

How residents behave: home range flexibility and dominance over migrants in a Mediterranean passerine



Michelangelo Morganti^{a,*}, Giacomo Assandri^{b,c}, José Ignacio Aguirre^a, Álvaro Ramirez^a, Mario Caffi^d, Francisco Pulido^a

^a Department of Zoology and Physical Anthropology, Complutense University of Madrid, Madrid, Spain

^b University of Pavia, Dept. of Earth and Environmental Sciences, Pavia, Italy

^c MUSE, Sezione Zoologia dei Vertebrati, Trento, Italy

^d Borgo San Giacomo, Italy

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Residency has repeatedly evolved in many migratory animals, some of which have preserved the anatomical adaptations to perform long-range movements. This is the case for partially migratory populations of Mediterranean passerines in which migrants and residents both have a migrant morphology. The question of how selection maintains residency in this situation remains unclear. Using radiotelemetry, we followed the resident fraction of a partially migratory population of blackcaps, *Sylvia atricapilla*, from eastern Spain and studied changes in home range size and habitat composition throughout three breeding and two wintering seasons. We then compared these birds with two groups of migratory blackcaps present in the area: in winter with migrants that breed in northern populations and in spring with migrants that breed locally. In addition, we observed aggressive interactions between individually marked birds to explore dominance relationships during winter. The home ranges of resident blackcaps were six times larger in winter than during the breeding season, but within each season, they were comparable in size to those of migrants. The habitats used by residents markedly differed between seasons as well as from those of migrants in winter, but not during the breeding season. In winter, resident birds were dominant over migrants, although migrants were generally larger. Overall, residents showed high between-season flexibility in home range size and habitat use. Winter home ranges of residents included breeding sites and more diverse types of habitats than those of northern migrants. This suggests that in winter, the importance of dominance for obtaining priority access to food may be high but not crucial, given that residents may reduce competition by feeding separately from migrants. Future studies should focus on whether residents show specific personalities and on the role of yearly oscillations in environmental conditions in maintaining residency in this type of partially migratory population.

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There is ample evidence showing that migratory birds have evolved morphological, physiological and behavioural adaptations that allow them to perform seasonal movements of various magnitudes (Hedenström, 2008; Hedenström & Møller, 1992; Vágási et al., 2015) and to exploit ecological niches that are only available during a short period of the year (Alerstam, Hedenstrom, & Åkesson, 2003; Dingle & Drake, 2007). However, it remains unclear which

behavioural and ecological features characterize a strictly resident bird (see Piersma, Pérez-Tris, Mouritsen, Bauchinger, & Bairlein, 2005). This question is particularly intriguing when applied to the resident fraction of partially migratory populations (defined as in Chapman, Brönmark, Nilsson, & Hansson, 2011), in which migrants and residents are morphologically identical and thus both potentially able to migrate. This has recently been found in blackcaps, *Sylvia atricapilla*, from coastal eastern Spain, which have probably evolved from migratory ancestors (Pérez-Tris, Bensch, Carbonell, Helbig, & Tellería, 2004) and maintain a migrant morphology although a large fraction of the population is resident (Morganti, Åkesson, & Pulido, 2015).

* Correspondence and present address: M. Morganti, Department of Earth and Environmental Sciences, University of Milan Bicocca, Milan, Italy.

E-mail address: michelangelomorganti@gmail.com (M. Morganti).

The main challenge of resident birds at temperate latitudes is to face radical seasonal changes in ecological conditions. However, the Mediterranean climate is mild even during winter, as is reflected by the fact that many birds breeding in northern Europe regularly winter in this area (SEO/BirdLife, 2012). Furthermore, food availability, often enhanced by extensive cultivation of olives, *Olea europaea*, seems not to be a strong limiting factor for frugivorous birds wintering in the southern Mediterranean area (Tellería, Blázquez, de la Hera, & Pérez-Tris, 2013). However, resources can be unevenly distributed across landscapes and in patches with milder temperatures and higher food availability the density of wintering birds can be huge (Carrascal, Seoane, & Villén-Pérez, 2012). This observation suggests that birds positively select specific wintering areas even in the Mediterranean region despite the overall favourable ecological conditions found at these latitudes when compared to those during winter months in northern regions. Furthermore, this indicates that interspecific and intraspecific competition can be very intense in the Mediterranean wintering quarters (De la Hera, Pérez-Tris, & Tellería, 2012; Pérez-Tris & Tellería, 2002; Tellería et al., 2013). As a consequence, food access may be seriously restricted for individuals with low competitive abilities. In blackcaps wintering in the Tarifa area, it has been observed that resident and northern migrants are spatially segregated at a landscape scale. Residents dwell in habitats that offer more varied fruit sources (Pérez-Tris & Tellería, 2002). This observation led Pérez-Tris and Tellería (2002) to suggest that this habitat segregation was a consequence of resident birds being dominant over migrants from northern populations, which would allow them to select the best habitat patches (De la Hera et al., 2012; Pérez-Tris & Tellería, 2002). On the other hand, as a general ecological rule, subordinate individuals within a population (usually juveniles and females) are more prone to be driven to suboptimal winter habitats (Marra, 2000) or to migrate (Gauthreaux, 1978; Ketterson & Nolan, 1976). It has been suggested that in partially migratory populations where there is an influx of migrants in winter, it is the dominant individuals of the local breeding population that may behave as residents, because they can compete with the migrants wintering in the area (see Berthold, 1986). According to this view, dominance should determine whether an individual stays in the breeding area all year or behaves as a migrant (e.g. Adriaensen & Dhondt, 1990; Bai, Severinghaus, & Philippart, 2012; Berthold, 1986; Gauthreaux, 1978; Lundberg, 1985). An alternative possibility, which better matches recent theoretical models on partial migration control (Pulido, 2011), is that dominance hierarchies do not determine the individual probability of migration in a given population. Even without the need of supposing the occurrence of dominance relationships, individuals behaving as resident may have an advantage over migrants thanks to the 'prior residency effect' (Cristol, Nolan, & Ketterson, 1990; Senar, Copete, & Metcalfe, 1990), which should enable them to maintain a territory with respect to competitors (see, for instance, Senar & Pascual, 2015).

However, to date, owing to practical difficulties in carrying out such tests in the wild, habitat choice and dominance have never been studied at the individual level. In particular, these aspects have never been studied in the blackcap or in other partial-migrants, in situations in which residents also interact with migrant conspecifics from northern latitudes in winter. For this reason, it is still unclear whether dominance relationships between resident and wintering migrants exist. Similarly, only information on the habitat composition of individual territories would allow us to test whether dominance or a prior residency effect determines which birds migrate or stay all year in the breeding areas. Here, we have overcome methodological problems by working during two

wintering and three breeding seasons, combining extensive ringing, radiotelemetry, fine-scale habitat mapping and observations of individually marked birds involved in aggressive interactions, to study the behavioural and ecological causes of partial migration in the blackcap.

Specifically, based on previous studies, we tested the following hypotheses. (1) Resident birds should adapt their home ranges throughout the year in terms of size and/or habitat composition. We expected resident blackcaps to have larger home ranges and habitats with a higher proportion of fruit trees in winter than in the breeding season. (2) The behavioural strategy of maintaining the same territory throughout the year (i.e. residency) should be rewarded in terms of occupancy of better patches within an area, with respect to migrant conspecifics. Therefore, we expected migratory birds, both those from the local breeding population and those from other breeding populations wintering in the area, to have home ranges that differ from those of resident conspecifics, particularly in size and/or habitat composition. (3) We expected that during winter, resident birds would outcompete migrants wintering in the same area. Higher dominance of residents than migrants would give them priority access to food.

Clarification of these questions could shed light on the mechanism driving the evolution and coexistence of residency and migration in areas in which during winter there is strong competition with migratory conspecifics breeding in other populations.

METHODS

Study Area

Field work was conducted along the Serpis river valley, in the municipality of Cocentaina (38°44'N–0°44'W, Alicante, Spain). The study area extends for about 2.5 km along the Serpis riverbank, covering a total of 77 ha. The main landscape is a hilly and Mediterranean environment (400–500 m above sea level), dominated by olive groves, but along the riverbank broadleaf vegetation with abundant underbrush and sparse cultivated fruit trees (e.g. *Ficus carica*, *Diospyros kaki*, *Punica granatum*) dominates. The climate is semiarid Mediterranean (annual rainfall: 263 mm/year, mean annual temperature: 13.4 °C). See Appendix 1 for further information about habitat characteristics.

Field Work and Bird Classification

Field work was carried out between 15 January and 20 February in 2011 and 2012 (wintering seasons) and from 20 April to 20 July in 2010, 2011 and 2012 (breeding seasons). Radio-tracking, ringing and observations of individual birds were conducted from dawn to dusk in alternating order across the day to homogeneously distribute each type of sampling during the whole daylight period. Blackcaps were trapped using mist nets and were individually marked with aluminium rings and a unique combination of colour rings to allow identification from a distance. Birds were sexed and aged, distinguishing juveniles in their first breeding or wintering season from adults, according to plumage (Jenni & Winkler, 1994). Although first-year birds from this population may undergo a complete juvenile moult, which will make them indistinguishable from adults, the percentage of these individuals is very low (<2%, Morganti, Aguirre, Onrubia, & Pulido, 2013). For this reason, it is likely that this potential error in ageing (i.e. first-year birds classified as adults based on plumage) may not affect the results of the present study. Moreover, the birds studied during the breeding seasons were exclusively actively reproducing birds, as determined by their presence

at a nest or by having a brood patch or cloacal protuberance (Svensson, 1992). Maximum wing chord, wing pointedness and tail length were measured with a ruler (± 0.5 mm). Right tarsus length and beak length were measured with an electronic calliper (± 0.01 mm). Wing pointedness was calculated as the difference between the distances from the tips of primary feathers 1 and 9 (numbered in decreasing order; Jenni & Winkler, 1994) to the wing tip. This measure is positively correlated with the pointedness of the wing (Pérez-Tris, Carbonell, & Tellería, 1999). All morphological measurements were taken by the same observer (M.M.), following standard ringing protocols (Svensson, 1992). Birds belonging to the wintering cohort were classified as wintering migrants (W) or residents (R) by means of a discriminant function (Morganti et al., 2015), which eventually allowed us to increase sample size of migrants in winter. For the breeding cohort, birds were classified as resident (R) or breeding migrants (M) based on individual capture–recapture histories (birds caught in at least two breeding seasons but not in winter were classified as ‘M’; birds caught during the breeding and wintering seasons were classified as ‘R’; see Morganti et al., 2015). Given the intense ringing activity performed throughout five consecutive seasons in a relatively reduced area, the probability that resident birds were wrongly classified as migrants is extremely low (for further details, see Morganti et al., 2015), especially if we take into account that residents maintain the same territory throughout the year (see below). Within the study area, the percentage of ringed birds increased from season to season, so that in the breeding season of 2012, 30% of all captured birds were ringed. Considering an annual survival rate of adults of about 46% in this region (see, Belda, Barba, & Monrós, 2007), we recaptured about 67% of all surviving birds, and almost 100% of birds present in the area (33% of the birds disperse). Most breeding birds were captured by individual identification of territories (singing males) and an extensive effort to capture the breeding pair in the territory. During the wintering seasons, birds were mainly trapped at common feeding places, where most of the observed individuals were colour-ringed after a few days from the beginning of the field season. The percentage of ringed birds at the feeding sites where we performed behavioural observations in winter 2012 was 61%. Unmarked birds were always present throughout the season, which could be because a small fraction of blackcaps move from site to site during winter instead of establishing home ranges (Belda et al., 2007).

Radiotracking and Home Range Calculation

We equipped a total of 57 blackcaps with radiotransmitters to calculate individual home ranges (30 in winter and 27 in the breeding season). Three individuals were tracked in consecutive breeding and wintering seasons. Individually tuned transmitters were attached to birds by means of a rubber leg-loop harness (Rappole & Tipton, 1991). SIKA receivers with range extensions between 138 and 174 MHz and Yagi antennas with flexible elements were used for tracking radio signals (for technical details, see www.biotrack.co.uk). Radiotags were attached to the birds at the beginning of the wintering seasons (17 January–3 February) or during the breeding seasons (four in April, 20 in May, three in June) and tracked as long as possible depending on the duration of the battery (about 40 days) until the end of the field season (20 February or 20 July). In a single day of tracking, we received one or more positions from each of the tagged individuals, and we planned the subsequent tracking session in order to have, at the end of the season, at least one individual position for each hour of daylight

and at least one for the roosting site. All points obtained for each individual were finally merged into a unique home range, which represents the area used throughout the season. Home ranges were based on a mean \pm SE (minimum–maximum) of 36.93 ± 1.57 (17–54) locations in winter and 28.00 ± 1.4 (16–50) locations in the breeding season for each blackcap.

Home ranges were calculated as fixed kernels at 95% using the ‘HRT tools’ extension (Rodgers, Carr, Smith, & Kie, 2005) for ArcGIS 9.3 (ESRI, Redlands, CA, U.S.A.). The kernel smoothing parameter (href) was individually adjusted by selecting the smallest value of href (rounded to the nearest 0.05) for which the external boundary of the kernel remains continuous, following the progressive method described in the HRT tools manual (Rodgers et al., 2005). Differences in home range size between seasons (winter versus breeding) and different categories of birds (R versus W and R versus M) were tested through ANOVAs.

Habitat Composition of the Home Ranges

We tested whether the home ranges of resident birds (R) included different habitat types in winter and spring and whether, within each season, this habitat composition differed from those of migrants (W and M birds). To this aim, we mapped the distribution of habitat types in the study area using aerial photos and assessed the borders of the polygons and pertinent habitat categories by mapping vegetation in the field. To improve the interpretability of the results, we reduced habitat types to six categories: brushes, bare areas, olive groves, mixed fruit orchards, deciduous forest patches with underbrush and tree cultivation (poplars and conifers) with no underbrush (see Appendix 1 for further details on habitat mapping).

Habitat proportions within each individual home range were used as dependent variables in MANOVAs that, using Pillai’s trace tests, verified significance of the differences in habitat composition between: (1) breeding and wintering seasons in the whole sample; (2) breeding and wintering seasons for R birds only; (3) R and W birds in winter; and (4) R and M birds during the breeding season. In the models, we accounted for potential confounding effects of other factors in determining differences in habitat composition by entering sex, age (first-year or adult) and year (2011 or 2012) as categorical predictors.

Interspecific competition may influence the settlement of a species within a given area (e.g. Freeman & Montgomery, 2015). This, however, is irrelevant for blackcaps in our study area, given that the most similar species present is the Sardinian warbler, *Sylvia melanocephala*, which occupies drier habitats than the blackcap and is very common outside the riverbanks where we conducted our study. Furthermore, if segregation mediated by interspecific interaction was important, it would probably affect blackcaps of different categories equally. Therefore, it will not alter our results.

Body Size and Body Condition Indices

We calculated body size and body condition indices of the wintering cohort following indications in Pérez-Tris and Tellería (2002, see Appendix 2) with the aim of exploring differences in body condition and body size between wintering migrants (W) and resident (R) birds and the relationship between these indices and dominance. Using general linear models, we explored whether birds of different age, sex and migration strategy (W versus R) showed significant differences in body size or body conditions. Successively, we used the same indices as predictors in

linear models exploring which factors determined individual dominance.

Dominance Analyses

Birds were classified according to their dominance using the ranking method originally proposed by Elo (1978) and successively adapted to animal systems, known as 'Elo-rating' (Neumann et al., 2011). This ranking procedure has several advantages when compared to other classical methods of ranking (e.g. I&SI, De Vries, 1998; David's score, David, 1987), since it is especially suited for studying highly open systems with a low number of interactions and in which the proportion of unobserved interactions is unknown, but probably high. Moreover, this method is independent of demographic changes and group composition, i.e. of the number of individuals present in the area when interactions occur (Neumann et al., 2011). Elo-rating is a progressive method, so individuals all start with the same score and progressively gain or lose points depending on the outcome of the interactions in which they are involved. The number of points won or lost in each interaction depends on the a priori probability of the outcome of that interaction. A dominant individual, for instance, will gain progressively fewer points for each interaction won, while a 'loser' that unexpectedly beats a 'winner' will gain many more points (see Neumann et al., 2011 for further details). This approach considers the development of the relationships within a group and is a good way to assess the personality of individuals. We applied this method to analyse behavioural interactions of blackcaps observed on a group of kaki trees, *D. kaki*, that they used as a feeding place in our study area during winter. Observations were performed by a single experienced observer (M. M.) with a telescope (Swarovski ATS 80 20–60) from a distance of ca. 55 m, which facilitated the correct identification of the colour-ring combination without influencing the natural behaviour of the birds. We considered aggressive interactions as the observation of a bird actively chasing another. We only considered interactions in which both individuals were identified by colour rings (58 interactions involving 32 individuals).

Analyses were carried out in R 3.1.2 (The R Foundation for Statistical Computing, Vienna, Austria, <http://www.r-project.org>), using the script provided by Neumann et al. (2011). We initially calculated scores maintaining the default values of 1000 for the starting score and 200 for K (the parameter used to calculate the number of points gained/lost in each interaction), but we successively repeated the score calculation varying the K value to 50 and 500 to control for the effect of its oscillation in the robustness of final outcomes (see Appendix 3 for further details). ' K ' also reflects the probability that a winning individual will win the following encounter, which is twice the probability of winning for an individual that never won previous encounters (Rutte, Taborsky, & Brinkhof, 2006). We used linear models (nlme package for R) to test whether dominance score was determined by sex, age (first-winter versus adults), migration strategy (W versus R), body size or body condition. We selected the best model based on AICc values through the dredge function of MuMIn library for R (Barton, 2015).

The feeding place was almost exclusively used by blackcaps. We observed very few individuals of other species. These were in descending order of abundance: chiffchaff, *Phylloscopus collybita*, thrushes (mainly *Turdus merula*) and Sardinian warbler. During observations, we also recorded aggressive interactions between blackcaps and other species. We found only sporadic interactions with chiffchaffs, which were systemically chased away, but with no other species. The frequency of interspecific interactions was so low

that it is unlikely that they affected habitat choice and interactions among wintering blackcaps.

Ethical Note

For the duration of the study (2010–2012), we obtained research permits for mist netting, measuring and radiotracking blackcaps for research purposes to M. M., F. P., J. I. A. and A. R. from the General Direction for the Management of Natural Environment of the Autonomous Region of Valencia [Permits protocol number: 2010/23552 and 401/12(FAU 12_043)]. Under these permits we mist-netted and ringed 1007 individual blackcaps (585 males, 327 females and 95 fledglings still in juvenile plumage) in this area throughout the study period (2010–2012). Mist nets were located and moved opportunistically depending on the time of day and the season. In most cases, we remained in a position where we could see the net and removed each bird as soon as it was captured. When nets were not visible to us, these were checked every 20 min. Birds were kept in individual cotton bags until ringing. Birds were ringed with one metal ring and up to three plastic rings, using a unique combination for each individual. Taking measurements and ringing took less than 5 min per bird throughout. Radiotransmitters (Pip41 tags by Biotrack, Wareham, U.K.) weighed ca. 0.42 g, which is about 2.3% of the mean weight (18.2 g) of blackcaps captured in our study area. Putting the tag on the bird normally needed 5–10 min. VHF transmitters of this type are commonly used on birds (Raim, 1978) and do not influence survival rates of small passerines (ca. 15 g; Anich, Benson, & Bednarz, 2009). The type of rubber attachment (Rappole & Tipton, 1991) naturally breaks and transmitters fall off after a few weeks. This ensures that birds need not to be trapped to remove the transmitter. In all bird manipulations, we followed standard guidelines of the national ringing manual of SEO/Birdlife (Pinilla, 2000) to minimize any possible disturbance. All procedures were performed in full accordance with the Directive 2010/63/EU on the protection of animals used for scientific purposes and fully meet the ASAB/ABS guidelines.

RESULTS

Home Range Size

Considering the whole sample, winter home range size was on average six times larger than breeding home ranges (mean area in $ha \pm SE$: winter season = 8.2 ± 0.9 , $N = 30$; breeding season = 1.4 ± 0.3 , $N = 27$; $F = 48.26$, $P < 0.001$). Similar differences in size were observed if only residents (R) were considered (mean area in $ha \pm SE$: winter season = 8.1 ± 1.4 , $N = 13$; breeding season = 1.3 ± 0.3 , $N = 5$; $F = 8.49$, $P = 0.010$; Fig. 1). During winter, the home range sizes of wintering migrants (W) and residents (R) were very similar (mean area in $ha \pm SE$: W = 8.2 ± 1.2 , $N = 17$; R = 8.1 ± 1.4 , $N = 13$; $F = 0.002$, $P = 0.963$). Equally, during the breeding season, the home ranges of resident (R) and migratory birds (M) were indistinguishable (mean area in $ha \pm SE$: R = 1.3 ± 0.3 , $N = 5$; M = 1.2 ± 0.2 , $N = 8$; $F = 0.098$, $P = 0.761$; Fig. 1). For three individuals that were tracked both in the wintering and in the breeding season, it was possible to map the overlap of breeding and wintering home ranges, showing that the wintering home range normally completely encloses the breeding home range (Fig. 2).

Habitat Composition of Home Ranges within and Between Seasons

MANOVA analyses showed that blackcaps had home ranges that differed significantly in their habitat composition between

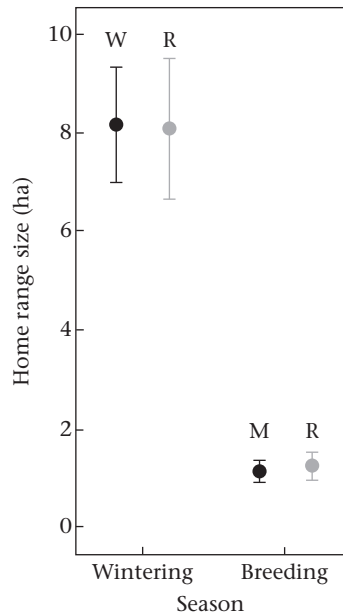


Figure 1. Seasonal differences in the home range sizes (mean \pm SE) of blackcaps in relation to the migratory status of birds: R: year-round residents; W: northern migrants wintering in the area; M: migrants that breed in the area but winter elsewhere.

wintering and breeding seasons. This held true both for the whole sample (Pillai's trace test, factor 'season': $F = 31.08$, $P < 0.001$, $N = 30$ wintering migrants (W)/27 breeding (R and M pooled)) and for resident birds (R; $F = 21.20$, $P < 0.001$, $N = 13$ wintering/5 breeding; Fig. 3). Specifically, the winter home ranges of R birds (Fig. 3a) were homogeneously composed of the different habitat types present in the study areas with the main exception of olive orchards, which alone cover $26.7 \pm 3.5\%$ (mean \pm SE) of the area, and other mixed fruit orchards ($12.2 \pm 0.8\%$). In contrast, habitat types were unevenly represented in breeding home ranges (Fig. 3b), with $55.8 \pm 10.3\%$ of their area composed of deciduous riparian forests with underbrush. Olive and mixed fruit orchards together covered less than 3% of the breeding home ranges.

During winter, the home ranges of residents (R) and wintering migrants (W) showed significant differences in habitat composition (Pillai's trace test, factor 'W/R': $F = 3.51$, $P = 0.018$, $N = 17W/13R$). Specifically, the home ranges of W birds (Fig. 3c) had a higher percentage of olive orchards with respect to other mixed fruit orchards than those of R birds (Fig. 3a). Further differences are found in the proportion of brush, which was much higher in W birds, and in the proportion of bare areas, which was higher in R birds. Both deciduous woods and tree cultivations were rarely frequented by wintering birds, but W birds had a higher proportion of the former in their home ranges than R birds.

During the breeding season, residents (R) and breeding migrants (M) had home ranges with similar proportions of habitat types (Pillai's trace test, factor 'M/R': $F = 1.28$, $P = 0.419$, $N = 8M/5R$; Fig. 3b, d). Sex, age and study year did not significantly affect the habitat composition of home ranges in any of these tests (see Table A4 for complete results of MANOVAs).

Body Size and Physical Condition in the Wintering Season

Linear models exploring the factors that potentially determine differences in body size and body condition in the wintering cohort

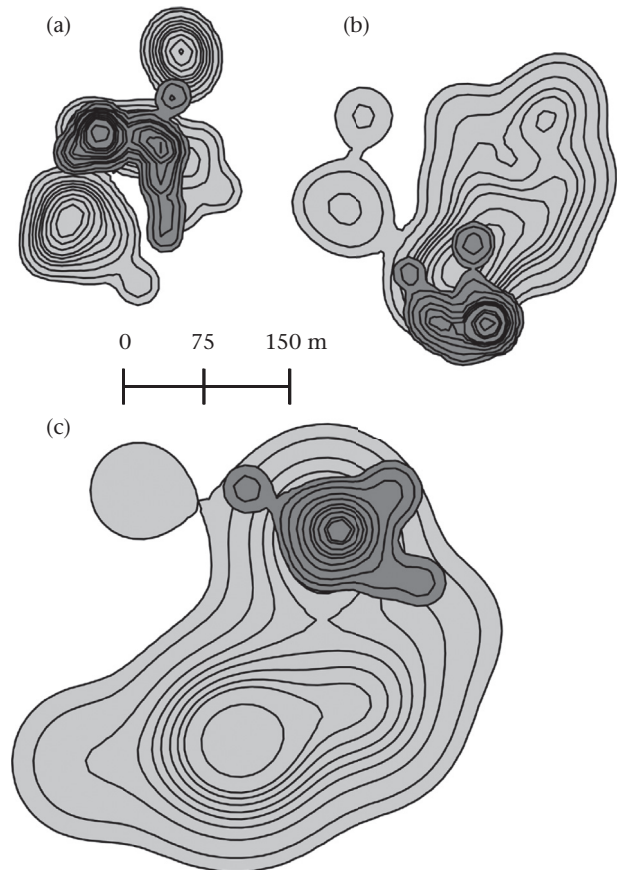


Figure 2. Overlap of wintering (pale grey) and breeding (dark grey) home ranges in three resident (R) individual blackcaps followed by radiotelemetry during both seasons in Cocentaina (Alicante, Spain). Contour lines identify intervals of 10% of the total home range; external bound represents fixed kernel at 95%. (a, c) First-year males; (b) adult male.

showed that adults were larger than juveniles ($\beta \pm SE = 0.477 \pm 0.10$, $P < 0.001$) and wintering migrants (W) larger than residents (R) ($\beta \pm SE = 0.599 \pm 0.12$, $P < 0.001$). The sexes also differed in body size, but in different ways. Males were larger than females among W, but smaller than females among R (Sex: $P = 0.170$; Sex*W/R: $\beta \pm SE = -0.643 \pm 0.22$, $P = 0.004$; Appendix Fig. A1a, b). Body condition did not differ significantly between any bird categories (Age: $P = 0.114$; W/R: $P = 0.814$; Sex: $P = 0.845$; Sex*W/R: $P = 0.243$; Appendix Fig. A1c, d).

Dominance in Wintering Season

The best selected linear model (based on AICc, see Appendix 3) exploring the factors affecting dominance score in the wintering cohort only retained body size and migration strategy (wintering migrants, W versus residents, R). This result was robust to variation in the scores assigned to each win or loss interaction (K value in Elo-rating procedure, Appendix Table A3). Therefore, the results presented here refer to dominance scores calculated using the default value of 200 for K .

In the best model, resident birds (R) had significantly higher dominance scores than wintering migrants (W; $\beta \pm SE = 141.40 \pm 58.63$, $P = 0.027$; Fig. 4a). The effect of body size was near to significance and indicated that larger birds tended to be

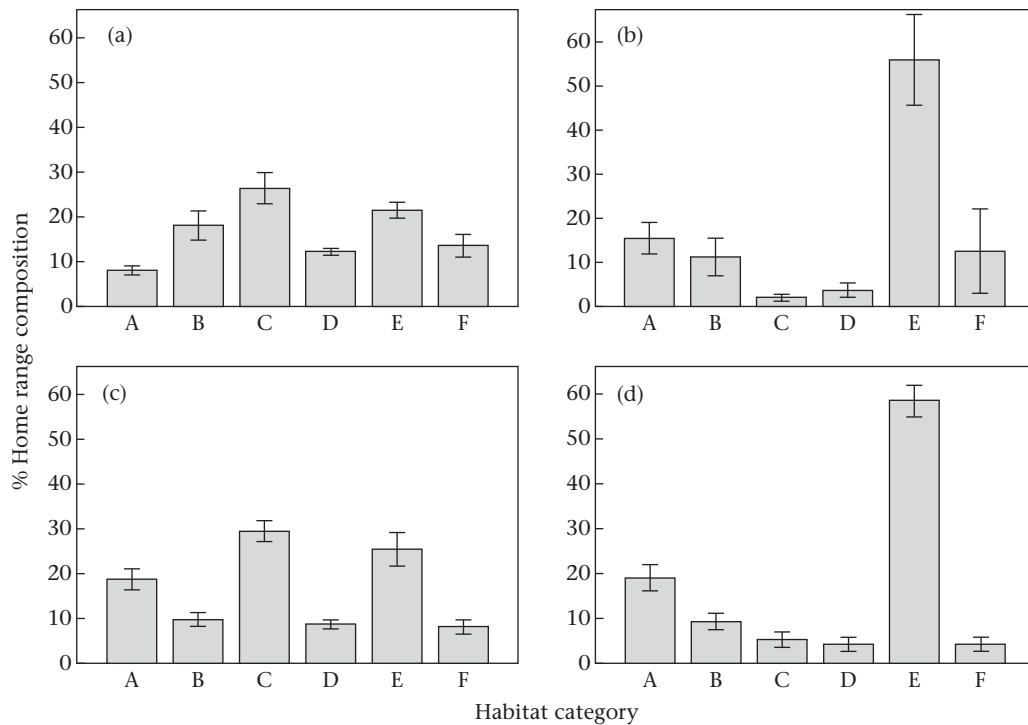


Figure 3. Habitat composition of home ranges in blackcaps differing in migratory behaviour in eastern Spain in both the winter and breeding seasons as calculated from radio-telemetry and habitat mapping. (a) Resident birds (R) in winter, $N = 13$; (b) R in the breeding season, $N = 5$; (c) wintering migrants (W), $N = 17$; (d) local migrants (M), $N = 8$. MANOVA revealed significant differences between (a) and (b) and (a) and (c). Habitat categories: A: brush; B: bare areas; C: olive groves; D: mixed fruit orchards; E: deciduous forest patches with underbrush; F: tree cultivation with no underbrush. Bars show proportion of each habitat type in the home range; whiskers indicate SE.

dominant over smaller conspecifics ($\beta \pm SE = 56.37 \pm 27.56$, $P = 0.056$; Fig. 4b).

In all cases, age and sex were not retained in the best model, while body condition was present in all the best equivalent models (those with $\Delta AICc < 2$; Appendix Table A3), but never reached significance.

DISCUSSION

Here we investigated the variability in size and habitat composition of home ranges in resident blackcaps from a Mediterranean breeding area and compared them to home ranges of migratory conspecifics that live in the same area during the breeding or wintering season. Furthermore, through behavioural observations in the wild, we verified whether resident blackcaps are able to outcompete conspecific wintering migrants at a common feeding place.

As expected, home range size differed markedly in resident birds between the breeding and nonbreeding seasons (from 8.2 ha in winter to 1.4 ha in the breeding season). During the breeding season, territoriality is more pronounced and oriented to a complete exclusion of conspecifics from a restricted area (breeding territory). This makes territorial behaviour during breeding very costly and imposes strict limits to the extent of the area that can be defended, as is the case for resident lesser spotted woodpeckers, *Dendrocopos minor*, which actively defend territories ca. 20 times smaller than their wintering home ranges during the breeding season (Wiktander, Olsson, & Nilsson, 2001). However, the fact that blackcaps shift their diet preferences from insects during reproduction towards fruits in autumn and winter (Jordano & Herrera, 1981) may also contribute to larger wintering home ranges,

because fruit tracking requires longer and more frequent movements (Tellería & Pérez-Tris, 2007; Tellería, Ramírez, & Pérez-Tris, 2008). The requirement of larger home ranges in winter may additionally be increased in a human-altered landscape, such as that studied here, where fruit resources are clumped in patches separated by large distances.

At the individual level, the three males we tracked during both seasons showed that wintering home ranges included the breeding home ranges (Fig. 2). This suggests that resident blackcaps gain some benefit from patrolling their breeding territory even during winter. We suggest that maintenance of a territory during winter may facilitate its defence against migrant intruders in spring because of the so-called 'prior residency effect', which generally allows the owner to keep the territory (Snell-Rood & Cristol, 2005; Tobias, 1997). The relevance of other factors (i.e. age, body size, dominance) in determining the outcome of territorial competition would be secondary in comparison with the advantage of the 'prior residency effect' (Cristol et al., 1990; Senar et al., 1990; Senar & Pascual, 2015). This mechanism is considered to be of general importance in determining the occurrence of partial migration across animal taxa and is the basic argument for the so-called 'arrival time hypothesis' about the evolution and maintenance of partial migration (Chapman, Brönmark, et al., 2011; Fudickar, Schmidt, Hau, Quetting, & Partecke, 2013; Ketterson & Nolan, 1976; Kokko, 2011). This hypothesis predicts that in a situation in which there is high intraspecific competition for high-quality territories, the territory-establishing sex (i.e. males) tends to be resident, especially in a high-density context (Ketterson & Nolan, 1976). Applied to our study, predictions from the arrival time hypothesis suggest that resident birds should have an advantage

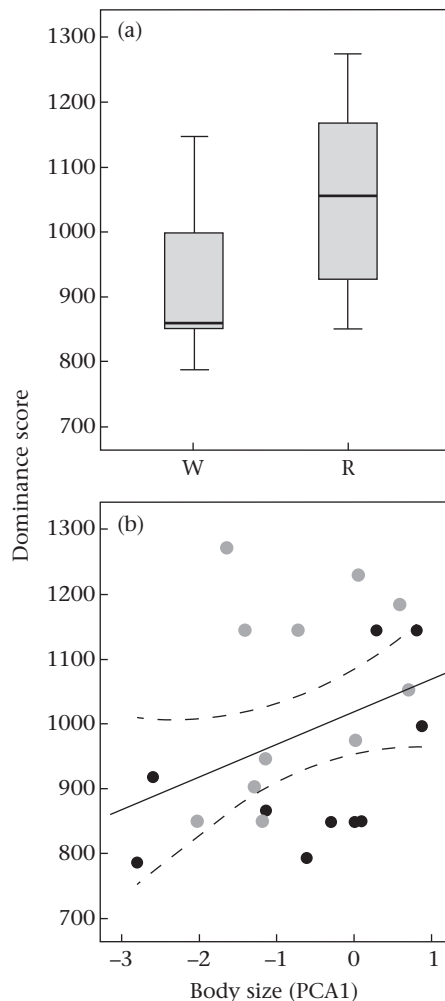


Figure 4. Factors determining dominance in wintering blackcaps from eastern Spain based on direct observations of colour-ringed individuals interacting at a natural feeding place. (a) Box plot comparison between the dominance score of year-round residents (R) and wintering migrants (W). Box limits represent 25% (lower limit) and 75% (upper limit) quartiles, while vertical lines represent the 5% and 95% percentiles. Black bold line in the boxes represents the median value. (b) Linear relationships of the dominance score with body size. Grey dots: R birds; black dots: W birds. Body size is calculated through a principal component analysis (see [Methods](#)) with positive values indicating larger overall sizes. Dashed lines represent 95% confidence intervals of the regression line.

over locally breeding migrants in maintaining their territories. Therefore, they could be expected also to have larger territories or better territories in terms of resource availability. However, our data did not support these predictions, since resident individuals had territories of similar sizes and habitat compositions to migrants breeding in the same area. It should be stressed that the 'prior residency effect', which explains why resident individuals may have access to better territories than migrants, does not imply a dominance relationship between the two groups of birds, given that 'owning' a territory gives an unbridgeable advantage with respect to any intruder (see, for instance, [Senar & Pascual, 2015](#)).

During winter, resident birds had similar home range sizes to wintering migrants originating from other breeding populations. However, in this case, home ranges had a significantly different habitat composition. An interesting difference we found was that home ranges of migrants included a slightly higher proportion of

olive orchards. This may be due either to W and R birds having different food preferences or to winter home ranges of residents including breeding home range (which may give them a 'prior residence' advantage in spring). Since breeding home ranges of residents were located in the bottom of the valley, they may have limited capacities to extend their winter home ranges up to olive orchards. Olives are an extremely energy-rich food source and are largely preferred by frugivorous birds wintering in the Mediterranean region ([Jordano & Herrera, 1981](#); [Rey, 1993](#)). Therefore, while having the same size, the habitat composition of home ranges of residents is probably suboptimal compared to home ranges of wintering migratory blackcaps. Residents probably compensate for the reduced quality of their winter home range with priority in access to food within their home range. In accord with this assumption, we found that residents are dominant over wintering migrants at the feeding sites. Eventually, residents and migrants will both obtain sufficient food to fill their needs even if they occupy different areas in the landscape. This finding is in accordance with the conclusion obtained with different methodologies in a wintering population from southern Spain (Tarifa area), where resident and migrant blackcaps occupied different habitats ([De la Hera et al., 2012](#); [Pérez-Tris & Tellería, 2002](#)) but had the same diet ([Tellería et al., 2013](#)). However, the comparison of the habitat composition of home ranges of resident and migratory blackcaps at our study site in winter also revealed that resident blackcaps had a higher proportion of mixed fruit orchards (in particular pomegranates, *P. granatum*, and kaki), as well as a higher proportion of bare areas and a lower one of other nonfruiting brushes. Bare areas have no clear functionality for blackcaps, but are probably part of their home ranges only as connection areas between other sites. The higher proportion of this habitat type in the home ranges of residents may be a consequence of the fact that residents must control and defend their breeding territories during winter. Therefore, their wintering home range has this 'burden' that forces resident birds to move over longer distances within the home ranges to reach feeding sites (i.e. fruit trees surrounded by bare soil). At the same time, the home range composition of residents seems to indicate that they can use a wider variety of feeding resources in winter than wintering migrants, which preferentially feed on olives. This is in line with previous findings on blackcaps in the Tarifa area: residents were more abundant in habitats with a higher variety of fruit sources ([Pérez-Tris & Tellería, 2002](#)). The use of habitats less preferred by migrants (i.e. fruit orchards), may have a further advantage for residents, because it reduces aggressive interactions with conspecifics, which are energetically costly, even for the winners ([Georgiev, Klimczuk, Traficonte, & Maestripietri, 2013](#)).

We found that the main feature determining dominance status in winter was being resident. Dominance status is often determined in birds by a series of factors with experience (age) and body size being the most relevant (e.g. [Barluenga, Barbosa, & Moreno, 2000](#); [Cristol et al., 1990](#); [Jahn, Levey, Hostetler, & Mamani, 2010](#)). Dominance of resident blackcaps was indirectly inferred in other populations with respect to both wintering migrants (Tarifa area, [De la Hera et al., 2012](#); [Pérez-Tris & Tellería, 2002](#)) and breeding migrants (southern France, [Berthold, 1986](#)), because in these cases residents were found in better, more productive habitats than migrants. However, for the breeding cohort, we previously found that M and R birds have analogous body size and wing shape and that composition of the two groups is similar in terms of sex and age classes ([Morganti et al., 2015](#)). Here, we further showed that M and R birds had similar home ranges in terms of size or habitat composition. It is, therefore, currently unclear what determines whether a bird from this partially migratory population migrates or

stays in the breeding area. There is some evidence obtained in a common-garden experiment that the incidence of migratory behaviour in this population is not controlled by genetic differences (Bulaić, 2016), as had previously been found in a partially migratory blackcap population from southern France (Berthold, Mohr, & Querner, 1990).

In the wintering cohort, we found no evidence that dominance may increase with age, and only a weak positive relation between body size and dominance score. If residents had been larger than wintering migrants, as was found in blackcaps from the Tarifa area (Pérez-Tris & Tellería, 2002), differences in body size would have been the main cause of the dominance of residents over migrants. However, this was not supported by our data. In fact, residents were generally smaller than wintering migrants in our study system. We thus argue that, at equal body size, residents are dominant over migrants, because they are more aggressive. This idea suggests that innate behavioural traits may be a more important source of differences in dominance than extrinsic differences such as those given by the 'prior residency effect' (see above). Indeed, aggressiveness should be related to sex and age too, and this may explain why in partially migratory blackcaps from southern France, Berthold (1986) found that males tended to be more resident than females. Even if the findings obtained so far do not suggest that differences in dominance between local residents and migrants are the prime drivers of the occurrence of partial migration in the population, it could be interesting to perform specific tests to study differences in dominance between the residents and breeding migrants in our partially migratory population. These experiments, however, would have to be conducted just before the start of migration, when birds 'decide' whether to stay or to leave the breeding area.

Overall, the dominance relationships and winter home ranges with higher habitat diversity were the key features driving the behaviour of year-round resident blackcaps. Our study was conducted over five consecutive seasons (two winters and three breeding seasons), so the data only control for variation in environmental conditions across 3 years that did not differ substantially. However, in the long term, strong oscillations in environmental conditions, such the loss of a crucial resource, may unbalance the relative viability of different behavioural strategies such as residency and migration. Moreover, the individual migratory status in partial migrant populations is considered to be highly flexible and sensitive to yearly oscillations in environmental conditions (Pulido, 2011). Indeed, a proportion of migrant and resident European robins, *Erithacus rubecula*, have been found to be affected by year-to-year weather oscillations, in a study that also showed different sensibilities to these factors across populations (Ambrosini et al., 2016).

A major result of our study is that resident blackcaps had the ability to reorganize the size and the habitat composition of their home ranges during the year according to their needs. In this process, the role of dominance appears to be important but not crucial, given that residents may also limit competition by using a wider variety of feeding habitats. Interestingly, dominance and more exploratory behaviour are often related behavioural traits that build specific personalities (Sih, Cote, Evans, Fogarty, & Pruitt, 2012; Sih et al., 2015), which may be characteristic of residents. Clearly, we need further insights into the role of animal personalities in determining the occurrence of partial migration (see Chapman et al., 2011b). We cannot exclude the possibility that variation in personalities is more important than intrinsic (age, sex, body size) or extrinsic (environmental oscillations) factors in determining the migratory status of an individual.

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Supplementary Material

Supplementary material associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.anbehav.2016.10.021>.

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APPENDIX 1. HABITAT MAPPING AND HOME RANGES

We mapped the distribution of habitat types in the study area using photointerpretation supported by a field confirmation of limits of the polygons and of habitat categories. Mapping was performed in ESRI ArcGIS 9.3 (ESRI, Redlands, CA, U.S.A.) and QGIS 1.7.4-Wroclaw (Quantum Gis Development Team, github.com/qgis/QGIS). In the first phase, habitat types were defined following EUNIS categories, as defined by Davies, Moss, and Hill (2004) and adding new categories when habitat types present in the study area were not available in the EUNIS categorization. Overall, in this first step, we identified 27 habitat types (Table A1). Successively, in order to reduce the number of habitat categories and to improve the power of the model, we merged habitats that had similar vegetation macrotypologies and considering differences in the presence of undergrowth. This procedure yielded six habitat typologies (Table A1). Habitat composition of home ranges was determined by measuring the coverage of each habitat category within individual home ranges. To avoid the problem of analysing data series that sum to 1 (unit sum constraint, see Aebischer, Robertson, & Kenward, 1993) and to normalize compositions (Aitchison, 1986), before carrying out the analyses we log ratio transformed habitat coverages within home ranges following the formula: $\ln(xi/xj)$ where xi represent the habitat proportion and xj the proportion of the most abundant habitat type (Aebischer et al., 1993). Since the log ratio transformation is equivalent to centring the $\ln(xi)$ in relation to their mean, the results of such analyses are independent of the component xj chosen as denominator in the log ratio transformation (Aebischer et al., 1993). To reduce type I error, zero values were replaced with 0.005 (Bingham & Brennan, 2004) before we calculated log ratios. Log transformed habitat proportions were eventually used as dependent variables in the MANOVAs to explore differences in home range composition between blackcaps belonging to different groups (R, W or M).

Table A1
Habitat typologies and relative EUNIS title considered in the habitat mapping

Final habitat typologies	Habitat (first classification)	EUNIS code	EUNIS title
Typology 1: brush	<i>Arundo donax</i> beds	C3.32	<i>Arundo donax</i> beds
	Sparsely wooded grasslands	E7	Sparsely wooded grasslands
Typology 2: bare areas	<i>Rubus</i> sp. shrublands	F3.2	Submediterranean deciduous thickets and brush
	Riparian vegetation	C3	Littoral zone of inland surface water bodies
	Running water	C2.2	Permanent nontidal, fast, turbulent watercourses
	Buildings	J2.1/J2.6	Scattered residential buildings/disused rural constructions
Typology 3: olive groves	Roads	J4.2	Road networks
	Dry grasslands	E1	Dry grasslands
	Bare soil	I1.5	Bare tilled, fallow or recently abandoned arable land
	Herbaceous communities of roadsides	J4.1	Disused road, rail and other constructed hard-surfaced
	Recent olive groves with no underbrush	G2.91	<i>Olea europaea</i> groves
	Recent olive groves with intermediate degree of underbrush	G2.91	<i>Olea europaea</i> groves
Typology 4: mixed fruit orchards	Ancient olive groves with no underbrush	G2.91	<i>Olea europaea</i> groves
	Ancient olive groves with intermediate degree of underbrush	G2.91	<i>Olea europaea</i> groves
	Ancient olive groves with high degree of underbrush	G2.91	<i>Olea europaea</i> groves
	Crops	I1.2	Mixed crops of market gardens and horticulture
Typology 5: deciduous forest patches with underbrush	Orchards	FB.31	Shrub plantations for ornamental purposes or for fruit, other than vineyards
	Gardens	I2.2	Small-scale ornamental and domestic garden areas
	Almond plantation	–	No Eunis title available
	Deciduous wood	G1.7C5/G2.12 /G1.3	<i>Celtis australis</i> woods/ <i>Quercus ilex</i> woodland/Mediterranean riparian woodland
	Poplar plantations with high degree of underbrush	G1.C1	Poplar plantations
Typology 6: tree cultivation with no underbrush	Poplar plantations with intermediate degree of underbrush	G1.C1	Poplar plantations
	Coniferous plantation	G5.4	Small coniferous anthropogenic woodlands
	<i>Pinus halepensis</i> forests with high degree of underbrush	G3.741	Iberian <i>Pinus halepensis</i> forests
	<i>Pinus halepensis</i> forests with intermediate degree of underbrush	G3.741	Iberian <i>Pinus halepensis</i> forests
	<i>Pinus halepensis</i> forests with no underbrush	G3.741	Iberian <i>Pinus halepensis</i> forests
	Poplar plantations with no underbrush	G1.C1	Poplar plantations

APPENDIX 2. BODY SIZE AND BODY CONDITION INDICES

We calculated body size and body condition indices for birds from the wintering cohort (according to Pérez-Tris & Tellería, 2002) to test for differences in these variables between wintering migrants (W) and resident birds (R) and to explore the relationship between these indices and dominance. We conducted a principal component analysis (PCA) with tarsus, beak, wing and tail length to obtain an index of structural body size. Components were varimax rotated to facilitate interpretation. The first principal component (PC1) explained 40.75% of the variance and was positively correlated with the four variables (eigenvalue = 1.630; factor loading for tarsus length = 0.384; beak length = 0.259; wing length = 0.883; tail length = 0.798). We used this principal

component as an index of structural body size. As a measure of individual fat accumulation, we used a fat score assigned by visual estimation of subcutaneous fat (Kaiser, 1993). This variable was transformed by calculating the logarithm of the squared score to meet normality. Transformed fat scores were positively related to weight (Pearson correlation: $r = 0.599$, $P < 0.001$). We regressed weight on structural body size ($\beta = 0.466$, $P < 0.001$) and fat content ($\beta = 1.267$, $P < 0.001$) and used unstandardized residuals of this regression as an index of body condition. Body size and body condition indices were unrelated (Pearson correlation: $r = -0.013$, $P = 0.773$). Before we conducted the main analyses, we explored the variation in body size and body condition indices in relation to migratory behaviour (R or W), age (first-year or adult) and sex (Fig. A1).

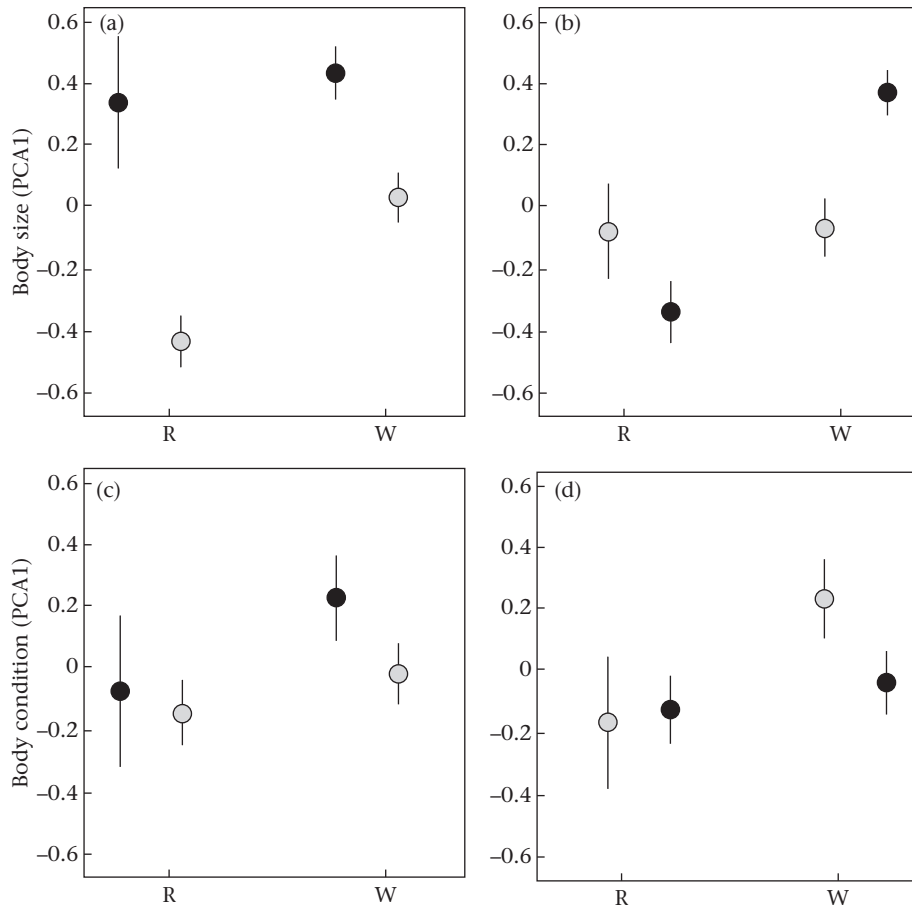


Figure A1. Mean \pm SE (a, b) body size and (c, d) body condition index of wintering blackcaps differing in migratory behaviour (wintering migrants, W, or residents, R). In (a) and (c), black dots represent adult birds ($N = 152$) and grey dots first-year birds ($N = 285$). In (b) and (d), black dots represent males ($N = 330$) and grey dots females ($N = 173$).

APPENDIX 3. DOMINANCE ANALYSIS

In the Elo-rating procedure, the choice of the parameter ‘ K ’ (see above) is of minor importance in large data sets that include many repeated interactions, but may strongly affect ranking in a short series of matches (Neumann et al., 2011), as may be the case in our study. We thus repeated the ranking procedure setting K to 500 and 50 and tested whether the best model

selected using the three different rankings ($K = 200, 500$ or 50) differed. Results of Elo-rating ranking of individuals are shown in Table A2. Prior to model selection, an outlier was eliminated from the database (an individual with dominance score near to 1600, see Table A2). Regardless of the K value setting, the best-selected model always included body size and migratory strategy (W versus R) as factors significantly determining dominance score (Table A3).

Table A2

Dominance scores and individual characteristics (see ‘Methods’) of 32 blackcaps observed in aggressive interaction with conspecifics during winter 2012 in Cocentaina (Alicante, Spain)

ID	Colour code	Sex	Age	W/R	Tarsus	Fat score	Body size	Condition	Dominance score		
									$K=200$	$K=500$	$K=50$
1	BMZR	Male	First-year	R	19.93	3	-1.629	-0.463	1275	1524	1063
2	BZMP	Male	Adult	W	20.66	2	0.208	-0.23	1557	1874	1215
3	GMGG	Male	Adult	R	20.06	2	-1.395	-0.684	1148	1269	1046
4	MGLO	Female	First-year	W	20.8	3	0.877	0.03	1000	1000	1000
5	MGZO	Male	Adult	R	20.97	4	-1.278	0.821	906	885	959
6	MOZG	Female	Adult	W	20.28	2	-1.123	1.51	869	862	933
7	MP,-	Female	Adult	R	19.36	2	-	-	967	970	975
8	MZBB	Male	First-year	R	20.25	3	0.065	0.348	1233	1223	1162
9	MZLL	Male	-	W	19.22	4	0	1.126	852	731	954
10	MZYB	Male	-	W	20.17	0	-	-	754	624	895
11	OBMZ	Female	-	Undet.	20.20	1	-	-	966	887	996
12	OLOM	Female	Adult	W	20.40	2	-	-	1072	1039	1064
13	OMPP	Female	Adult	W	20.80	2	-	-	940	937	966

(continued on next page)

Table A2 (continued)

ID	Colour code	Sex	Age	W/R	Tarsus	Fat score	Body size	Condition	Dominance score		
									K=200	K=500	K=50
14	OMPZ	Male	—	Undet.	21.05	2	—	—	982	996	972
15	PBOM	Male	First-year	R	19.80	1	0.027	−0.265	978	979	985
16	PMPY	Female	Adult	W	20.16	2	−0.603	1.307	796	573	948
17	PYLM	Female	Adult	W	22.12	3	0.298	−2.31	1148	1269	1046
18	PZGM	Female	First-year	W	19.23	2	−2.787	−0.226	789	626	932
19	RMPY	Male	Adult	R	20.69	1	−0.716	1.031	1148	1269	1046
20	RMZY	Female	Adult	W	18.22	3	−2.58	−0.7	921	776	991
21	YMOB	Male	Adult	R	21.72	2	0.597	0.769	1188	1370	1054
22	YMZB	Male	First-year	R	21.25	2	−1.179	−0.524	852	731	954
23	ZGBM	Male	Adult	W	19.05	2	0.819	−1.325	1148	1269	1046
24	ZGMO	Male	First-year	R	21.06	3	0.718	−0.806	1056	1158	1006
25	ZMBB	Male	—	Undet.	—	2	—	—	968	967	982
26	ZMBP	Male	Adult	W	20.15	2	0.014	−0.3	852	731	954
27	ZMZB	Male	First-year	R	20.23	1	−1.133	0.585	949	975	965
28	ZPMG	Male	First-year	Undet.	20.40	4	0.048	−0.06	1211	1374	1068
29	ZYBM	Male	First-year	W	20.76	2	0.092	0.284	852	731	954
30	ZYOM	Male	Adult	R	19.45	4	−2.014	0.704	852	731	954
31	ZYPM	Male	First-year	W	19.87	6	−0.285	4.543	852	731	954
32	ZZMO	Female	First-year	W	20.17	3	—	—	919	919	961

Dominance was calculated by the Elo-rating method setting K at different values (Neumann et al., 2011). Birds are ranked from highest to lowest dominance score. W = northern originating individuals wintering in the area, R = local year-round residents. W and R birds were discriminated based on a morphological discriminant function (Morganti et al., 2015).

Table A3

Influence of changing the K parameter on the final dominance model

Rank	Factors	AICc	Δ AICc
K=200 (default value)			
1	W/R+BSIZE	272.45	0
2	W/R+BSIZE+BCOND	272.46	0.01
3	BCOND	273.5	1.05
4	Null model	273.75	1.3
K=50			
1	W/R+BSIZE	232.64	0
2	W/R	233.39	0.75
3	Null model	233.73	1.09
4	BSIZE	233.82	1.18
5	W/R+BSIZE+BCOND	233.94	1.3
6	W/R+BCOND	234.26	1.62
7	BCOND	234.29	1.65
K=500			
1	W/R+BSIZE	295.91	0
2	W/R+BSIZE+BCOND	295.96	0.05
3	W/R+BCOND	297.28	1.37
4	Null model	297.46	1.56

The table compares the results of model selection exploring the factors affecting dominance scores assigned with Elo-rating methods when the value of K is higher (500) or lower (50) with respect to the default (200) score. K represents the scores assigned to each interaction won or lost in the Elo-rating progressive method (see Methods in main text). W/R = migration strategy W or R; BSIZE = body size index; BCND = body condition index.

Table A4

Full results of MANOVA analyses

Predictor	Test statistics	F	df	P
Winter vs breeding season (full data set)				
Season	0.764	31.083	5, 48	<0.001
Year	0.161	1.842	5, 48	0.123
Age	0.034	0.333	5, 48	0.89
Sex	0.034	0.341	5, 48	0.886
Winter vs breeding season (only R birds)				
Season	0.922	21.204	5, 9	<0.001
Year	0.557	2.263	5, 9	0.136
Age	0.274	0.68	5, 9	0.65
Sex	0.132	0.272	5, 9	0.917
R vs W birds (wintering season)				
W/R	0.455	3.506	5, 21	0.018
Year	0.333	2.097	5, 21	0.106
Age	0.167	0.847	5, 21	0.532
Sex	0.064	0.289	5, 21	0.914
R vs M birds (breeding season)				
M/R	0.615	1.275	5, 4	0.419
Year	0.728	2.137	5, 4	0.241
Age	0.836	4.076	5, 4	0.099
Sex	0.674	1.649	5, 4	0.324

The tests explore which factors predict differences in habitat composition and home ranges within and between seasons. Predictors in the models were season (wintering/breeding); migration strategy (R/W or R/M); age (first-year/adult); sex (males/females) and year (2011/2012).