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Additional Information

# **Similar dispersal patterns between two closely related birds with contrasting migration strategies**

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1 **Abstract**

2

3 Studying dispersal is crucial to understand metapopulation and sink-source dynamics and invasion  
4 processes. The capability to disperse is especially important for species living in fragmented  
5 habitats like wetlands. We investigated the distribution of natal and breeding dispersal distances and  
6 philopatry in Spanish populations of two closely related reedbed-nesting birds, the Moustached  
7 Warbler *Acrocephalus melanopogon* and the Eurasian Reed Warbler *Acrocephalus scirpaceus*.  
8 These warblers are morphologically very similar, but differ in migration strategy and, in our study  
9 area, in population size. Our aims were to find the best model for dispersal distances and to assess  
10 the occurrence of intra- or interspecific differences in dispersal patterns. We used ringing data from  
11 the Spanish marking scheme and selected recaptures to avoid including migrating individuals. In  
12 both species, most individuals were philopatric but dispersing birds were able to cross large  
13 distances (up to more than 100 km), suggesting the capability to compensate for habitat  
14 fragmentation. We found the heavy-tailed Cauchy distribution to be the best conceptual description  
15 for our data, in all cases but natal dispersal of Moustached Warblers. Among Eurasian Reed  
16 Warblers, natal philopatry was lower than breeding philopatry. We found no significant interspecific  
17 differences. This does not confirm the hypothesis of higher dispersal ability in long distance  
18 migrants (like Eurasian Reed Warblers) than in resident/short distance migrant bird species (like  
19 Moustached Warblers). The similarity in dispersal patterns among the two warblers may be  
20 explained by their close phylogenetic relatedness, similar constraints imposed on both species by a  
21 patchy habitat or similar evolutionary pressures.

22

23

24 **Keywords** *Acrocephalus melanopogon*; *Acrocephalus scirpaceus*; dispersal; long-distance  
25 dispersal; spatial ecology; philopatry

## 26 **Introduction**

27

28 Studying dispersal is crucial in population biology. It is an important element in metapopulation and  
29 sink-source dynamics (Begon et al. 2006), in colonization and invasion processes (Hengeveld 1994,  
30 Shigesada et al. 1995), and should be taken into account when studying the processes underlying  
31 adaptation (Lambrechts et al. 1999). Dispersal is also related to gene flow and, consequently, to the  
32 degree of genetic differentiation among populations (Bohonak 1999, Frankham et al. 2010). Thus,  
33 information about dispersal is of critical importance for conservation, especially for species living  
34 in fragmented habitats (e.g. Van Houtan et al. 2010). Dispersal in birds has been the object of many  
35 studies, but the high movement capability of most bird species implies important problems of data  
36 collection (Koenig et al. 1996, Paradis et al. 1998 and reference therein). Indeed, small-scale study  
37 areas are likely to underestimate the frequency of long-distance dispersal events (Koenig et al.  
38 1996, Paradis et al. 1998). In spite of being relatively rare, such events are likely to be important in  
39 population dynamics (Nathan et al. 2003) and in determining the genetic structure of populations  
40 (Ibrahim et al. 1996). A ringed bird may be recovered anywhere, thus recapture data from ringing  
41 databases are not spatially limited and can provide useful information about dispersal (Paradis et al.  
42 1998, 2002).

43 In this study, we used data from the Spanish marking scheme to investigate large-scale  
44 dispersal patterns of two closely related reedbed-nesting birds, the Eurasian Reed Warbler  
45 *Acrocephalus scirpaceus* Hermann 1804 and the Moustached Warbler *Acrocephalus melanopogon*  
46 Temminck 1823. These species are similar in size (~ 10 g) and are both insectivorous, but they  
47 differ in migration strategy. Their population sizes in Spain are also highly different. The Eurasian  
48 Reed Warbler (hereafter Reed Warbler) is a common breeding bird in Spain (679000 - 1320000  
49 individuals, Carrascal and Palomino 2008) and migrates over long distances, wintering in sub-  
50 Saharan Africa (Kennerley and Pearson 2010). The Spanish population of Moustached Warbler is  
51 sedentary or migrate over short distances, is distributed across a highly discontinuous range and has

52 been estimated in 484 - 1777 breeding pairs (Castany and López 2006). Distribution maps of both  
53 species in Spain are available at *Atlas Virtual de las Aves Terrestres de España* (Carrascal et al.  
54 2005; <http://www.lmcarrascal.eu/atlas/mapasalfab.html>). The breeding habitat of both species is  
55 highly fragmented, because of the natural patchy distribution of wetlands and the habitat loss due to  
56 human activities (Van Vesseem et al. 1997, Paracuellos and Telleria 2004, Silva et al. 2007).

57 Our aims were: 1) to obtain new information about dispersal ability and philopatry in  
58 Spanish populations of the two species, the Reed Warbler and the Moustached Warbler; 2) to find  
59 the best conceptual description of dispersal distances in these warblers, among a set of simple  
60 models (one-two parameters, see Table 1 for details) with clear biological meaning; 3) to assess the  
61 occurrence of intraspecific differences in dispersal patterns, between natal dispersal (from the birth  
62 place to a breeding site) and breeding dispersal (between breeding sites); 4) to assess the occurrence  
63 of interspecific differences in dispersal patterns between the two species: long-distance migrants are  
64 suggested to have higher dispersal ability than sedentary/short-distance migrant species (Paradis et  
65 al. 1998). Genetic data suggest that this pattern also occurs among our study species, given the  
66 higher differentiation among Spanish populations of Moustached Warbler than among Reed  
67 Warblers breeding in Spain and Morocco (Ceresa et al. 2015). In addition, Reed Warblers have  
68 more pointed wings than Moustached Warblers (Kennerley and Pearson 2010), indicating higher  
69 flight efficiency (Norberg et al. 1998) and, consequently, a possibly higher dispersal capability.  
70 Concerning our model set, we fitted distance data to the normal, the exponential and the Cauchy  
71 distributions. The normal distribution describes a low diffusion through space, determined by  
72 various external stochastic factors ('random walk'; Van Houtan et al. 2007). Dispersal distances will  
73 follow an exponential distribution if moving individuals have a constant probability of settling  
74 (Paradis et al. 2002). Finally, the Cauchy distribution is heavy-tailed, and as such it predicts more  
75 frequent long-distance dispersal events than the exponential distribution (Paradis et al. 2002).

76

## 77 **Methods**

78

79 **Data selection**

80

81 The starting database was made available by 'Banco de datos de anillamiento del remite ICONA –  
82 Ministerio de Medio Ambiente' (2015). It included all recoveries of individuals ringed in Spain  
83 (including those birds recovered outside the country) from year 1962 to 2013 and provided recovery  
84 distances to the nearest km. The ringing effort on the two species increased throughout the years, up  
85 to reaching the maximum number of marked individuals in the decade 2001-2010 (6425  
86 Moustached Warblers and 229671 Reed Warblers; SEO/BirdLife 2016a,b). Consequently, also the  
87 majority of the collected recovery data (> 80%) are referred to birds ringed during that decade and  
88 the following years. Ringing and recoveries occurred at overall 1127 different localities, among  
89 these the Moustached Warbler was recorded at 103 sites and the Reed Warbler at 1099 sites.

90         In this study, we only considered birds ringed during the breeding season and recovered  
91 during the breeding season of following years. We defined two age classes: juveniles for individuals  
92 ringed in their year of birth and adults for birds ringed later. Natal dispersal was estimated by using  
93 birds ringed as juveniles, while to estimate breeding dispersal we used birds ringed as adults  
94 (Paradis et al. 1998). We excluded those birds whose age was unknown when ringed. Periods  
95 adopted as breeding season were 1 June – 31 July for the Reed Warbler (Cantos and Tellería 1994)  
96 and 1 April – 31 May for the Moustached Warbler (Castany 2003). Juvenile Reed Warblers ringed  
97 in May (early fledged individuals) were also included. We checked the geographical coordinates  
98 provided in the database to ensure they corresponded to the ringing/recovery localities, when they  
99 did not we corrected them. Given the intrinsic characteristics of our dataset, we could not  
100 investigate fine-scale movements of birds within each breeding area, thus all dispersal events  
101 described in this work consist in displacements from a natal/breeding site towards a different patch  
102 of suitable habitat. To obtain reliable information about dispersal distances, it was very important to  
103 avoid including individuals ringed/recovered when migrating. The periods we adopted as breeding

104 season excluded the main migration periods of the study species (Cantos and Tellería 1994, Castany  
105 2003, Peirò 2003, Kennerley and Pearson 2010), but even so we risked including some late/early  
106 migrating individuals. Examining recoveries of Reed Warblers, we observed that the direction of  
107 most of the largest recorded distances approached or corresponded to the North-East – South-West  
108 axis, followed by most individuals migrating through the Iberian Peninsula (e.g. Procházka et al.  
109 2011). We then discarded the largest dispersal distances when orientated along the NE – SW axis  
110 (Paradis et al. 1998). As a result of this selection, all dispersal distances larger than 290 km were  
111 removed and recoveries were not preferentially oriented along this axis ('migratory axis' vs. all  
112 other directions:  $\chi^2_1 = 1.041$ ,  $P = 0.308$ ). Including all the data did not anyway affect the results of  
113 our study (i.e. we obtained very similar outputs from data analysis). For Moustached Warblers we  
114 found a low number of dispersing individuals, thus we could not assess if distances were  
115 preferentially orientated in some direction. We then used all available recoveries for this species. A  
116 further possible risk was to include birds that were not actually breeding when recaptured, e.g. in  
117 several passerine species some individuals do not breed during their first potential breeding season  
118 (Cooper et al. 2009 and reference therein). However, such individuals are likely to be waiting for an  
119 opportunity to obtain a territory/mate (Newton 1992) or looking for extra-pair copulations (see e.g.  
120 Blomqvist et al. 2005 for the Moustached Warbler). Thus, even when occurring in our dataset, such  
121 individuals were probably recovered close to their potential breeding sites (Paradis et al. 1998).

122

### 123 **Statistical analysis**

124

125 Within the set of selected recoveries, we first calculated the proportion of philopatric and dispersing  
126 individuals among juveniles and adults of the two species and carried out inter- and intraspecific  
127 comparisons by means of chi-square ( $\chi^2$ ) test of independence (Winkler et al. 2004). To compare the  
128 distribution of dispersal distances among species and age classes we used the two-samples  
129 Kolmogorov-Smirnov test. Interspecific comparisons were carried out by considering natal and

130 breeding dispersal both jointly (i.e. using all data per species) and separately. In order to find the  
131 best dispersal model among our set (see Introduction) we fitted dispersal distances to the normal,  
132 the exponential and the Cauchy distributions using package `fitdistrplus` 1.0-4 (Delignette-Muller  
133 and Dutang 2015) in R 3.1.1 (R Core Team 2014). For the Cauchy distribution, we always fixed the  
134 location parameter at  $x = 0.1$ . We ranked models using the Akaike Information Criterion (AIC), and  
135 considered the model with lower AIC as the best one (Burnham and Anderson 2002).

136         Ideally, spatial variation in sampling effort should be taken into account when studying the  
137 distribution of dispersal distances (e.g. Van Houtan et al. 2007), because it is likely to determine a  
138 spatial variation in recovery rates, but we lacked the necessary data. As suggested by Paradis et al.  
139 (1998), the bias resulting from spatial variation in recovery rates may be reduced if the number of  
140 potential recovery sites is large (like in this study), and interspecific comparisons are unlikely to be  
141 affected when species are studied over the same area, because spatial variation in recovery rates  
142 would be similar.

143

## 144 **Results**

145

146 Both natal and breeding philopatry were high in both species: the proportion of philopatric  
147 individuals was 98 % and 92 % respectively in juvenile and adults Moustached Warblers, 91 % and  
148 94 % in juvenile and adult Reed Warblers. Among Reed Warblers, natal philopatry was lower than  
149 breeding philopatry ( $\chi^2_1 = 6.273$ ,  $P = 0.012$ ), while we found no significant difference among  
150 Moustached Warblers ( $\chi^2_1 = 1.066$ ,  $P = 0.302$ ) or among species (all data:  $\chi^2_1 = 0.128$ ,  $P = 0.721$ ;  
151 juveniles:  $\chi^2_1 = 2.285$ ,  $P = 0.131$ ; adults:  $\chi^2_1 = 0.233$ ,  $P = 0.629$ ). Some of the relatively rare  
152 dispersing individuals were recovered at long distance (Fig. 1); birds dispersing further than 100 km  
153 were found in all categories excepted the juvenile Moustached Warblers (the category with lower  
154 sample size,  $N = 50$ ). According to the Kolmogorov-Smirnov test we found no significant difference  
155 in distribution of dispersal distances among the two species (all data:  $D = 0.026$ ,  $P = 1$ ; juveniles:  $D$



156 = 0.075,  $P = 0.963$ ; adults:  $D = 0.030$ ,  $P = 1$ ) and among age classes (Reed Warbler:  $D = 0.041$ ,  $P =$   
157  $0.590$ ; Moustached Warbler:  $D = 0.06$ ,  $P = 1$ ). According to the AIC values, the Cauchy distribution  
158 provided the best model for dispersal distances in all cases, excepted the natal dispersal of  
159 Moustached Warblers (Table 2). In this last case, the exponential distribution obtained the lower  
160 AIC (Table 2). The estimated scale parameter  $\gamma$  of Cauchy distribution was very similar among  
161 species and age classes (Table 2), i.e. increasing distance the probability of dispersal events  
162 decreased in a similar way. The normal distribution always resulted to be the worst model for our  
163 dispersal data (Table 2; Fig. 2).

164

## 165 **Discussion**

166

167 Although in both species most individuals were philopatric, dispersing birds were able to cross  
168 large distances, suggesting the capability to compensate for habitat fragmentation. We found a  
169 heavy-tailed distribution to be the best model for dispersal distances, consistently with similar  
170 previous studies (Paradis et al. 2002, Winkler et al. 2005, Van Houtan et al. 2007, 2010). The  
171 exception represented by natal dispersal of Moustached Warblers, where the exponential  
172 distribution was selected as the best model (Table 2), should be cautiously considered because of  
173 the low sample size. Long-distance dispersal cases are rare, thus reduced samples are likely to fail  
174 in detecting them. When losing these events, heavy-tailed distributions, given their characteristics  
175 (see the Introduction), will result as less adequate to describe dispersal distances. Further  
176 investigation using additional data will be needed to assess if juvenile Moustached Warblers from  
177 our study populations are able to disperse over long distances. The good dispersal ability of Reed  
178 Warblers was also found in British populations (Paradis et al. 1998) and was confirmed by the low  
179 genetic differentiation among European populations (Kralj et al. 2010, Procházka et al. 2011,  
180 Ceresa et al. 2015). Our results about this species indicate that in our study population juveniles  
181 disperse more frequently than adults, but with similar probability of settling with increasing

182 distance, which indicates that dispersal ability is not different among the two age classes.

183         The two species showed a similarly low tendency to disperse, possibly caused by the  
184 reduced opportunities of finding new breeding sites and/or by the high costs of dispersal (e.g.  
185 increased mortality, physiological costs; Waser et al. 1994, Plissner and Gowaty 1996). At a  
186 marshland in Hungary, Vadász et al. (2008) found higher natal and breeding site fidelity in  
187 Moustached than in Reed Warblers, and in both species breeding site fidelity was higher than natal  
188 site fidelity. The results of Vadász et al. (2008) can not anyway be compared with ours, because in  
189 the first case the authors used returning rates at a single site (mortality and dispersal can not be  
190 distinguished), while we compared the proportion of recoveries obtained at and outside each ringing  
191 site. Ceresa et al. (2015) found that gene flow among Spanish populations of the two warblers,  
192 although occurring, was partly limited or even restricted. The high natal and breeding philopatry we  
193 found in both species may help to explain such limitation in gene flow, as hypothesized by Ceresa et  
194 al. (2015).

195         The lack of significant differences in the distribution of dispersal distances between the two  
196 species and the high similarity in the estimated Cauchy scale parameter (Table 2) contrast with the  
197 hypothesis of higher dispersal ability in Reed Warblers (long-distance migrants) than in Moustached  
198 Warblers (resident/short distance migrants). Indirect information from genetic data indicated that  
199 Spanish populations of both species have a good dispersal capability, consistently with our results,  
200 but also showed lower population differentiation in Reed than in Moustached Warblers (Ceresa et  
201 al. 2015), indicating higher gene flow in the first species. Consistently with a limited gene flow, for  
202 Moustached Warblers we found no case of dispersal between the three populations considered in  
203 Ceresa et al. (2015), i.e. one small isolated inland population, one at the Mediterranean coast and  
204 one on the Mallorca Island. These populations are separated by the sea or by large land zones where  
205 the species does not breed. We found dispersal cases only between marshlands along the  
206 Mediterranean coast of Spain, the only area of the country where the breeding range is relatively  
207 continuous (see Castany and López 2006). Unfortunately, as far as we know there are no available

208 genetic data to compare birds from different breeding sites along the coast. The Mallorca Island  
209 hosts the largest Spanish population of Moustached Warblers (~ 500 breeding pairs) and has been  
210 the object of intense ringing activity (Castany 2003). The lack of recoveries from or towards this  
211 island is consistent with the restricted gene flow between the Mallorcan population and those of the  
212 mainland, which suggested that the sea represents an effective barrier for this species (Ceresa et al.  
213 2015). The extinction of several bird species on Barro Colorado Island (Panama) showed that water  
214 can represent a barrier to immigration (Willis 1974, Robinson 1999), and other studies suggest that  
215 water bodies are more effective barriers than land areas of the same width, at least for some species  
216 (Hodges and Kremets 1996, Machtans et al. 1996). Unlike Moustached Warblers, Reed Warblers  
217 showed low populations differentiation even when the breeding sites were separated by the sea  
218 (Ceresa et al. 2015). According to the authors, the interspecific difference in population  
219 differentiation could be due to differences in dispersal ability, breeding site fidelity, capability of  
220 crossing the sea, population size or breeding range patchiness (Ceresa et al. 2015). Our results do  
221 not support the first two possible explanations, thus the lower population differentiation in Reed  
222 than in Moustached Warblers is more likely to be determined by the more continuous breeding  
223 range/larger population size (see the references in the Introduction) and the higher capability of  
224 crossing stretches of sea of the first species. This comparison among ringing data and genetic  
225 information should be anyway cautiously considered. For example, differences in gene flow may  
226 also be influenced by possible interspecific differences in the fitness costs of dispersal, and we have  
227 no information about this issue. The similarity in dispersal patterns between the two species may be  
228 explained by their close phylogenetic relatedness (Sutherland et al. 2000). Furthermore, both  
229 warblers breed in a naturally patchy habitat, thus their dispersal ability may have evolved according  
230 to the same need of crossing more or less wide areas of unsuitable habitat to find new breeding  
231 sites.

232

233

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237 **References**

238

239 Banco de datos de anillamiento del remite ICONA – Ministerio de Medio Ambiente (2015) Datos  
240 de anillamiento y recuperaciones en España. Ministerio de Agricultura, Alimentación y Medio  
241 Ambiente, SEO/BirdLife, ICO, EBD-CSIC y GOB. Madrid

242

243 Begon M, Townsend CR, Harper JL (2006) Ecology: from individual to ecosystems, 4th edn.

244 Blackwell Publishing, Oxford

245

246 Blomqvist D, Fessl B, Hoi H, Kleindorfer S (2005) High frequency of extra-pair fertilisation in the  
247 moustached warbler, a songbird with a variable breeding system. Behaviour 142:1133-1148

248

249 Bohonak AJ (1999) Dispersal, gene flow, and population structure. Q Rev Biol 74: 21-45

250

251 Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical  
252 information-theoretic approach. Springer Verlag, New York

253

254 Cantos FJ, Tellería JL (1994) Stopover site fidelity of four migrant warblers in the Iberian  
255 Peninsula. J Avian Biol 25:131-134

256

257 Carrascal LM, Palomino D (2008) Las aves comunes reproductoras en España. Población en 2004-  
258 2006. SEO/BirdLife, Madrid

259

260 Carrascal LM, Weykam S, Palomino D, Lobo JM, Díaz L (2005) Atlas Virtual de las Aves Terrestres  
261 de España. <http://www.vertebradosibericos.org/atlasaves.html>

262

263 Castany J (2003) El carricerín real (*Acrocephalus melanopogon*) en el P. N. del Prat de Cabanes-  
264 Torreblanca. Doctoral thesis. University of Valencia  
265  
266 Castany J, López G (2006). El carricerín real en España. I Censo Nacional (2005). SEO/BirdLife,  
267 Madrid  
268  
269 Ceresa F, Belda EJ, Kvist L, Rguibi-Idrissi H, Monrós JS (2015) Does fragmentation of wetlands  
270 affect gene flow in sympatric *Acrocephalus* warblers with different migration strategies? J Avian  
271 Biol doi:10.1111/jav.00589  
272  
273 Cooper NW, Murphy MT, Redmond LJ, Dolan AC (2009) Density-dependent age at first  
274 reproduction in the eastern kingbird. Oikos 118:413-419  
275  
276 Delignette-Muller ML, Dutang C (2015) fitdistrplus: An R Package for Fitting Distributions. J Stat  
277 Softw 64:1-34 URL <http://www.jstatsoft.org/v64/i04/>  
278  
279 Frankham R, Ballou JD, Briscoe DA (2010) Introduction to Conservation Genetics, 2nd edn.  
280 Cambridge University Press  
281  
282 Hengeveld R (1994) Small step invasion research. Trends Ecol Evol 9:339-342  
283  
284 Hodges MF Jr, Kremetz DG (1996) Neotropical migratory breeding bird communities in riparian  
285 forests of different widths along the Altamaha River, Georgia. Wilson Bull 108:496-506  
286  
287 Ibrahim KM, Nichols RA, Hewitt GM (1996) Spatial patterns of genetic variation generated by  
288 different forms of dispersal during range expansion. Heredity 77:282-291

289

290 Kennerley P, Pearson D (2010) Reed and Bush Warblers. Christopher Helm Publishers Ltd., London

291

292 Koenig WD, Van Vuren D, Hooge PN (1996) Detectability, philopatry, and the distribution of

293 dispersal distances in vertebrates. Trends Ecol Evol 11:514-517

294

295 Kralj J, Procházka P, Fainová D, Patzenhauerová H, Tutiš V (2010) Intraspecific variation in the

296 wing shape and genetic differentiation of reed warblers *Acrocephalus scirpaceus* in Croatia. Acta

297 Ornithol 45:51-58

298

299 Lambrechts MM, Blondel J, Caizergues A, Dias PC, Pradol R, Thomas DW (1999) Will estimates

300 of lifetime recruitment of breeding offspring on small-scale study plots help us to quantify

301 processes underlying adaptation? Oikos 86:147-151

302

303 Machtans CS, Villard MA, Hannon SJ (1996) Use of riparian buffer strips as movement corridors

304 by forest birds. Conserv Biol 10:1366-1379

305

306 Nathan R, Perry G, Cronin JT, Strand AE, Cain ML (2003) Methods for estimating long-distance

307 dispersal. Oikos 103:261-273.

308

309 Newton I (1992) Experiments on the limitation of bird numbers by territorial behaviour. Biol Rev

310 Camb Philos Soc 67:129-173

311

312 Norberg UM (1989) Vertebrate Flight, Mechanics, Physiology, Morphology, Ecology and

313 Evolution. Springer Verlag, Berlin

314

315 Paracuellos M, Tellería JL (2004) Factors affecting the distribution of a waterbird community: the  
316 role of habitat configuration and bird abundance. *Waterbirds* 27:446-453  
317

318 Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal  
319 in birds. *J Anim Ecol* 67:518-536  
320

321 Paradis E, Baillie SR, Sutherland WJ (2002). Modeling large-scale dispersal distances. *Ecol Model*  
322 151:279-292  
323

324 Peirò, IG (2003) Intraspecific variation in the wing shape of the long-distance migrant Reed  
325 Warbler *Acrocephalus scirpaceus*: effects of age and distance of migration. *Ardeola* 50:31-37  
326

327 Plissner JH, Gowaty PA (1996) Patterns of natal dispersal, turnover, and dispersal costs in eastern  
328 bluebirds. *Anim Behav* 51:1307-1322  
329

330 Procházka P, Stokke BG, Jensen H, Fainová D, Bellinvia E, Fossøy F, Vikan JR, Bryja J, Soler M  
331 (2011) Low genetic differentiation among reed warbler *Acrocephalus scirpaceus* populations across  
332 Europe. *J Avian Biol* 42:103-113  
333

334 R Core Team (2014) R: A Language and Environment for Statistical Computing. R Foundation for  
335 Statistical Computing <<http://www.R-project.org>>  
336

337 Robinson WD (1999) Long-term changes in the avifauna of Barro Colorado Island, Panama, a  
338 tropical forest isolate. *Conserv Biol* 13:85-97  
339

340 SEO/BirdLife (2016a) *Acrocephalus melanopogon*. Anillamientos por década.



341 <http://www.anillamientoseo.org/>. Accessed 19 February 2016

342

343 SEO/BirdLife (2016b) *Acrocephalus scirpaceus*. Anillamientos por década.

344 <http://www.anillamientoseo.org/>. Accessed 19 February 2016

345

346 Shigesada N, Kawasaki K, Takeda Y (1995) Modeling stratified diffusion in biological invasions.

347 *Am Nat* 146:229-251

348

349 Silva JP, Phillips L, Jones W, Eldridge J, O'Hara E (2007) Life and Europe's wetlands, restoring a

350 vital ecosystem. Office for Official Publications of the European Communities, Luxembourg

351

352 Sutherland GD, Harestad AS, Price K, Lertzman KP (2000) Scaling of natal dispersal distances in

353 terrestrial birds and mammals. *Conservation Ecology* 4:16 URL

354 <http://www.consecol.org/vol4/iss1/art16>

355

356 Vadász C, Németh Á, Karcza Z, Loránt M, Biró C, Csörgő T (2008) Study on breeding site fidelity of

357 *Acrocephalus* Warblers in Central Hungary. *Acta Zool Acad Sci Hung* 54 (Suppl. 1):167-175

358

359 Van Houtan KS, Pimm SL, Halley JM, Bierregaard RO Jr, Lovejoy TE (2007) Dispersal of

360 Amazonian birds in continuous and fragmented forest. *Ecol Lett* 10:219-229

361

362 Van Houtan KS, Bass OL Jr, Lockwood J, Pimm SL (2010) Importance of estimating dispersal for

363 endangered bird management. *Conserv Lett* 3:260-266

364

365 Van Vessum J, Hecker N, Tucker GM (1997) Inland wetlands. In: Tucker GM, Evans MI (eds)

366 *Habitats for birds in Europe: A conservation strategy for the wider environment*. BirdLife

367 Conservation Series 6. BirdLife International, Cambridge  
368  
369 Waser PM, Creel SR, Lucas JR (1994) Death and disappearance: estimating mortality risk  
370 associated with philopatry and dispersal. *Behav Ecol* 5:135-141  
371  
372 Willis EO (1974) Populations and local extinctions of birds on Barro Colorado Island, Panama.  
373 *Ecol Monog* 44:153-169  
374  
375 Winkler DW, Wrege PH, Allen PE, Kast TL, Senesac P, Wasson MF, Llambías PE, Ferretti V,  
376 Sullivan PJ (2004) Breeding dispersal and philopatry in the tree swallow. *Condor* 106:768-776  
377  
378 Winkler DW, Wrege PH, Allen PE, Kast TL, Senesac P, Wasson MF, Sullivan PJ (2005) The natal  
379 dispersal of tree swallows in a continuous mainland environment. *J Anim Ecol* 74:1080-1090

380 Table 1. Distributions adopted for modelling dispersal distances ( $d$ )

381

Distribution	Probability density function	Parameters (name)
Normal	$\frac{1}{\sigma\sqrt{2\pi}} e^{-(d-\mu)^2/2\sigma^2}$	$\mu$ (mean), $\sigma$ (standard deviation)
Exponential	$\lambda e^{-\lambda d}$	$\lambda$ (rate)
Cauchy	$\frac{1}{\pi\gamma} \left[ \frac{\gamma^2}{(d-x)^2 + \gamma^2} \right]$	$x$ (location), $\gamma$ (scale)

382 Table 2. AIC values for three dispersal models (the best model for each data category is highlighted  
 383 in bold), sample size (n) and the estimated Cauchy scale parameter ( $\gamma$ ) with the 95% confidence  
 384 intervals (CI)

385

Species	Data category	n	AIC values			$\gamma$ (95% CI)
			Cauchy	Exponential	Normal	
Reed Warbler	All data	1808	<b>693</b>	6509	14466	0.108 (0.102 – 0.113)
	Natal dispersal	476	<b>416</b>	1961	4017	0.111 (0.101 – 0.122)
	Breeding dispersal	1332	<b>278</b>	4500	10372	0.106 (0.101 – 0.112)
Moustached Warbler	All data	125	<b>20</b>	468	1022	0.106 (0.087 – 0.125)
	Natal dispersal	50	-27	<b>-53</b>	185	0.102 (0.073 – 0.131)
	Breeding dispersal	75	<b>49</b>	352	652	0.109 (0.083 – 0.135)

386 **Figure legends**

387

388 Fig. 1 Natal and breeding dispersal distances in Spanish populations of Moustached and Reed

389 Warbler, obtained from ringing data

390

391 Fig. 2 Cumulative density functions (CDF) of the observed data (black solid line) and of the fitted

**392**