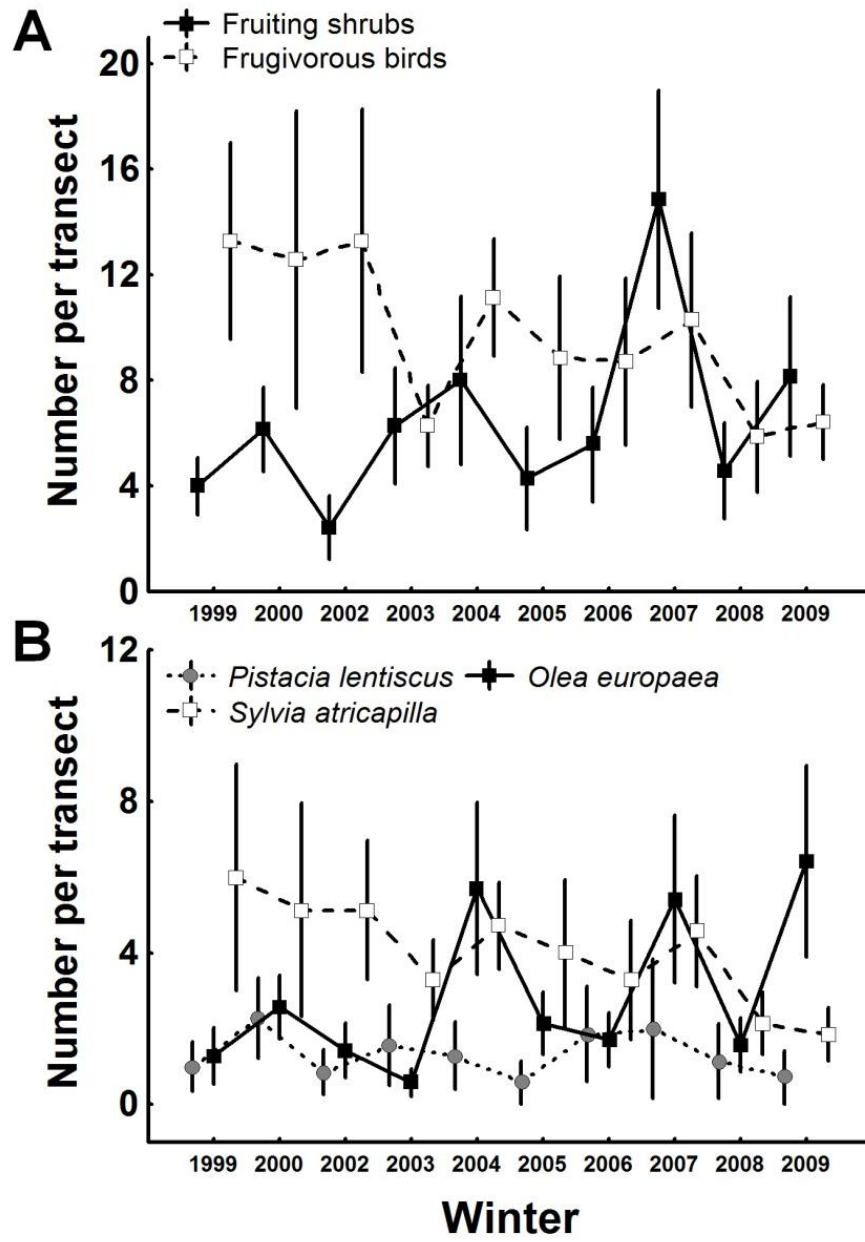
Figure 1. *Above.* Among-winter changes (mean \pm SE) in frugivorous bird and fruiting shrub abundance (number of shrubs that were in fruit) in seven 500-m long transects in San Carlos forest. *Below.* Abundance patterns of Wild Olives, Lentiscs and Blackcaps.

Figure 2. Energy (mean \pm SE) provided by fruits in San Carlos forest and daily energy requirements of Blackcaps and the whole community of frugivorous birds in two years of low (2008) and high (2009) fruit crop.

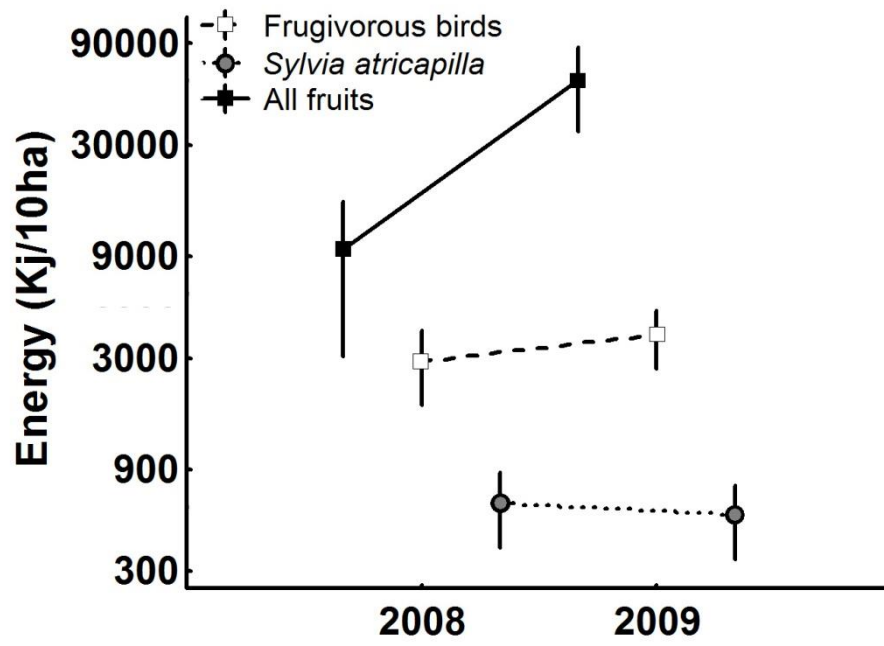
Figure 3. Abundance of fruiting shrubs per transect in San Carlos forest. The main graph shows abundance (mean \pm SE) obtained from the mean scores of the 10 winters of monitoring during which changes in fruit abundance were assessed. The histogram shows the number of samples in which seeds of the different fruit species were recorded ($n = 760$ food samples).

Figure 4. Variation in bill width (above) and size index of Wild Olives (below) consumed by male and female Blackcaps according to age and migratory status (means \pm 0.95 % CI).

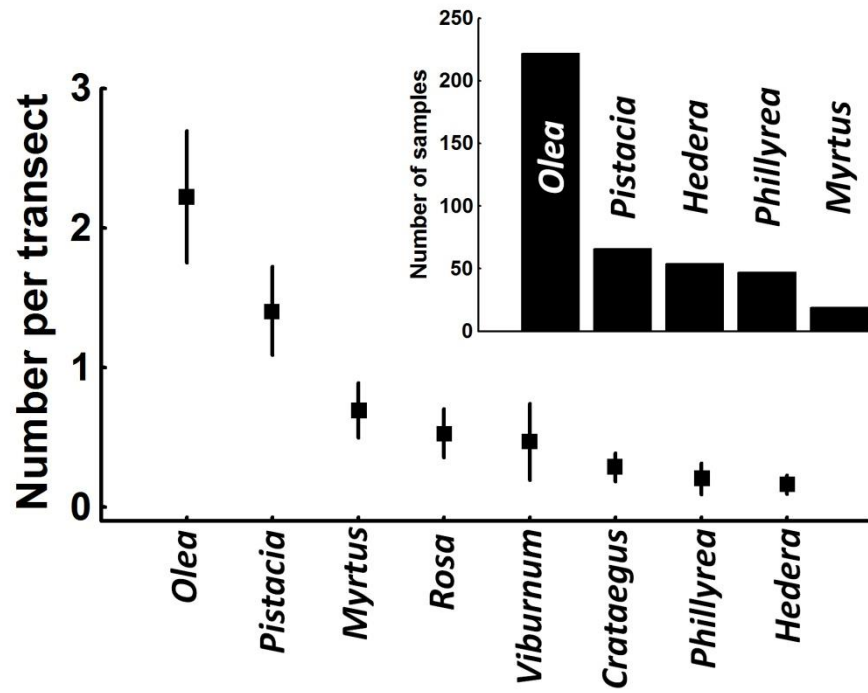
Tellería et al. Figure 1.



Tellería et al. Figure 2.



Tellería et al. Figure 3.



Tellería et al. Figure 4.

