

1 **Running head: *Tracking of spring migrating Eurasian Teal***

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3 **Spring migratory routes and stopover duration of satellite tracked Eurasian Teal *Anas crecca***  
4 **wintering in Italy**

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17 Identifying an organism's migratory strategies and routes has important implications for  
18 conservation. For most species of European ducks, information on the general course of migration,  
19 revealed by ringing recoveries, is available, whereas tracking data on migratory movements are  
20 limited to the largest species. In the present paper, we report the results of a tracking study on  
21 Eurasian Teal, the smallest European duck, captured during the wintering period at three Italian  
22 sites. The departure date of spring migration was determined for 21 individuals, and for 15 the  
23 entire spring migratory route was reconstructed. Most ducks departed from wintering grounds  
24 between mid-February and March following straight and direct routes along the Black Sea-  
25 Mediterranean flyway. The breeding sites, usually reached by May, were spread from central to  
26 North-Eastern Europe to east of the Urals. The migratory speed was slow (approximately 36 km/d  
27 on average), because most birds stopped for several weeks at stopover sites, mainly in south-eastern  
28 Europe, especially at the very beginning of migration. The active flight migration segments were  
29 covered at much higher speeds, up to 872 km/d. Stopover duration tended to be shorter when birds  
30 were closer to their breeding site. These results, based on the largest satellite tracking effort for this  
31 species, revealed for the first time the main features of the migratory strategies of individual Teal  
32 wintering in Europe, such as the migration timing and speed and stopover localisation and duration.

33

34 **Keywords:** Anatidae, telemetry, flyways, wildfowl, migratory strategy

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36

37 Migration constitutes a prominent feature of avian life cycle, as the majority of species are  
38 migratory to some extent (Newton 2008). Flight is energetically demanding (Johansson *et al.* 2014)  
39 explaining why for many birds most migration time is actually spent in stopover/staging sites in  
40 order to gain the energy needed for the subsequent flights (Alerstam & Lindström 1990,  
41 Hedenström & Lindström 2014). The availability of suitable stopover sites is thus critical for a  
42 successful migration and identifying their geographical distribution and how they are distributed  
43 along the migratory routes is essential for a proper understanding of the migratory strategies of a  
44 given species (Newton 2008, Chernetsov 2012). Traditionally, the linkages between the areas  
45 visited by migrants are investigated by means of ringing and field counting (Bairlein 2003, Newton  
46 2008), but these techniques cannot offer an accurate description of bird migration patterns, given  
47 their intrinsic biases due to the non-random distribution of data collectors and to the often limited  
48 number of re-encounters (Thorup *et al.* 2014, Giunchi *et al.* 2015, Si *et al.* 2015), nor can they  
49 account for individual variability in migratory strategy. The recent advances in tracking  
50 technologies permit unprecedented opportunities for reconstructing the migration of many bird  
51 species, even of relatively small size (Wikelski *et al.* 2007, Bridge *et al.* 2011, Bridge *et al.* 2013,  
52 Kays *et al.* 2015). In this way, valuable information can be collected on individual variability in  
53 various aspects of the migratory behaviour, such as routes followed, departure dates and number  
54 and location of stopover sites visited (Strandberg *et al.* 2009).

55

56           Migratory waterfowl, and dabbling ducks in particular, are an essential component  
57 of wetland ecosystems where they play key functional roles (Post *et al.* 1998, Green and Elmberg  
58 2014, Viana *et al.* 2016). They can be dispersing vectors for many plants (Brochet *et al.* 2010a,  
59 2010b, Green *et al.* 2016), invertebrates (Green & Figuerola 2005) and pathogens (Altizer *et al.*  
60 2011), so identifying their migratory routes and how stopover sites are linked can be important for  
61 understanding the dispersal pathways of several organisms and diseases. Dabbling ducks are also  
62 important quarry species across Europe (Elmberg *et al.* 2006, Madsen *et al.* 2015, Guillemain *et al.*  
63 2016). As emphasized by the EU management directives, the sustainability of this hunting activity  
64 and, more generally, effective management strategies of populations have to be based on accurate  
65 scientific data including the migratory ecology of these species, like the timing of their pre-breeding  
66 migration (Arzel *et al.* 2006, Madsen *et al.* 2015).

67

68           Tracking data on migratory movements of European ducks are still scarce and the  
69 available information mainly refers to the largest species (e.g. van Toor *et al.* 2013, Gehrold *et al.*

70 2014, Parejo *et al.* 2015). In the present paper, we report the results of a tracking study on the  
71 Eurasian Teal *Anas crecca* (hereafter Teal), the smallest of European waterfowl, which is among the  
72 most abundant ducks in Europe (Carboneras *et al.* 2017), with the breeding population being  
73 estimated at 557,000-915,000 pairs (Staneva & Burfield 2017). While the breeding population trend  
74 is still unknown, the species is not considered of conservation concern in Europe (Staneva &  
75 Burfield 2017). Nevertheless, the importance of Teal as a quarry species, being one of the most  
76 hunted European ducks (Guillemain & Elmberg 2014, Guillemain *et al.* 2016), makes it crucial to  
77 collect as much information as possible on its biology and migratory behaviour in order to develop  
78 effective regulation on a continental scale (Guillemain & Elmberg 2014). In the Western Palearctic,  
79 Teal migration has been studied with ring-recoveries (Wolff 1966, Guillemain & Elmberg 2014,  
80 Guillemain *et al.* 2017), and only a few birds have been tracked by satellite, mostly in central East-  
81 Asia (Gaidet *et al.* 2010, Takekawa *et al.* 2010, Iverson *et al.* 2011, Bridge *et al.* 2014).

82

83 Our study aims to: 1) determine the phenology of spring migration of a sample of  
84 female Teal wintering in three Italian wetlands; 2) identify the main stopover/staging areas for  
85 tracked Teal; 3) characterize Teal migratory strategies at the individual level. The results, based on a  
86 total of 21 tracked female Teals, represent the largest dataset on spring migration of this species  
87 collected in Europe and provide relevant details on their migratory strategy, such as migration speed  
88 and stopover duration.

89

90

## 91 **METHODS**

92

### 93 **Study animals and PTT characteristics**

94 From 2013 to 2016, 29 female Eurasian Teal were captured while wintering in different areas of the  
95 Italian Peninsula (Table S1). Females were chosen because males are thought to follow their mate to  
96 their breeding grounds (Guillemain & Elmberg 2014). We could not include eight birds because the  
97 PTT stopped working before the start of spring migration. It was impossible to assess whether this  
98 was due to PTT failure or bird mortality.

99

100 Captures took place in December-January using mist-nets or decoy traps in sites  
101 located in central [TUS: San Rossore Estate (43.70° N, 10.30° E), Pisa, Tuscany,  $n = 5$ ] and

102 northern Italy [LOM: Quinzano D'Oglio (45.29° N, 10.01° E) and Gambara (45.27° N, 10.30° E),  
103 Brescia, Lombardy, N = 4; VEN: Valle Morosina (45.29° N, 12.13° E), Padua, Veneto,  $n = 12$ ] (Fig.  
104 1). Captures were made in different areas in order to obtain more generalizable results. The capture  
105 sites were characterized by very different management policies: the San Rossore Estate is a  
106 protected area, whereas hunting was allowed in the remaining capture sites. In particular, Valle  
107 Morosina is a hunting reserve where abundant food was provided to wintering ducks (mostly teal)  
108 throughout the hunting season.

109  
110 Birds were ringed, measured according to standard ringing procedures (Busse &  
111 Meissner 2015) and aged following Rousselot and Trollet (1991). Each duck was equipped with a  
112 solar-powered Argos Platform Transmitter Terminal (PTT, model PTT-100 9.5 g, Microwave  
113 Telemetry Inc.) using a home-made Teflon harness (see Roshier & Asmus 2009 for details, Fig. S1)  
114 and then released. The total weight of the tag corresponded to < 3.5 % of the bird's body weight. In  
115 order to find the best trade-off between tag duration and number of fixes, we used two duty cycles:  
116 6 hours on/16 hours off (6/16; 10 individuals) and 10 hours on/48 hours off (10/48; 11 individuals)  
117 (see Table S1 for details). The "off" hours allowed the PTT to recharge the batteries and save  
118 energy. In five of the 10/48 birds the PTT activated whenever charged, even before the end of the 48  
119 hour "off" period. The PTTs with different duty cycles were almost equally distributed among  
120 capture sites (see Table S1). The data obtained through Argos in the period 28 December 2013 – 30  
121 June 2016 were stored and then filtered in Movebank ([www.movebank.org](http://www.movebank.org)) by means of the Hybrid  
122 Douglas Filter specifically developed for bird migration datasets (Douglas *et al.* 2012; see Table S2  
123 for details). The filter tagged as outliers a median of 5% of collected fixes per bird (*interquartile*  
124 *range*,  $IQR = 4-6\%$ , *range* = 2-11%). All Teal were followed for only one spring migration except  
125 for VEN05 and TUS04 that were tracked for two and three successive years, respectively (Fig. S2  
126 and S3). Unless stated otherwise, we considered only the first migration of these two birds to  
127 control for pseudoreplication (Hurlbert 1984).

128

## 129 **Data analysis**

130 Following release, all tagged birds stayed in their wintering areas for a period of time, moving short  
131 distances between successive locations (*median* = 0.9 km,  $IQR = 0.4, 1.9$  km, *range* = 0, 19.4 km).  
132 We identified the start of spring migration when a bird moved > 30 km in any direction with no  
133 return to the wintering site. The starting date of migration was defined as the mean date between the  
134 last location in the wintering area and the first location during migration. Given that ring-recoveries  
135 have shown that during the wintering period Teal can move for > 30 km within a relatively short  
136 time period (< 30 days; Brochet *et al.* 2009), the estimated starting date used in this paper might

137 underestimate the actual timing of spring migration, as it may refer to late wintering movements not  
138 related to migration. We assumed that a Teal completed its spring migration (CM Teal hereafter,  $n =$   
139 15) if: (1) it stopped in the same delimited area, moving very short distances between successive  
140 locations ( $< 4$  km), for more than one month between the end of April and June (see Guillemain &  
141 Elmberg 2014) or (2) its last locations were recorded during the breeding season (after the end of  
142 April) and in a plausible breeding area (see Guillemain & Elmberg 2014), in case the PTT stopped  
143 transmitting before the end of June. For CM Teal satisfying criterion (1), the arrival date at the  
144 breeding site was assessed as the day the Teal first reached the area where they stayed between the  
145 end of April and June. We have no information to assess whether the PTT of the remaining six  
146 individuals stopped working before they reached a plausible breeding area because of tag failure or  
147 bird mortality.

148

149           Because of the PTT duty cycles used, we could not identify stopovers lasting less  
150 than 48 h for all tracked birds, and so staging/stopover sites were defined as areas where Teals  
151 stayed for  $> 48$  hours and moving for  $\leq 30$  km between successive locations, and the geographic  
152 position of the stopover site was identified by averaging the coordinates of all locations assigned to  
153 that stopover area (van Wijk *et al.* 2012). It should be noted that the number of missed stopovers of  
154 1 or 2 days was probably low, as estimated by considering the five CM Teals tagged with 6/16 PTT  
155 (median = 1, range = 0 - 2).

156

157           Distances between successive stopovers were calculated by considering the shortest  
158 distance between consecutive stopover sites to account for the variable sampling effort among  
159 animals (i.e., different number of fixes/animal). It should be noted, however, that the difference  
160 between the distances measured in this way and the distances measured by considering the most  
161 accurate fix per duty cycle (following Hewson *et al.* 2016) was very small (ca. 1 km for most birds).  
162 The only exception to this pattern were LOM02 and LOM03 that made an extended back and forth  
163 movements to reach their first stopover site, which was located not far from the wintering area (Fig.  
164 S4).

165

166           For each CM Teal we counted the number of stopovers, the time spent in each  
167 stopover area, the distance travelled between successive stopovers, the total migration length (days)  
168 and travelled distance (as the sum of distances between all stopover sites) and the straightness index  
169 (Batschelet 1981), i.e. the ratio between the shortest distance between wintering and breeding site  
170 and the total distance travelled (see above) from the wintering to the breeding grounds. The index  
171 can range from 0 to 1, with values close to 1 indicating a nearly straight path. All distance

172 measurements were done using the orthodromic Vincenty ellipsoid method by means of the package  
173 *geosphere* 1.5-5 (Hijmans 2016) in R 3.4.0 (R Core Team 2017).

174

## 175 **Statistical analysis**

176 We investigated whether there was a site-specific effect on bird's weight and departure date, given  
177 the different latitudes and management policies at the capture sites. We then tested whether  
178 migration distance was correlated with the migratory strategy of tagged birds, in particular with the  
179 departure and arrival dates, number of days spent migrating, number of stopover sites used and the  
180 duration of the longest stopover. In the last four analyses, departure date was also included in the  
181 model as a covariate. We also investigated whether late-migrating birds tended to shorten stopover  
182 duration after controlling for the length of the migratory step immediately before the stopover, as a  
183 proxy of the energy consumed before the stopover. We also tested whether the length of a given  
184 migration step was affected by the duration of the previous stopover, used as a proxy of the amount  
185 of energy accumulated during stopover. Finally, we examined whether the overall number of  
186 stopover sites and the departure and arrival dates of migration were related to the duration of the  
187 longest stopover. All the analyses were performed by means of (Generalized) Linear Models or  
188 (Generalized) Linear Mixed Models using bird ID as random intercept, using the package *lme4* 1-  
189 1.13 (Bates *et al.* 2015) in R 3.4.0 (R Core Team 2017). The error distribution was chosen  
190 depending on the data to be analysed. Data exploration was carried out following the protocol  
191 described in Zuur and Ieno (2016). Overdispersion was checked by comparing residual deviance  
192 with residual degrees of freedom (for the GLM) or by using the function *dispersion\_glm* in the  
193 *blme4* 1.1 R-package (for the GLMM; Körner-Nievergelt *et al.* 2015); if the data were  
194 overdispersed we used the corresponding *quasi* distribution (for the GLM) or included an  
195 observation level random effect (GLMM; Harrison 2014). All predictors were standardized to  
196 improve the interpretability of regression coefficients (Schielzeth 2010). When explorative analyses  
197 provided some evidences of non-linear relationships, we included a quadratic term in the model. No  
198 model simplification was performed. Following Körner-Nievergelt *et al.* (2015), after fitting each  
199 model, we simulated 1000 values from the joint posterior distribution of the model parameters using  
200 the function *sim* of the R-package *arm* 1.9-3 (Gelman & Hill 2007; Gelman & Su 2016). The 2.5%  
201 and 97.5% quantiles of the simulated values were used as lower and upper limits of the 95%  
202 Credible Intervals (*95CrI*). (Pseudo)  $R^2$  were calculated using the R-package *MuMIn* 1.40.0 (Bartoń  
203 2017); for GLMM we reported the marginal  $R^2$ , which represents the variance explained by fixed  
204 factors only (Nakagawa & Schielzeth 2013). All the geographical analysis and plots were made  
205 using QGIS Essen 2.14 (QGIS Development Team 2015).

206



207

## 208 RESULTS

209

210 Teals captured in Veneto were heavier than those captured in the other two sites (linear model,  $N =$   
211  $21$ ;  $\beta_{\text{Veneto.vs.Tuscany}} = 60.5$ ,  $95CrI = 29.9, 91.2$ ;  $\beta_{\text{Veneto.vs.Lombardy}} = 102.3$ ,  $95CrI = 69.3, 134.5$ ;  $R^2_{adj} = 0.70$ ;  
212 Fig. 2), with a median for all captured birds of 337 g ( $IQR = 290 - 361$  g).

213

### 214 Course and timing of migration

215 The routes followed by the tracked Teals were all directed towards Central and Eastern Europe (Fig.  
216 1). The estimated median departure date from wintering grounds was 14 March ( $IQR = 15$  February  
217 - 02 April,  $N = 21$ ). There was a tendency for Teals captured in Veneto to depart earlier than those  
218 captured in Lombardy and in Tuscany (linear model,  $n = 21$ ;  $\beta_{\text{Veneto.vs.Tuscany}} = -27.1$ ,  $95CrI = -55.4$ ,  
219  $1.8$ ;  $\beta_{\text{Veneto.vs.Lombardy}} = -25.0$ ,  $95CrI = -59.1, 7.3$ ;  $R^2 = 0.11$ ; Fig. 2).

220

221 The proportion of CM birds belonging to the different sites is reported in Fig. S5;  
222 general information on spring migration statistics is reported in Table 2. Teals that completed spring  
223 migration (CM Teals) migrated for about 80 days ( $median = 77$  days) to cover more than 2500 km  
224 ( $median = 2739$  km). The total migratory speed was quite slow ( $median = 36$  km/day), but the  
225 active flight migration segments were covered at much higher speeds, up to 872 km/day ( $median =$   
226  $222.9$  km/day). Overall, Teals followed a relatively straight and direct route towards their breeding  
227 grounds (straightness index generally  $> 0.9$ ). The two birds tracked for more than one spring  
228 migration (Fig. S2 and S3), showed different patterns: VEN05 migrated to the same breeding site in  
229 two successive years following a very similar route, while TUS04 changed its breeding site between  
230 the first and the second year (distance between breeding site centroids: 629 km), returning to the  
231 same breeding area frequented during the second year also in the third year of tracking (Fig. S3). In  
232 the second year of tracking, the TUS04 PTT did not send data between 26 November 2014 and 6  
233 February 2015.

234

235 The onset of migration did not depend on the total migration distance (linear model,  
236  $N = 15$ ;  $\beta_{\text{migration.distance}} = -5.5$ ,  $95CrI = -19.4, 7.2$ ;  $R^2 = 0$ ), but when controlling for migration  
237 distance, the number of days spent on migration correlated with the start of migration, with late-  
238 departing birds migrating faster, and the effect was non-linear (linear model,  $n = 15$ ;  $\beta_{\text{departure.day.linear}} =$   
239  $-20.7$ ,  $95CrI = -30.5, -10.9$ ;  $\beta_{\text{departure.day.quadratic}} = 8.5$ ,  $95CrI = 0.19, 17.1$ ;  $\beta_{\text{migration.distance}} = 9.6$ ,  $95CrI =$   
240  $0.71, 18.4$ ;  $R^2 = 0.70$ ; Fig. 3).

241



242 The median arrival date to breeding ground for CM Teals was 20 May ( $IQR = 1$   
243 May - 5 June,  $n = 12$ ). The arrival to the breeding grounds was positively associated with the  
244 distance of migration, but not to the departure date of migration (linear model,  $n = 15$ ;  $\beta_{migration.distance}$   
245  $= 11.3$ ,  $95CrI = 1.4, 21.1$ ;  $\beta_{departure.day} = 7.2$ ,  $95CrI = -3.7, 17.7$ ;  $R^2 = 0.26$ ), i.e. birds arriving late to  
246 their breeding grounds not necessarily departed late from their wintering grounds, but usually  
247 migrated longer distances (Fig. S6).

248

### 249 **Stopover location and duration**

250 As reported in Table 2, CM Teals frequented a median of four stopovers lasting  $> 48$  h, whose  
251 spatial distribution is shown in Fig. 1. The number of used stopover sites did not depend on the  
252 departure day or on the migration distance (GLM with Poisson error distribution,  $n = 15$ ;  $\beta_{departure.day}$   
253  $= -0.02$ ,  $95CrI = -0.29, 0.24$ ;  $\beta_{migration.distance} = 0.16$ ,  $95CrI = -0.08, 0.43$ ;  $R^2 = 0.11$ ).

254

255 Stopover duration was affected by the interaction between the arrival day at the  
256 stopover site and the length of the migration step immediately before the stopover (GLMM with  
257 Poisson error distribution and bird and observation as random effects,  $n = 15$ ;  $\beta_{distance.before.stopover} =$   
258  $0.03$ ,  $95CrI = -0.16, 0.20$ ;  $\beta_{arrival.date.stopover} = -0.75$ ,  $95CrI = -0.94, -0.56$ ;  
259  $\beta_{distance.before.stopover*arrival.date.stopover} = -0.31$ ,  $95CrI = -0.49, -0.13$ ;  $SD_{bird.ID} = 0.33$ ;  $SD_{Observation} = 0.46$ ;  $R^2$   
260  $= 0.55$ ). Earlier stopovers were longer and their duration increased relative to the length of the  
261 migration step immediately before the stopover. For late stopovers the relationship was inverse and  
262 less strong (Fig. 4). The length of each stopover significantly affected the length of the following  
263 migration step (linear mixed model with bird as random effect,  $n = 15$ ;  $\beta_{stopover.length} = 189.9$ ,  $95CrI =$   
264  $95.2, 273.1$ ;  $SD_{bird.ID} = 18.0$ ;  $R^2 = 0.23$ ), i.e. longer stopovers were followed by longer flights before  
265 the next stop (Fig. S7).

266

267 All birds showed at least one stopover of  $\geq 10$  days and for most of them (11 out of 15)  
268 the longest stopover (hereafter: LS) lasted  $\geq 20$  days. Its duration strongly affected the overall  
269 migratory length, spanning over almost half of the total number of days spent on migration ( $median$   
270  $= 40\%$ ,  $IQR = 30\% - 60\%$ ,  $n = 15$ ). For most birds (13 out of 15), the LS occurred in the first half of  
271 their migratory journey, often at its very beginning (Fig. 5). The duration of the LS only marginally  
272 depended on migration distance, but it was inversely related to the departure day from wintering  
273 ground (linear model,  $n = 15$ ;  $\beta_{migration.distance} = 7.93$ ,  $95CrI = -2.33, 18.12$ ;  $\beta_{departure.day} = -10.73$ ,  $95CrI$   
274  $= -20.46, -0.86$ ;  $R^2 = 0.37$ ; Fig. 6). The overall number of stopover sites used was not affected by  
275 the duration of the LS (GLM with Poisson error distribution,  $n = 15$ ;  $\beta_{max.stopover.duration} = -0.03$ ,  $95CrI$   
276  $= -0.29, 0.21$ ;  $R^2 = 0$ ), i.e. Teals staying for longer at a single site were not characterized by a

277 smaller number of stops. The duration of the LS was also not significantly associated with the  
278 arrival to the breeding grounds (linear model,  $n = 15$ ;  $\beta_{\text{max.stopover.duration}} = 5.46$ ,  $95CrI = -6.30, 16.17$ ;  
279  $R^2 = 0$ ).

280

281

## 282 **DISCUSSION**

283

284 To our knowledge, this is the first satellite tracking study on the migration of Eurasian Teal  
285 wintering in Europe. Some Teals have been tracked in the past, but they were from the eastern  
286 portion of the distribution range of the species (see e.g. Gaidet *et al.* 2010, Takekawa *et al.* 2010,  
287 Iverson *et al.* 2011, Bridge *et al.* 2014) and no specific analysis regarding their movements was  
288 reported. While the migratory course and destinations of the species are quite well known thanks to  
289 the large number of ringing recoveries (Guillemain & Elmberg 2014, Guillemain *et al.* 2017), the  
290 present results add valuable information on several aspects of migration strategies such as timing,  
291 speed of travel and stopover length. As birds were tagged in three sites characterized by different  
292 management policies and two of them (TUS and VEN) are within areas hosting a Teal wintering  
293 population of national importance (Zenatello *et al.* 2014), our data are likely to be representative of  
294 the migratory behaviour of Teals wintering in Italy.

295

### 296 **Performances of the tracking system**

297 For 21 of the 29 tagged females we were able to determine the departure date for spring migration,  
298 and 15 of them were followed for at least the whole spring migration. Compared with studies on  
299 other species of Anatidae, this outcome was satisfactory, both considering the hunting pressure on  
300 this species (Guillemain & Elmberg 2014, Guillemain *et al.* 2016) and the high rate of equipment  
301 failures in wildfowl studies (see e.g. Miller *et al.* 2005, Haukos *et al.* 2006, Yamaguchi *et al.* 2008,  
302 van Toor *et al.* 2013, Gehrold *et al.* 2014). The impact of the extra weight/drag due to the tag, which  
303 likely affects survival and behaviour of tracked birds, cannot be dismissed (see Barron *et al.* 2010,  
304 Lameris & Kleyheeg 2017). A variety of tag effects, including lack of, has been reported for  
305 backpack attachments in wildfowl (Lameris & Kleyheeg 2017); only one published paper (Hupp *et al.*  
306 *et al.* 2015, on Northern Pintails *Anas acuta*) reported a delay in migration due to tagging, which  
307 however was not significant when considering the departure date..

308

### 309 **Migratory courses and timing of departure**

310 As expected considering the data from ringing recoveries (Spina & Volponi 2008, Guillemain *et al.*  
311 2009, Calenge *et al.* 2010) and isotope analyses (Guillemain *et al.* 2014), birds followed the Black

312 Sea-Mediterranean flyway. The plausible breeding sites of tagged Teals spread over a vast area,  
313 from central to North-Eastern Europe, even east of the Urals. In the two birds tracked for more than  
314 one year, VEN05 was faithful to its breeding site, while TUS04 moved between the first and the  
315 second year of tracking (Fig. S2). Even if based on two birds only, our data partially support the  
316 philopatry of this species reported in the literature (Guillemain & Elmberg 2014), while suggesting  
317 that Teal behaviour can be probably more flexible.

318

319 Most birds departed from wintering grounds between mid-February and March, i.e.  
320 well after the end of our capture effort and within the temporal window estimated from ringing  
321 recoveries for Teals wintering in Italy (Spina & Volponi 2008) and France (Guillemain *et al.* 2006,  
322 Caizergues *et al.* 2011). Birds from Veneto tended to be the first to leave their wintering location,  
323 and this was probably related to the hunting management of the site, where abundant food is  
324 provided until the end of the hunting season on 31 January. Afterwards, the high competition for a  
325 reduced amount of resources would have urged at least a fraction of birds to leave the area.

326

### 327 **Migration speed and stopover pattern**

328 The actual speed of migration recorded in our sample was quite variable but was often above the  
329 speeds reported for the species estimated using ringing data (Clausen *et al.* 2002, Guillemain &  
330 Elmberg 2014). The maximum speed recorded (872 km/day), however, was below the record of  
331 1285 km/day reported by Clausen *et al.* (2002) for an autumn migrating radio-tagged Teal. The total  
332 migratory speed was below the theoretical overall upper speed limit for a flapping flying bird of ~  
333 0.3 kg (see Hedenström & Ålerstam 1998); this speed was rather slow also compared to other birds  
334 of similar size (see Nilsson *et al.* 2013), especially considering that, according to migration theory  
335 (Kokko 1999), spring migration should be faster than autumn migration (but see Nilsson *et al.*  
336 2013, Kölzsch *et al.* 2016).

337

338 The slow total migratory speed of tracked birds was mainly due to the long time  
339 spent in stopover areas especially at the very beginning of migration. Given that several studies  
340 (reviewed in Guillemain & Elmberg 2014) indicate that Teals are income rather than capital  
341 breeders (Arzel *et al.* 2007), it seems unlikely that these stops were used by birds to accumulate  
342 energy reserves for the next breeding season. Long stops are not uncommon among spring  
343 migrating dabbling ducks (e.g. North American Pintails, Miller & Takekawa 2005).

344

345 As stops of several weeks often characterise a staging strategy of migration, i.e.

346 when birds store fuel before crossing an ecological barrier (Warnock 2010), it could be  
347 hypothesized that Teals also take advantage of these long stops to accumulate energy before a long  
348 non-stop flight. This hypothesis seemed supported by the significant positive relationship between  
349 the length of the stopover and the distance of the successive flight (Fig. S7), although it does not  
350 appear that tracked Teals had to face significant ecological barriers during their journeys. Also, the  
351 long distance of the non-stop flights after stopovers might be biased because short stops may have  
352 remained undetected due to the PTT duty cycles (but see Methods). Actually, some wildfowl  
353 migrating overland are known to follow a stepping-stone strategy, taking advantage of the food they  
354 find *en route* (Viana *et al.* 2013). The few available data suggest that Teals do not optimize their  
355 migration schedule to maximize food availability at spring (and autumn) stopover sites (Arzel &  
356 Elmberg 2004, Arzel *et al.* 2008), which seems to contradict the need of high fuelling rate requested  
357 for a true staging strategy.

358  
359 Even though we have no information regarding fuelling rates at the stopover sites  
360 we have identified, it is known that the time spent foraging by Teals in early spring is relatively  
361 short and it is unlikely that they increase body reserves much before the next departure (Arzel *et al.*  
362 2007). The weight of wintering Teals increases noticeably in mid-winter and then declines into early  
363 March (Fox *et al.* 1992, Guillemain & Elmberg 2014), and it seems unlikely that migrating birds  
364 accumulate again a large amount of reserves along the route after having lost it just before  
365 departing. Teals might have to move from their previous wintering area because of a decrease in  
366 food availability, having then to wait to avoid the high individual costs of early arrival to the  
367 breeding grounds, as demonstrated for other Anseriformes (see Kölzsch *et al.* 2016 and references  
368 therein). The total length of migration in birds departing later was shorter after controlling for the  
369 distance of migration (Fig. 3), but birds departing first did not arrive earlier to their breeding  
370 grounds. This suggests that some birds moved earlier from wintering sites because they were  
371 searching for food resources and not because they were pressed by the urge of arriving sooner to  
372 their destination.

373  
374 Birds showing prolonged stopovers departed earlier from the wintering site than  
375 others (Fig. 6), either because they were forced to leave it due to resource depletion or because  
376 previously inaccessible resources (e.g. because of ice cover) became available elsewhere in late  
377 winter. For instance, birds from the Veneto capture site may have started migration when the  
378 artificial provision of food strongly decreased, and they tended to be the first to leave their  
379 wintering site, also showing the most prolonged and earliest longest stopover (LS).

380

381                   Regardless the reason why the majority of tracked Teals spent several weeks in  
382 single sites, it seems that these stopovers play an important ecological role, because some of them  
383 are used by different birds and also because two of three journeys of birds with multiple years used  
384 the same sites. Eleven of the 15 LS identified for Teals that completed spring migration (CM Teals)  
385 were included in a Natura2000 site ([www.eea.europa.eu/data-and-maps/data/natura-8](http://www.eea.europa.eu/data-and-maps/data/natura-8); Fig. S8).

386  
387                   As recorded for other species (e.g. Eurasian Woodcocks *Scolopax rusticola*; Arizaga  
388 *et al.* 2014), stopover duration tended to be shorter when close to the breeding site (Fig. 5),  
389 indicating that competition for breeding sites might be an important driver of the migratory  
390 behaviour of the species. The short stopover duration in the latter part of the trip might be also due  
391 to the increased foraging activity during the final migration steps (Arzel *et al.* 2007).

392  
393                   To conclude, the present findings shed light on Eurasian Teal spring migration  
394 providing relevant information to define their migratory phenology and strategies at the individual  
395 level. As suggested by Stafford *et al.* (2014), to identify the key factors possibly affecting Teal  
396 migration, it will be fundamental to integrate the knowledge on individual movements with  
397 environmental data. This will provide an overall understanding of the biology of this species and  
398 address further research and management issues at the continental scale.

399

400

401 This research was funded by the hunting associations Associazione Cacciatori Migratori Acquatici and Federazione  
402 Italiana della Caccia (National Section; Regional Sections: Lombardia, Marche, Toscana; Provincial Sections: Brescia,  
403 Livorno, Lucca, Pisa), by several hunting districts (A.T.C., Ancona 1, Brescia, Foggia, Macerata 2, Pesaro 2, Ravenna  
404 2, Rovigo 3, Venezia 5), by Associazione “La Gru”, CST Marche, Ente Produttori Selvaggina Veneto, and Sig. F.  
405 Gandolfi. For a detailed list, please see: <http://www.progettoanatisatellitare.com>.

406 We would like to thank all the people who helped us in the field: F. Avogadro di Valdenigo, M. Basile, D. Bianchi, C.  
407 Biondo, F. Bosio, F. Budrago, C. Caccamo, F. Carpita, F. Chini, G. Cirani., P. Dall’Antonia, S. del Carlo, A. Labate, F.  
408 Licata, A. Lucchetta, L. Marcato, G. Marzano, R. Mencacci, A. Piccinotti, A. Salvati, N. Semperboni, P. Tinti, A.  
409 Valfrido. Thanks in particular to the Migliarino-San Rossore-Massaciuccoli Regional Park, the AZV Valle Morosina –  
410 Ghebo Storto Estate, and to the ringers: A. Galardini, R. Gambogi, G. La Gioia, A. Mazzoleni, L. Sattin.  
411 Prof. A. Massolo kindly revised the English wording. The manuscript was greatly improved thanks to the comments by  
412 Dr. M. Guillemain, Prof. A.D. Fox and two anonymous reviewers.

413 All protocols performed in studies involving animals comply with the ethical standards and Italian laws on animal  
414 welfare. All procedures involving animals were approved by the Italian Istituto Superiore per la Protezione e la Ricerca  
415 Ambientale (ISPRA).

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640 **SUPPORTING INFORMATION**

641

642 Additional Supporting Information may be found in the online version of this article:

643

644 **Table S1.** Summary information of tracked Teals

645 **Table S2.** Settings used for the Movebank's Hybrid Douglas Filter

646 **Figure S1.** Details of the attachment procedure: a) checking the position of the harness  
647 before completing the deployment; b) harnessed teal ready to be released.

648 **Figure S2.** Spring migration of VEN05 in two successive years. The dot shows the  
649 breeding ground and the star the wintering area.

650 **Figure S3.** Spring migration of TUS04 in three successive years

651 **Figure S4.** Spring migration of LOM02 and LOM03.

652 **Figure S5.** Proportion of tagged birds belonging to the three capture sites which completed  
653 spring migration

654 **Figure S6.** Arrival day in relation to (a) departure day and (b) migration distance.

655 **Figure S7.** Distance travelled after a stopover in relation to stopover duration

656 **Figure S8.** Locations of the longest stopover for each Teal with a completed migration in  
657 relation to Natura2000 sites

658

659 **Table 1.** Descriptive statistics for each Teal migratory journey. The asterisks indicate data from the second or third year  
660 of tracking for teal TUS04 and VEN05. The second year for TUS04 is missing because the PTT did not send data from  
661 26 November 2014 to 06 February 2015. 1Y: 1<sup>st</sup> calendar year (Euring age code 3); 2Y: 2<sup>nd</sup> calendar year (Euring age  
662 code 5); Ad: > 2<sup>nd</sup> calendar year (Euring age code 6). Teal with no statistics did not complete their migration and were  
663 taken into consideration only for the analysis of the starting date of migration.

664

ID teal	Age	Starting date of migration	Arrival date in breeding grounds	Migration length (days)	Number of stopovers	Mean stopover permanence (days)	Distance travelled per day (km)	Days of flight	Straightness Index
LOM02	Ad	06 Mar	23 May†	78	3	21	12	14	0.94
LOM03	2Y	11 Mar	10 May†	60	6	9	47.3	7	0.97
LOM04	Ad	13 Mar	-	-	-	-	-	-	-
LOM05	Ad	09 Mar	26 May	47	4	6	59.2	22	0.89
TUS01	1Y	03 Apr	-	-	-	-	-	-	-
TUS04	2Y	02 Feb	30 May	117	4	26	36.3	14	0.89
TUS04***	Ad	03 Mar	18 May	45	3	9	95.1	18	1
TUS06	1Y	06 May	-	-	-	-	-	-	-
TUS09	2Y	27 Mar	12 Jun	77	4	15	42.9	15	0.97
TUS10	Ad	09 Apr	-	-	-	-	-	-	-
VEN01	2Y	06 Feb	30 Apr	83	5	14	16.4	14	0.80
VEN02	2Y	06 Feb	10 Jun	124	5	21	30.5	17	0.98
VEN03	Ad	31 Mar	-	-	-	-	-	-	-
VEN04	Ad	09 Feb	31 May†	111	7	13	25.3	20	0.88
VEN05	Ad	15 Mar	04 Jun	81	6	11	40.5	13	0.95
VEN05**	Ad	02 Mar	22 May	81	5	15	39.9	8	0.96
VEN05***	Ad	18 Mar	-	-	-	-	-	-	-
VEN06	Ad	16 Feb	14 May	87	3	25	27.1	12	0.90
VEN07	Ad	23 Jan	-	-	-	-	-	-	-



<b>VEN09</b>	2Y	03 Mar	12 May	70	6	10	39.1	7	0.94
<b>VEN10</b>	2Y	20 Feb	28 Apr	67	2	32	26	2	0.94
<b>VEN12</b>	Ad	18 Mar	02 May	45	3	13	43.1	5	0.84
<b>VEN13</b>	Ad	15 Mar	09 Apr	25	2	9	68.2	6	0.98
<b>VEN17</b>	2Y	21 Apr	20 Jun	60	4	13	29.9	9	0.95

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† Date of the last location recorded

665 **Table 2.** Summary statistics for the Teal with a completed spring migration journey at their first year of tracking ( $n =$   
666 15). The total speed of migration is the measure of the total distance travelled divided by the migration length, whereas  
667 the actual speed of migration is the result of the total distance travelled between successive stopovers divided by the  
668 travelling days.

669

	<b>Median</b>	<b>Interquartile range</b>	<b>Range</b>
<b>Number of stopover</b>	4	3-6	2-7
<b>Total distance travelled (km)</b>	2739	1768-3060	940-4252
<b>Migration length (days)</b>	77	60-85	25-124
<b>Travelling days</b>	13	7-15	2-22
<b>Total speed of migration (km/day)</b>	36.3	26.6-43.0	12.1-68.2
<b>Actual speed of migration (km/day)</b>	222.9	168.5-345.8	67.2-871.8
<b>Travelling days/migration length</b>	0.15	0.12-0.18	0.03-0.47
<b>Time at stopover/time airborne</b>	5.7	4.6-7.5	1.1-32.5
<b>Straightness index</b>	0.94	0.89-0.96	0.80-0.98

670

## 671 Captions

672

673 Figure 1. Capture sites, migratory routes and stopover location for Teals with a completed spring migration journey  
674 migrating over short (a) or long distances (b). The different symbols indicating capture sites (TUS = Tuscany, LOM =  
675 Lombardy, VEN = Veneto) indicate different management policies: triangle = hunting area; diamond = protected area;  
676 star = hunted area with food being provided throughout the hunting season. The small dark dots show the end of the  
677 spring migratory route. The size of the dots along the migratory route is proportional to the number of days the teal  
678 remained in the stopover area. The cross shows the first fix of TUS04 during the second year of tracking, whose PTT  
679 did not send data between 26 November 2014 and 6 February 2015.

680 Figure 2. Weights (a) and departure dates (b; Julian day, 1 = 1<sup>st</sup> of January) of captured teals grouped according to their  
681 age (1Y: 1<sup>st</sup> calendar year; 2Y: 2<sup>nd</sup> calendar year; Ad: >2<sup>nd</sup> calendar year). The lines indicate the median for each of the  
682 three capture sites. In (b) only the first migration was considered for TUS04 and VEN05.

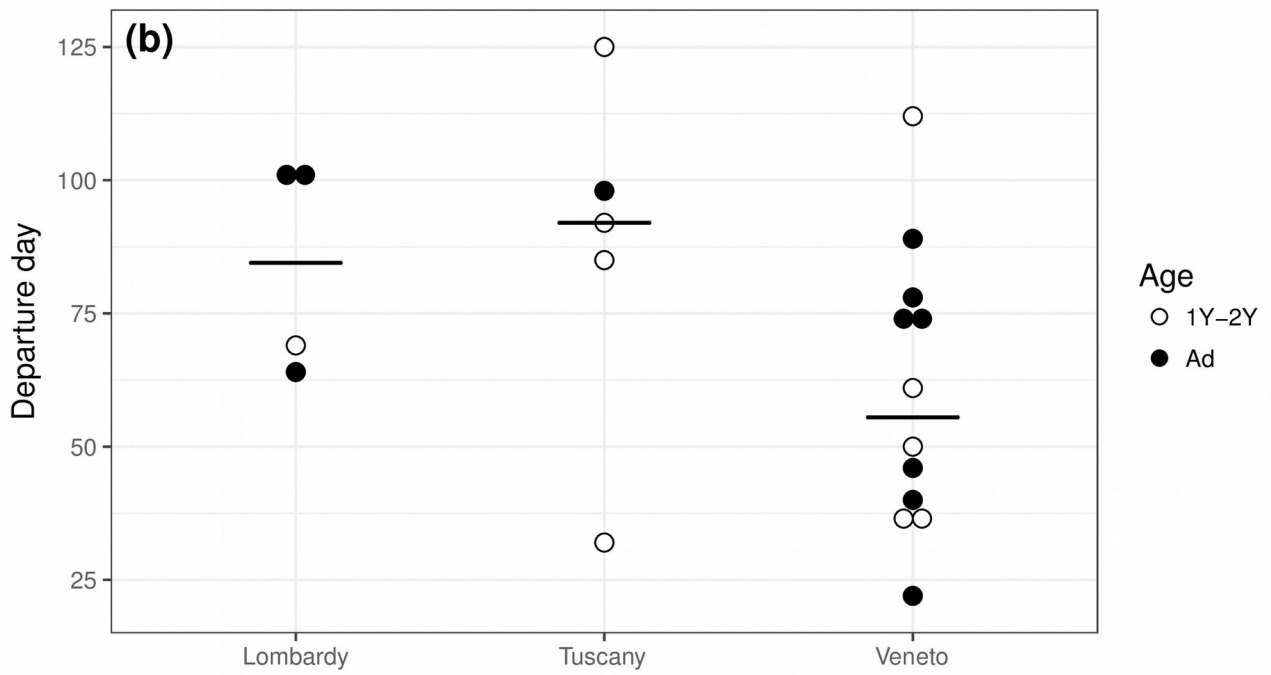
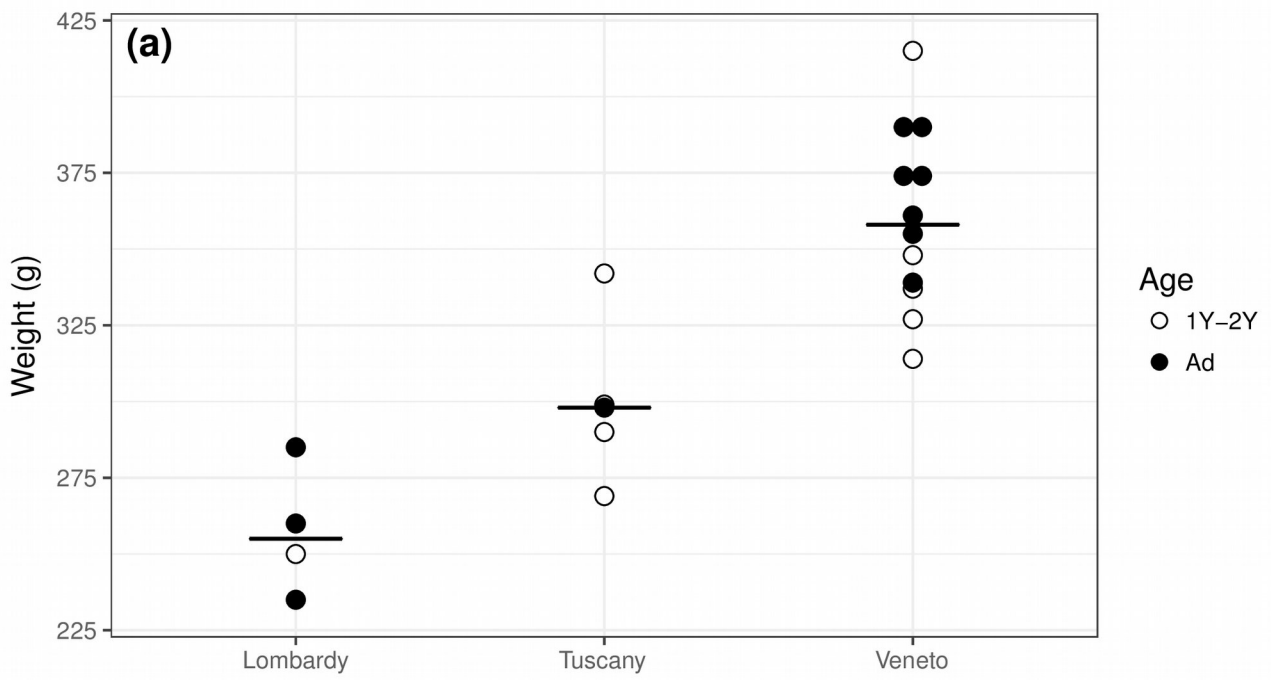
683 Figure 3. Migration length in relation to departure day (a) and migration distance (b). Open dots: first or second  
684 calendar year birds; filled dots: adult birds. Bold lines: fitted lines of the linear model  $migration.length \sim$   
685  $departure.day.linear + departure.day.quadratic + migration.distance$ ; dotted lines: 95% credible intervals.

686 Figure 4. Predicted effect of the length of the migratory step before stopover on stopover duration for different arrival  
687 days at stopover site as derived from the model:  $stopover.length \sim distance.before.stopover + arrival.date.stopover +$   
688  $distance.before.stopover * arrival.date.stopover + (1|bird.ID) + (1|observation)$ . Variables were standardized before the  
689 analysis (actual mean and *SD* are reported in brackets). For earlier stopovers ( $-1$  *SD* arrival day; black line) the  
690 relationship between stopover duration and previous migratory step is positive, whereas for late stopovers the  
691 relationship is null (average arrival day; grey line) or even negative ( $+1$  *SD* arrival day; light grey line).

692 Figure 5. Distribution of stopover duration for the 15 Teals with a completed spring migration journey. Dots are filled  
693 according to the fraction of covered route before the stopover.

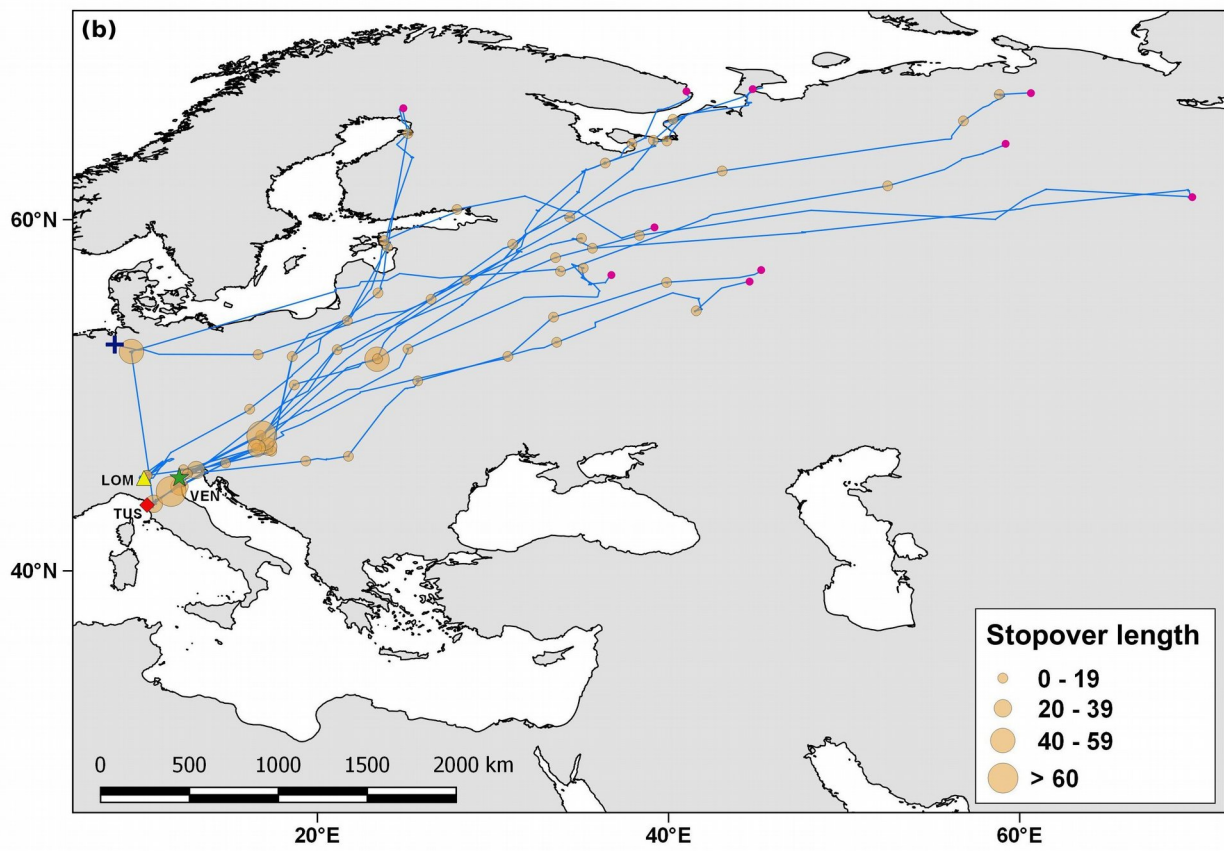
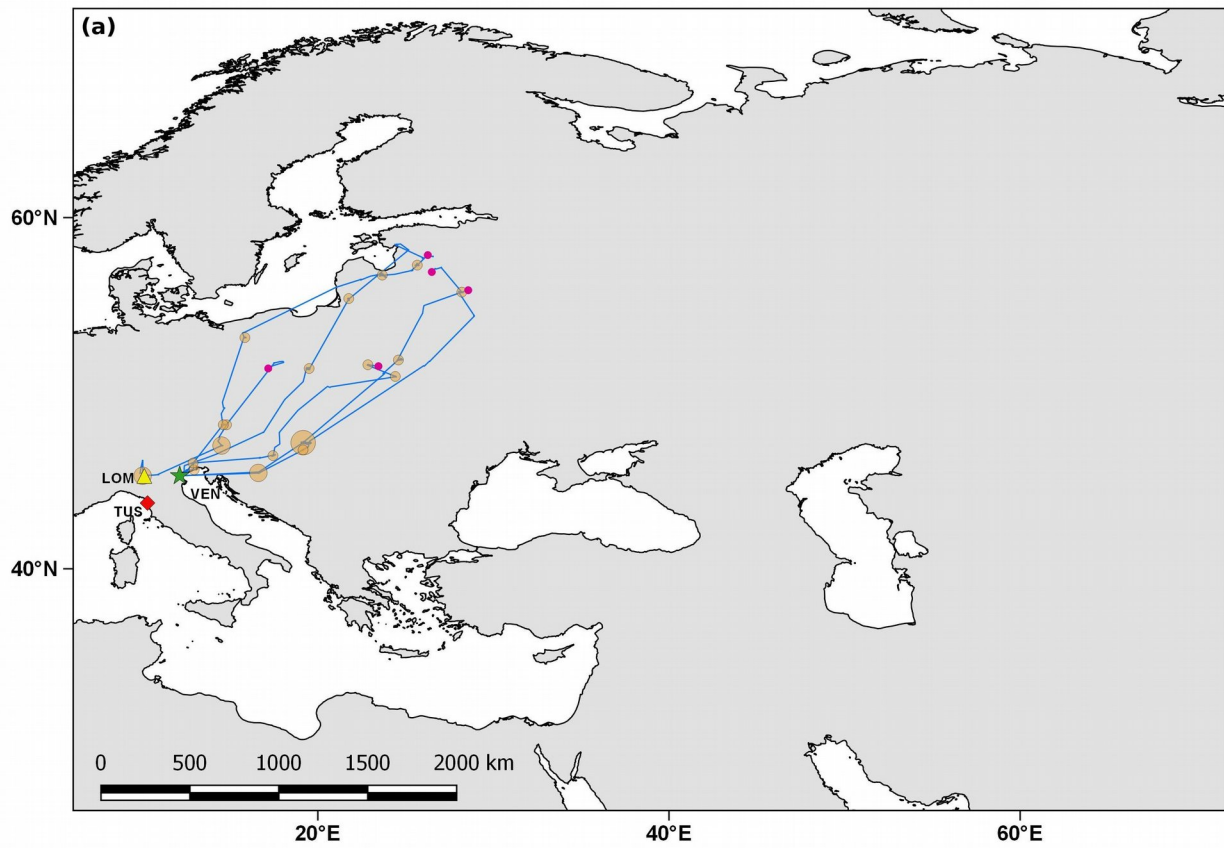
694 Figure 6. Duration of the longest stopover (LS) in relation to departure day (a) and migration distance (b). Open dots:  
695 first or second calendar year birds; filled dots: adult birds. Bold lines: fitted lines of the linear model  
696  $max.stopover.duration \sim departure.day + migration.distance$ ; dotted lines: 95% credible intervals.

697



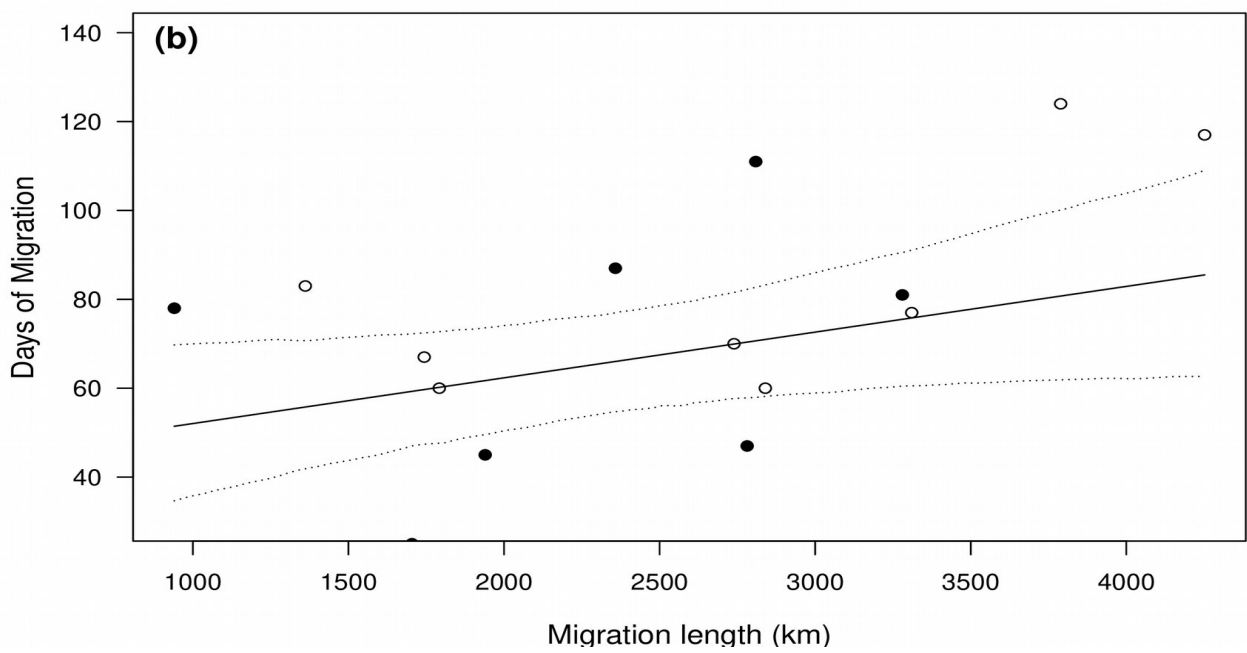
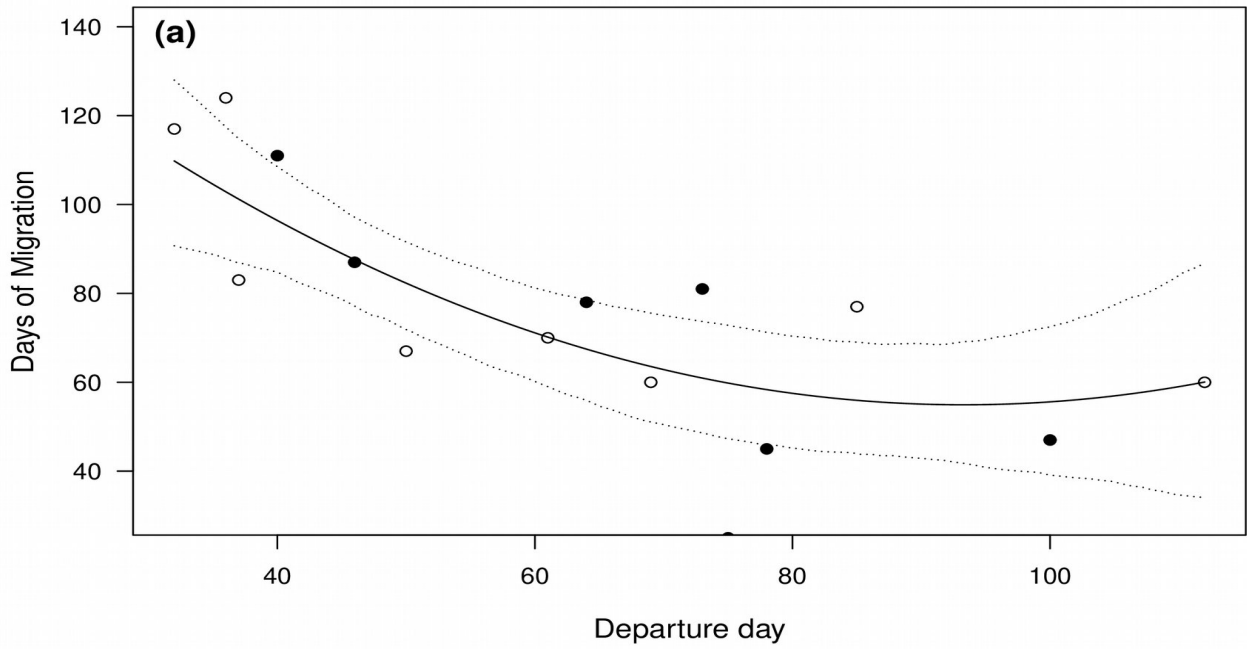
698 Fig. 1

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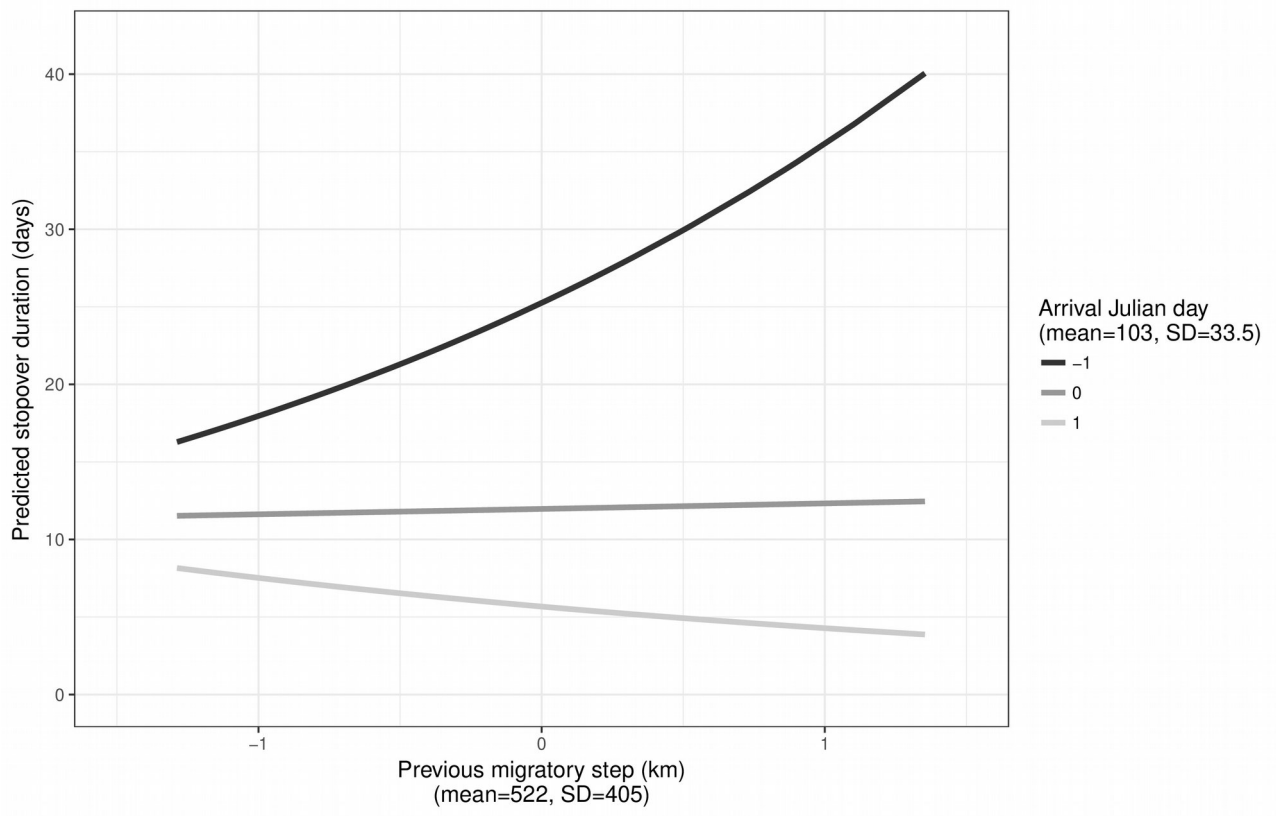
700 Fig. 2

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702 Fig. 3

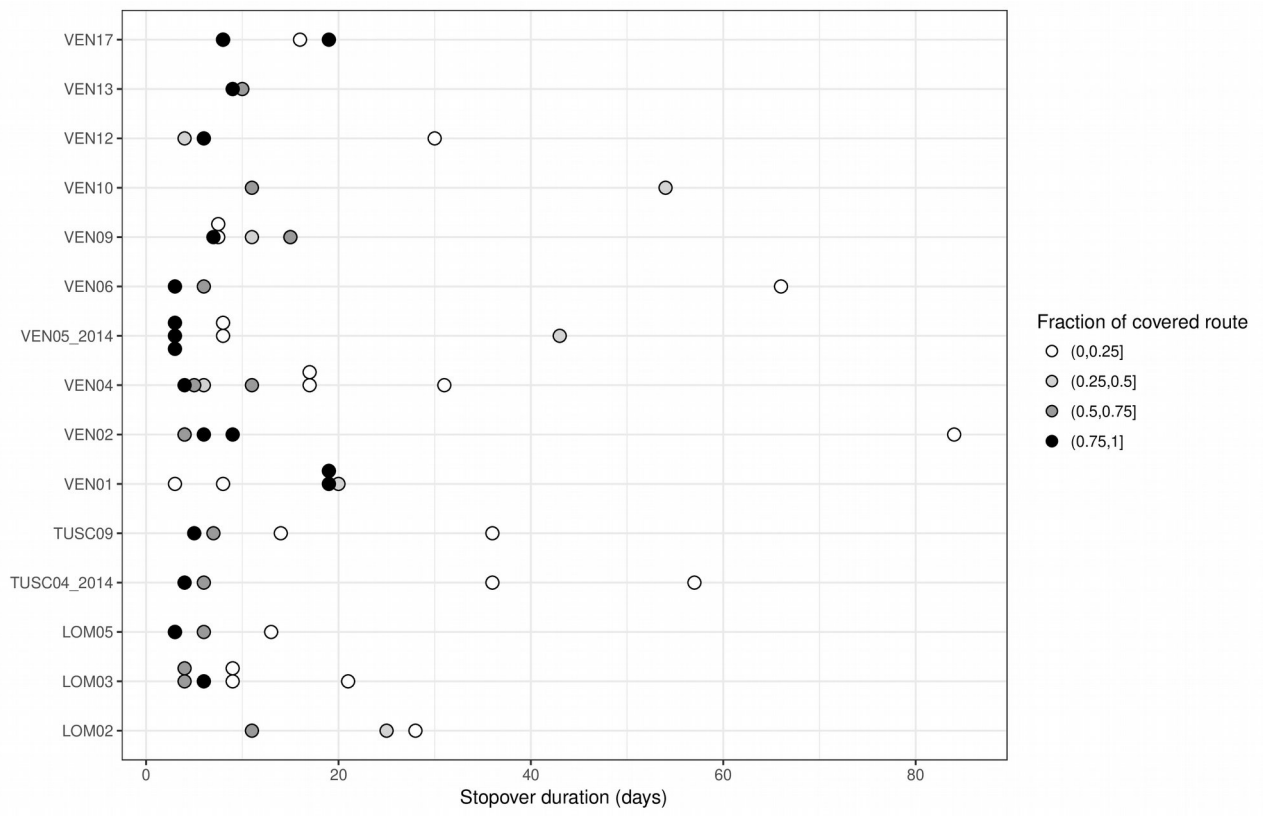
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704 Fig. 4

705





706 Fig. 5

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