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3	Habitat segregation by breeding origin in the declining
4	populations of European Robins wintering in southern Iberia
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Mediterranean woodlands and associated shrub formations of southern Iberia are key 23 habitats for migratory bird conservation. In some bird species, migratory and sedentary 24 conspecifics meet together in these areas during winter, but our understanding of how 25 26 each population group is distributed over available habitats and the factors that determine their spatial organization are still unclear. This seriously limits our ability to 27 assess their vulnerability to ongoing environmental changes affecting wintering habitats 28 in this region. We used hydrogen isotopic signatures of feathers (δD_f) to shed light on 29 the habitat distribution of seasonally sympatric European Robin Erithacus rubecula 30 populations wintering in Campo de Gibraltar that are currently facing a drastic decline. 31 32 In contrast to previous studies that used morphological methods to distinguish the migratory behaviour of wintering Robins in this area, our isotopic approach revealed 33 that sedentary Robins were not outcompeted upon the arrival of migrants and remained 34 35 in the woodlands where they reproduce, which agrees with the results obtained in other regions. Interestingly, we also found that migratory Robins with a closer breeding origin 36 37 (higher δD_f values) had more chances of occupying woodlands than migrants coming from further away. Altogether, our results suggest that the role of breeding origin in 38 shaping the distribution of Robins during winter in Campo de Gibraltar is more relevant 39 than the effects of sex, age or body size, which might facilitate the evolution of local 40 adaptations for the exploitation of each habitat type. 41

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43 Keywords: Deuterium, habitat selection, intraspecific interactions, rectrix feathers.

Mediterranean woodlands in southern Iberia are recognised as key habitats for avian 45 46 conservation (Blondel & Aronson 1999). The most humid sectors of the Mediterranean mountains contain moist, sometimes relict, submediterranean woodlands (De Dios et al. 47 48 2009) that have the particularity of hosting isolated bird populations of typically Eurosiberian species at the southwestern edge of their breeding distribution (Cramp 49 1988, 1992). Some of these peripheral bird populations, which normally exhibit a 50 sedentary life style (Tellería et al. 2001a), seem to have an independent evolutionary 51 52 history (Pérez-Tris et al. 2004) and could be locally adapted to Mediterranean conditions (Pérez-Tris & Tellería 2002a, Carbonell et al. 2003), thus constituting 53 54 singular entities of high conservation value (Crandall et al. 2000). Increasing evidence suggest that these forests are seriously threatened by global warming and other 55 anthropogenic alterations (Peñuelas et al. 2002, De Dios et al. 2009), which could 56 57 detrimentally affect many of the forest bird populations that depend on these habitats year-round or during key periods of their annual cycle (e.g. wintering; Tellería et al. 58 59 2005).

These moist forests, as well as other more thermic habitats, such as the 60 Mediterranean shrublands, also play an essential role as wintering destination for many 61 bird populations breeding in Western Europe (Busse 2001, Møller et al. 2011). Seasonal 62 migration leads, in some bird species, to the co-occurrence of sedentary and migratory 63 conspecifics within the same wintering grounds (De la Hera et al. 2012). In this 64 heterogeneous landscape consisting of a mosaic of shrubland and woodland patches, 65 66 individuals with different breeding origins could show structured patterns of distribution between wintering habitats. This spatial patterning would be promoted if coinciding 67 68 bird populations markedly differ in competitive ability, phenology of relevant lifehistory events (e.g. timing of arrival to wintering grounds) and/or winter habitat 69

preferences (Webster & Marra 2005, Clobert et al. 2009). The existence of high degrees 70 71 of habitat segregation between populations not only would be important as potential drivers of ecological and evolutionary divergence (Bearhop et al. 2005), but would also 72 73 have paramount implications for management and conservation of key wintering habitats (Webster *et al.* 2002). However, if the spatial organization is mainly driven by 74 individual characteristics (e.g. sex, age) and not by population-specific attributes, we 75 would expect that individuals from different breeding origins end up mixing in both 76 77 woodlands and shrublands during winter.

The current paradigm in southern Iberia assumes that sedentary and migratory 78 populations of several avian species prefer woodlands over shrublands for 79 overwintering. Whereas fruit availability is large enough to satiate the bird community 80 in both habitats (Tellería et al. 2013), woodlands provide more diverse fruit crops and a 81 82 more sheltered habitat that may reduce predation risk and the effects of adverse weather conditions (Cuadrado 1997, Tellería & Pérez-Tris 2004). Under intense intraspecific 83 84 competition for the occupancy of woodlands (Pérez-Tris & Tellería 2002b, Tellería & Pérez-Tris 2004, Campos et al. 2011b), a combination of potentially interrelated factors 85 such as age, sex, body size and population origin could affect the competitive status of 86 individuals and their distribution between habitats (Piper 1997). Since the occupancy of 87 habitats of different quality may have downstream consequences on future reproduction 88 and survival, the way in which migratory and sedentary individuals are distributed 89 between available habitats during winter may impact the demography of each 90 91 population group, potentially interacting with other factors that regulate their populations (Webster & Marra 2005, Harrison et al. 2011). Although this knowledge is 92 93 essential to assess the vulnerability of these bird populations to ongoing environmental

changes in the region (Herrero & Zavala 2015), our understanding of the wintering 94 95 ecology and distribution of seasonally sympatric populations is yet not well understood. Wintering populations of the European Robin Erithacus rubecula (hence forth 96 97 Robin) in the woodland-shrubland mosaics of Campo de Gibraltar (Cádiz, southern Spain) are currently facing a drastic decline (> 40% of reduction) with climate change 98 as the main potential driver (Tellería 2015). To ascertain the relative impact of these 99 deteriorating conditions on co-existing migratory and sedentary Robins and to 100 101 understand their wintering interactions, reliable methods for distinguishing between population groups are necessary. Morphological classification functions (MCF) have 102 103 been traditionally used to distinguish local sedentary Robins from migrants in this region, since the latter show longer and more pointed wings than the former (Pérez-Tris 104 et al. 2000). Research based on MCF suggests that more than 30% of the sedentary 105 106 population (primarily young and female birds) is displaced from woodlands to 107 shrublands during winter by arriving migratory Robins (Tellería et al. 2001b, Tellería & 108 Pérez-Tris 2004). In wintering areas where sedentary Robins are not present, 109 hierarchical relationships among migrants are mainly determined by sex and age (Catry et al. 2004, Campos et al. 2011a). However, wherever sedentary Robins occur, 110 observational and experimental research suggests that they should be dominant over 111 112 recently-arrived migrants (Tobias 1997, Campos et al. 2011b), which does not fit with 113 the between-habitat distribution patterns observed in Campo de Gibraltar. A potential 114 explanation for this contradiction lies in the unsuitability of morphology to identify the 115 population origin of Robins (Ellrich et al. 2010). In fact, a recent study reveals that MCF 116 implemented in Campo de Gibraltar actually assign erroneously a high proportion of 117 migrants to the sedentary group (particularly juveniles and females; De la Hera *et al.* 2017), which could explain the unexpected large number of sedentary Robins 118

previously found in shrublands. This encourages the use of alternative, more reliable,
approaches of population differentiation (e.g. stable isotope analyses; Rubenstein &
Hobson 2004) in order to clarify this controversy.

122 Another interesting question that remains to be tested at a more local scale is whether migrants with different breeding origins also show non-random distributions 123 between available habitats during winter (see Catry et al. 2016, Ambrosini et al. 2016). 124 This could be possible in migratory Robins wintering in southern Iberia that have a 125 126 broad range of geographic origins (Bueno 1998, Korner-Nievergelt et al. 2014) and, therefore, might show variation in life-history characteristics that could promote spatial 127 128 segregation during winter (e.g. timing of arrival to wintering grounds, trophic specialization; Tobias 1997, Catry et al. 2016). A recent study detected a more 129 insectivorous wintering diet in migratory Robins that had a more northern breeding 130 131 origin (Catry et al. 2016). This finding supports the existence of variation in the 132 wintering strategies of Robins and the idea that different populations could be best 133 suited for the exploitation of particular habitats, which might result in a certain degree 134 of migratory connectivity at a habitat scale in other wintering areas (Webster *et al.* 2002). 135

In this study, we used hydrogen isotopic signatures measured from feathers (δD_f) 136 to clarify how breeding origin and other individual characteristics (sex, age and body 137 138 size) might affect habitat distribution of wintering Robins in Campo de Gibraltar, a glacial refuge during the Pleistocene with a singular resident avian community (Pérez-139 140 Tris et al. 2015). We first analysed whether sedentary Robins (which only breed in woodlands and were identified from δD_f values) were able to remain in woodlands 141 142 during winter or, whether they were partially displaced to shrublands, as MCF suggest (Tellería et al. 2001b). Secondly, we took advantage of the geographic variation in 143

hydrogen isotope ratios to test whether breeding origin (estimated from δD_f values)
contributed to explain the between-habitat (shrubland vs. woodlands) arrangement of
migratory Robins during winter.
METHODS
Fieldwork and individual bird data collection
Our study area was located in Campo de Gibraltar, within the protected areas of Los
Alcornocales and Estrecho de Gibraltar Natural Parks (Cádiz, Spain). This is a
mountainous area whose most humid sectors are dominated by well-developed
woodlands embedded in a matrix of extensive shrublands. Cork Oaks Quercus suber,
the Terciary relict Mirbeck's Oaks Quercus canariensis and large specimens of wild
Olives Olea europaea sylvestris are the most representative tree species in the canopy of
woodlands. Woodlands also show a varied array of berry-producing shrubs that grow in
the understory and normally fruit during winter. Among them, smaller Olives, Mastics
Pistacia lentiscus, Mock Privet Phillyrea latifolia, Common Myrtle Myrtus communis
and Laurustinus Viburnum tinus are the most common species. On the other hand,
shrublands are less complex habitats largely dominated by Mastics and small shrubby
Olives.
Within these large protected areas, our fieldwork was concentrated in two
localities representing woodlands (San Carlos Tiradero, 36°09'48"N, 5°34'56"W, and
San Carlos Carretera, 36°09'54"N, 5°34'55"W) and two localities representing
shrublands (Almodóvar, 36°09'03"N, 5°37'54"W, and Betis, 36°05'11"N, 5°42'09"W),

where we captured wintering Robins using mist-nets and mesh-clap traps. Trapping 169 170 sessions took place during two different winters (2006/07 and 2013/14) spanning the traditional winter season in this area (from mid-November to mid-February; 171 172 SEO/Birdlife 2012). Each trapped Robin was aged as adult or juvenile using plumage characteristics (Jenni & Winkler 1994), and a set of body size-related morphological 173 traits were measured: tarsus length, bill length, maximum wing chord, eighth primary 174 175 (P8) length (P1 being the innermost primary) and tail length (see Svensson 1992). Two 176 experienced ringers (IdH and JP-T), that have their measurements standardized, took all previous morphological measurements in winter 2006/07, and one of these two (IdH) in 177 winter 2013/14. Additionally, we used a syringe to extract a sample of blood from the 178 jugular vein that was used for molecular sexing (Griffiths et al. 1998), and collected one 179 180 tail feather (rectrix 5; Jenni & Winkler 1994) for isotopic analyses.

181 In order to determine the existing variation in δD_f values in the local sedentary population at Campo de Gibraltar, we also captured Robins during the breeding period 182 183 in the same woodlands sampled in winter. Shrublands were not visited during the 184 reproductive season because densities of breeding Robins are very low in this habitat type (Tellería et al. 2001b). Likewise, we also collected feathers from birds breeding in 185 Álava (Northern Spain, 42°54'02"N, 2°32'07"W), where the Robin population is mostly 186 187 migratory (De la Hera et al. 2014). Both breeding populations were sampled in August 188 2006, when juvenile Robins are abundant and most adults had their tail feathers recently moulted, and in May 2014, when the tail feathers produced the previous year by 189 190 breeders had yet not been moulted. This procedure provided comparable feather 191 samples to those collected during the winters of 2006/07 and 2013/14, respectively.

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193 Hydrogen isotopic analyses of feathers

195 Deuterium, the heavy stable isotope of hydrogen, becomes progressively less common in rainfall from south-western Europe, where our study site is located, towards the 196 197 northeast (Hobson et al. 2004). This isotopic variation is transferred to the feathers of Robins through the diet during plumage production. Consequently, the isotopic 198 signatures of the tail feathers collected from Robins wintering in Campo de Gibraltar 199 will provide information on the localities where these birds grew their feathers during 200 201 summer (Rubenstein & Hobson 2004). Accordingly, we expect δD_f values to be lower (more negative) in Robins from more distant geographic origins (Catry et al. 2016). 202 203 Collected feathers were first cleaned with a chloroform:methanol solution to remove impurities and a subsample of 0.35mg of feather mass weighted into silver 204 205 capsules. Hydrogen isotopic measurements were obtained by coupled pyrolysis/isotope-206 ratio mass spectrometry using a high temperature conversion elemental analyser (TC/EA) 207 interfaced to a Thermo Scientific Delta V Plus. This was configured through a 208 CONFLO IV for automated continuous flow gas-isotope ratio mass spectrometer (CF-209 IRMS). Deuterium/Protium ratios were expressed in delta notation (δD_f) in units per mil (%), and normalized according to the VSMOW-SLAP scale using the values obtained for 210 three keratin standards: Keratin-SC Lot SJ (expected $\delta D = -121.6\%$, observed $\delta D = -$ 211 212 121.0‰ ± 0.22SE), Caribou hoof (expected δD = -197.0‰, observed δD = -197.8‰ ± 0.26SE) and Kudo horn (expected $\delta D = -54.1\%$, observed $\delta D = -55.1\% \pm 0.44SE$). For 213 214 a subsample of 20 individuals, hydrogen isotopic ratios were measured twice, which provided a highly significant repeatability ($r_i = 0.98$, $F_{19,20} = 130.9$, P < 0.001), 215 216 supporting the reliability of obtained δD_f measurements.

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218 Statistical analyses

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220 We classified wintering Robins as migratory or sedentary using their δD_f values (see Results) and tested whether sedentary birds were more common in woodlands than in 221 222 shrublands. We used Generalized Linear Mixed Models (GLMM) for this purpose, where the migratory behaviour of Robins was analysed (migratory = 0, sedentary = 1) in 223 response to sex, age, habitat and all their two-way interactions as fixed effects factors, 224 and winter of capture and site as random effects. In order to obtain composite indices of 225 226 body size, and given the large number of potentially-interrelated morphological traits obtained from each individual Robin, we performed a Principal Component Analysis 227 228 (PCA) that considered the five morphological traits measured, which gave rise to two independent main components of body size (PC1 and PC2, see Results). In order to 229 explore whether variation in PC1 and PC2 was affected by the migratory behaviour of 230 231 Robins, we performed Linear Mixed Models where population (migratory or sedentary), 232 sex, age and all possible two-way interactions were included as fixed effects factors, 233 and winter of capture as a random factor. 234 After excluding potential sedentary birds from the data, we also explored which factors (i.e. body-size, age, sex, breeding origin) better explained the occupancy of each 235 habitat type by migratory Robins wintering in Campo de Gibraltar. For that purpose, we 236 237 performed another GLMM that included habitat as a binomial response variable 238 (shrubland = 0; woodland = 1), sex, age and their interaction as fixed effects factors,winter as a random factor, and δD_f , PC1 and PC2 as continuous predictors. All models 239 240 were fitted in R version 3.4.0 using the package *lme4* for GLMM and package *nlme* for the Linear Mixed Models (method REML). 241 242

243 **RESULTS**

245	We captured, measured and sampled 42 breeding Robins in summer (18 in Álava and
246	24 in Gibraltar) and 149 wintering Robins in Campo de Gibraltar. Robins captured in
247	Campo de Gibraltar during the breeding period did not show significant variation
248	between years in their δD_f values ($F_{1,22} = 2.69$, $P = 0.116$). Considering a normal
249	distribution of this trait (Shapiro Wilk test: $W = 0.97$, $P = 0.717$; mean \pm SD = -
250	27.59 \pm 6.62, <i>n</i> = 24), we expected that 97.5% of the sedentary Robin population would
251	show a δD_f value higher (less negative) than -40.57‰ (i.e. mean minus 1.96×SD).
252	Álava breeders showed more negative values (Shapiro Wilk test: $W = 0.90$, $P = 0.051$;
253	left-skewed distribution with mean \pm SD = -53.75 \pm 12.75, <i>n</i> = 18) than Gibraltar
254	breeders (site effects: $F_{1,40} = 74.5$, $P < 0.001$), with only one individual exceeding
255	marginally this -40.57‰ threshold (Fig. 1). It was additionally considered that most of
256	the migratory Robins wintering in Campo de Gibraltar came from farther North-
257	Northeast than Álava (Bueno 1998, Korner-Nievergelt, et al. 2014), since the breeding
258	densities of the species south of Álava are relatively low compared to North and Central
259	European migratory populations, and a sedentary life style will be prevalent in many
260	Iberian populations (Martí & Del Moral 2003, Tellería 2012). For these reasons, we
261	used the abovementioned threshold to distinguish local sedentary $(> -40.6\%)$ from
262	migratory Robins (< -40.6‰) in our study site during winter (Fig. 1).
263	When this δD_{f} -based criteria was applied to the 149 Robins captured in Campo
264	de Gibraltar during winter, the 39 Robins with δD_f values greater than -40.6‰ (i.e.
265	sedentary) were mostly restricted to woodlands (37 out of the 83 birds caught in this
266	habitat; Table 1), while their presence was very rare in shrublands (only two out of 66

birds trapped; Table 1). This led to highly significant between-habitat differences in the

268 occurrence of sedentary birds (Table 2). These results differed markedly from the

habitat distribution of sedentary Robins that would have been inferred from the
morphology-based approach (i.e. MCF) that was traditionally used in this region to
assign the migratory behaviour of Robins (see Table S1).

Our morphological PCA gave rise to two Principal Components (Table 3). PC1 was associated with the length of flight-related body measurements (i.e. wing, P8 and tail length), which was interpreted as an index of the development of the flight apparatus. The second component (PC2) was strongly determined by tarsus and bill length, so that it was considered an index of skeletal size. Migratory Robins showed a more developed flight apparatus (PC1) than sedentary conspecifics (Table 4), but did not differ in their skeletal size (Table 4).

The GLMM that analysed a set of candidate traits (i.e. age, sex, body size and breeding origin) that could explain the wintering habitat distribution of migrants (n =110) revealed a significant effect of δD_f values. Thus, migrants with a closer breeding origin were more likely to occur in woodlands than counterparts coming from more distant locations (Table 5, Fig. 1). In turn, age, sex or body size (estimated by both PC1 and PC2) did not significantly affect the spatial organization of migratory Robins during winter.

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288 DISCUSSION

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Our results showed that sedentary Robins are able to remain in the same woodlandswhere they breed during winter, in spite of the massive arrival of overwintering

migrants. Interestingly, the migratory contingent also showed some degree of habitat

segregation, with migrants occupying woodlands having a closer breeding origin than

migratory conspecifics occurring in shrublands. On the other hand, sex, age or body size

did not affect the spatial distribution of migratory Robins. Altogether, our study

supports the idea that breeding origin has a more relevant role than initially suggested in

shaping the spatial distribution of Robins in Campo de Gibraltar during winter.

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299 Habitat distribution of migratory and sedentary Robins: underlying causes

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301 The fact that sedentary Robins virtually only occur in woodlands during winter agrees with what has been observed in other Iberian areas that host sedentary Robins (Campos 302 303 et al. 2011b), and contradicts the original idea that, in Campo de Gibraltar, part of the 304 sedentary population (mostly female and young birds) was outcompeted and excluded from woodlands upon the arrival of migrants. This latter possibility had been suggested 305 306 by previous studies that made use of morphological variation to infer the migratory 307 behaviour of wintering Robins (Tellería et al. 2001b, Tellería & Pérez-Tris 2004). 308 However, these morphological approaches are now considered inappropriate, while 309 isotopic analyses seem to provide a more reliable discrimination of the population origin of Robins (Rubenstein & Hobson 2004, De la Hera et al. 2017). 310

The observed distribution of sedentary Robins confined to woodlands could be a 311 312 general rule in other species showing migratory and sedentary counterparts in Campo de 313 Gibraltar during winter, since the same pattern of distribution has been previously 314 described in the other well-studied species in the area, the Eurasian Blackcap (De la 315 Hera et al. 2012). Sedentary blackcaps have a larger skeletal size than migrants and this 316 trait, together with an early occupancy of the best habitats, are considered the main 317 determinants of their dominance over migrants for the use of woodlands (Pérez-Tris &Tellería 2002b). However, the absence of differences in structural size between 318

migratory and sedentary Robins suggests that sedentary Robins might benefit primarily
from an early occupancy of woodlands to be dominant (irrespective of age or sex) over
all migratory birds that arrive later (Tobias 1997, Snell-Rood & Cristol 2005).

322 Several studies have detected that age and sex are the main factors explaining the wintering distribution of migratory Robins when sedentary counterparts are absent 323 (Figuerola et al. 2001, Catry et al. 2004, Campos et al. 2011a). However, we did not 324 find biases in the population composition (with regard to age and sex) of migrants 325 326 occupying woodlands and shrublands, neither did structural size affect habitat distribution. The breeding origin was the only factor explaining the habitat distribution 327 328 of migrants, a pattern that Catry et al. (2016) did not find when comparing one woodland and one distant shrubland in Portugal that only hosted migratory Robins. 329 Although we do not completely rule out the possibility that age, sex and other additional 330 331 factors (e.g. cryptic trophic segregation within habitats; see Catry et al. 2016, Neto et al. 332 2017) played a role in the distribution of Robins in Campo de Gibraltar, their effects, if 333 existing, seem to be of minor importance in this region.

334 A limitation of our study that needs to be considered is that it is based on the isotopic characterization of only two breeding populations with a modest sample size. 335 Our data suggest that the δD_f threshold used to distinguish the migratory behaviour of 336 337 Robins would assign erroneously only a small percentage ($\sim 2.5\%$) of the sedentary population. Although our study would have benefitted from a more extensive sampling 338 of Iberian migratory Robins, current knowledge of their migration ecology suggests that 339 340 the proportion of Iberian migrants wintering in southern Iberia that are potentially susceptible to be erroneously assigned as sedentary, is very low (see Results). This 341 342 supports the idea that our isotopic approach is providing a much more realistic view

than previous morphology-based studies of how migratory and sedentary Robins are
distributed between habitats in Campo de Gibraltar (De la Hera *et al.* 2017).

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346 Ecological and evolutionary implications of observed habitat distribution

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348 Shrublands strongly differ from woodlands in several key habitat characteristics (e.g. vegetation structure, food abundance and diversity, predation risk) which could promote 349 350 specialization in the exploitation of each habitat type in the different populations (Tellería et al. 2008). Recent research supports the existence of different wintering 351 352 strategies in Robins, and such variation could be associated with their breeding latitude (Catry et al. 2016). Alternative wintering strategies have been suggested for some 353 passerine species (Senar et al. 1994, Neto et al. 2017), including Robins (Cuadrado 354 355 1997), and this variation could be reflected in differences in avian morphological 356 characteristics between habitat types (Desrochers 2010). In addition to the marked 357 morphological differences between sedentary and migratory Robins (see above), we found that migratory Robins coming from further away (more negative δD_f) had smaller 358 structural size and more concave wings than migrants with a closer breeding origin, but 359 size of flight morphology (PC1) or wingtip pointedness was not significantly associated 360 361 with δD_f (See Section 3 in Supplementary Material). These latitudinal patterns might 362 support the existence of latitudinal variation in the lifestyles of overwintering migratory Robins, although this variation did not result in consistent morphological differences 363 364 between migrants occupying woodlands and shrublands in our study (See Section 4 in 365 Supplementary Material).

366 Understanding whether the observed patterns of spatial segregation has resulted367 in habitat specialization is of paramount importance, because each scenario would have

368 different consequences for individual fitness and population dynamics (Webster et al. 369 2002, Harrison et al. 2011). For example, if habitat specialization does not occur, we would assume that Robin populations with more distant breeding origins will be more 370 371 likely to occupy the supposedly low-quality shrublands than sedentary or migratory counterparts breeding closer to the wintering grounds. This would cause inequalities 372 between Robins wintering in different habitats that might lead to individual differences 373 in short-term (e.g. winter survival) and long-term fitness consequences (e.g. carry-over 374 375 effects in subsequent life-history stages), with the potential to affect the abundance of each population group (Harrison et al. 2011). However, if observed structured patterns 376 377 gave rise to some degree of specialization between habitat types, differences in wintering conditions between Robins adapted to woodlands or shrublands are expected 378 to be small, with less variation in the short or long-term consequences for individual 379 380 fitness (Webster & Marra 2005).

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382 Conservation prospects for woodland-shrubland mosaics

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Global warming scenarios predict drastic changes in habitat configuration in southern 384 Iberia (Peñuelas et al. 2002, Herrero & Zavala 2015). These ongoing alterations might 385 386 explain the current decline observed in the breeding and wintering populations of Robins in Campo de Gibraltar (Tellería 2015), which could be representative of the 387 challenges that other typically Eurosiberian species might be facing in their southern 388 389 limits of their distributional range. Climate-induced increase in summer drought is 390 expected to progressively deteriorate Mediterranean woodlands, potentially becoming 391 shrub-type formations (Herrero & Zavala 2015), with few opportunities for latitudinal or altitudinal displacement to new areas (De Dios et al. 2009). These changes in 392

vegetation composition might affect detrimentally both migratory and sedentary 393 394 populations of Robins and other avian species (Pérez-Tris et al. 2002b, Tellería et al. 2005). However, these impacts are expected to be more dramatic on local sedentary 395 396 birds that are intimately bound to woodlands year-round, and for which shrublands would not constitute a suitable alternative habitat in the long-term. Consequently, 397 management actions aiming to attenuate the effects of climate change and other threats 398 on these Mediterranean woodlands are essential, not only for preserving their intrinsic 399 400 value (Ojeda et al. 2000), but also for guaranteeing the conservation of their singular breeding bird populations. 401

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413

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Table 1. Distribution of the 149 Robins captured during winter in Campo de Gibraltar

according to habitat, site, population (migratory and sedentary, according to δD_f values)

and age (adult and juvenile).

	Migratory Robins		Sedentary Robins			
	$(\delta D_{\rm f} < -40.6\%$	($\delta D_{\rm f} > -40.6\%$)				
Sites	Adults	Juveniles	Adults	Juveniles	Total	
Woodlands						
San Carlos Carretera	11	13	12	4	40	
San Carlos Tiradero	7	15	14	7	43	
Shrublands						
Almodóvar	17	17	0	1	35	
Betis	14	16	1	0	31	

Table 2. Results of the GLMM that tested for differences between habitats (shrublands
and woodlands) in the occurrence of sedentary birds, controlling for other potential
confounding factors (age and sex), in the 149 Robins captured during winter in Campo
de Gibraltar.

Random Effects:	Variance \pm Std. Dev				
Year	0.24 ± 0.49				
Site	$1.99E^{-9}\pm 4.46E^{-5}$				
Fixed effects:	Estimate±SE	Z value	Р		
Intercept	-4.04 ± 1.46	-2.78	0.005		
Sex (Male)	1.16 ± 1.58	0.73	0.463		
Age (Juvenile)	0.27 ± 1.57	0.17	0.864		
Habitat (Woodlands)	3.94 ± 1.44	2.73	0.006		
$\text{Sex} \times \text{age}$	-0.72 ± 0.93	-0.77	0.443		
Sex \times habitat	-0.17 ± 1.58	-0.11	0.916		
Age \times habitat	-1.16 ± 1.58	-0.73	0.466		

Table 3. Results of the PCA (KMO = 0.74; Bartlett's test of sphericity: $\chi^2_{10} = 415.7$, *P* < 0.001) analysing five morphological measurements taken from the 149 wintering Robins captured in Campo de Gibraltar, showing correlation coefficients (factor loadings), eigenvalues and the percentage of variance explained by each component.

	PC1	PC2
Tarsus length	0.18	0.74
Bill length	0.23	0.60
Wing length	0.56	-0.17
P8 length	0.56	-0.22
Tail length	0.54	-0.09
Eigenvalue	2.792	1.004
Explained variance	0.56	0.20

Table 4. Results of the Linear Mixed Models that analysed the variation in flight morphology (PC1) and structural size (PC2) for the 149 Robins

579 captured during winter in Campo de Gibraltar.

	Flight morphology (PC1)		Structural size (PC2)			
Random Effects:	Standard deviation		Standard deviation			
Year	0.41			0.18		
Residual	1.16			0.98		
Fixed effects:	Estimate±SE	t value	Р	Estimate ±SE	t value	Р
Intercept	-0.13 ± 0.35	-0.37	0.709	0.02 ± 0.21	0.11	0.913
Age (Juvenile)	-0.56 ± 0.26	-2.13	0.035	-0.15 ± 0.22	-0.69	0.492
Sex (Male)	2.21 ± 0.33	6.71	< 0.001	-0.24 ± 0.28	-0.87	0.384
Population (Sedentary)	-1.53 ± 0.38	-4.05	< 0.001	0.45 ± 0.32	1.42	0.157
$Age \times sex$	0.16 ± 0.41	0.38	0.704	-0.01 ± 0.35	-0.04	0.968
Age \times population	0.11 ± 0.48	0.24	0.813	0.03 ± 0.40	0.08	0.939
Sex \times population	-0.82 ± 0.46	-1.79	0.075	0.17 ± 0.39	0.43	0.664

Table 5. Results of the GLMM that analysed the factors (sex, age, body size and
breeding origin) that better explained the habitat distribution (shrublands vs. woodlands)
of the 110 migratory Robins wintering in Campo de Gibraltar.

Random Effects:	Variance \pm Std. Dev			
Year	0.09 ± 0.30			
Fixed effects:	<i>Estimate</i> ± <i>SE</i>	Z value	Р	
Intercept	1.50 ± 1.09	1.38	0.168	
Sex (Male)	$\textbf{-0.42}\pm0.79$	-0.53	0.599	
Age (Juvenile)	$0.41{\pm}0.53$	0.77	0.443	
PC1	0.23 ± 0.19	1.23	0.219	
PC2	0.24 ± 0.23	1.05	0.295	
$\delta D_{\rm f}$	0.03 ± 0.01	2.20	0.028	
Sex x age	0.48 ± 0.89	0.54	0.591	

586 Figure legends.

587

- **Figure 1.** δD_f values of Robins captured during breeding in Álava and Campo de
- 589 Gibraltar (lower box), and during winter in the two distinctive habitat types (woodlands
- and shrublands) available in Gibraltar (upper box). The broken grey line shows the δD_f
- threshold used to distinguish the migratory behaviour of wintering birds according to
- 592 the observed δD_f distributions of breeding Robins.

