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

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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.

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).

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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). Radiotracking, 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