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3 **Spring migration strategies of Whinchat *Saxicola rubetra* when successfully crossing**  
4 **potential barriers of the Sahara and the Mediterranean Sea**

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19 **Keywords:** geolocator, migrant, migratory capability, migration speed, migration stop-overs.

20 The flexibility for migrant land birds to be able to travel long distances rapidly without stop-overs, and  
21 thus to cross wide inhospitable areas such as deserts and oceans, is likely to be a major determinant  
22 of their survival during migration. We measured variation in flight distance, speed, and duration of major  
23 stop-overs (more than two days), using geolocator tracks of 35 Whinchats *Saxicola rubetra* that  
24 migrated successfully from central Nigeria to Eastern Europe in spring, and how these measures  
25 changed, or depended on age, when crossing the barriers of the Sahara or the Mediterranean Sea.  
26 Thirty-one percent of Whinchats crossed at least the Sahara and the Mediterranean before a major  
27 stop-over; 17% travelled over 4,751 km on average without any major stop-overs. Flight distance and  
28 speed during, and duration of major stop-overs after, crossing the Mediterranean Sea were  
29 indistinguishable from migration over Continental Europe. Speed during a migration leg was lowest  
30 crossing Continental Europe and fastest, with longer duration major stop-overs afterwards, when  
31 crossing the Sahara, but there was much individual variation, and start date of migration was also a  
32 good predictor of stop-over duration. As the distance travelled during a leg increased, so major stop-  
33 over duration afterwards increased (1 day for every 1000km), but the speed of travel during the leg had  
34 no effect. There were no differences in any migration characteristics with age, other than an earlier start  
35 date for adult birds. The results suggest that adaptive shortening or even dropping of daily stop-overs  
36 may occur often, allowing rapid, long-distance migration at the cost of major stop-overs afterwards, but  
37 such behaviour is not restricted to or always found when crossing barriers, even for birds on their first  
38 spring migration. The results may highlight the importance of stop-over sites rather than barrier width  
39 as the likely key component to successful migration. Individual variation in spring migration may indicate  
40 that small passerine migrants like Whinchats may be resilient to future changes in the extent of barriers  
41 they encounter, although this may not be true of first autumn migrations or if stop-over sites are lost.

42

43 The capability for migrant land birds to travel long distances without stop-overs, and thus to cross  
44 unsuitable or hostile habitats such as deserts and oceans, is likely to be a major determinant of their  
45 survival during migration (Newton 2008). Such 'migratory barriers' may act as a constraint to migration,  
46 selecting for specialist physiology or behaviour (i.e. migratory capability) during migratory flights  
47 (Lockwood *et al.* 1998, Mettke-Hofmann & Greenberg 2005, Vagasi *et al.* 2016), because stop-overs  
48 are unavailable or unsuitable. For example, the crossing of migratory barriers such as the Sahara has  
49 been associated with high mortality risk for a number of species, and migrants may mitigate this risk by  
50 shortening the period they spend migrating over barriers through faster migration or by avoiding them  
51 where possible (Klaassen *et al.* 2014, Lok *et al.* 2015). This may be particularly true for small passerine  
52 migrants, where billions of birds with relatively limited capacity for fuel storage (Alerstam *et al.* 1990,  
53 Alerstam *et al.* 2003) migrate 5 – 10,000 kilometres twice annually in the Palearctic-African and Nearctic  
54 migration flyways, crossing the Sahara desert and the Mediterranean Sea (Hahn *et al.* 2009), or the  
55 Caribbean Sea respectively (Faaborg *et al.* 2010). The potential for these barriers in the flyways to  
56 become more significant is increasing with climate and habitat change, as the width of habitat unsuitable  
57 for migratory fuelling or refuelling increases (Doswald *et al.* 2009). Furthermore, the capacity of migrants  
58 to adapt to such changes may be confounded by concurrent shifts in range and migratory timings due  
59 to changes in climate and habitat suitability (Walther *et al.* 2002, Both *et al.* 2006, Chen *et al.* 2011),  
60 and such shifts may change the route and hence length of migration, potentially reducing  
61 fitness/survival. There is therefore an urgent need to understand the migratory capability of small  
62 passerine migrants, and how flexible they can be when crossing potential migratory barriers, particularly  
63 as populations of many Afro-Palearctic long-distance migrant bird species have been declining for the  
64 last 50 years (Sanderson *et al.* 2006, Vickery *et al.* 2014).

65 Testing migratory capability in small passerines is currently mostly limited to data from  
66 successful migrations. Passerines are generally too small to track except by archival tags such as  
67 geolocators where the bird must be recaptured to download its movement data (Bridge *et al.* 2013).  
68 Consequently, migratory data is only available for individuals that have successfully made two  
69 migrations (from breeding to non-breeding location and back, or vice-versa). Any individuals that used  
70 migration strategies that failed do not contribute data: larger birds that can be satellite tagged, for  
71 example, and so providing information of location of death, have shown that this mortality during  
72 migration may be particularly associated with crossing barriers like the Sahara (Strandberg *et al.* 2010)

73 or the Mediterranean sea (Oppel *et al.* 2015). A further limitation of geolocator tags is that stop-over  
74 durations of less than two days cannot realistically be measured, so geolocators can only indicate major  
75 stop-overs between migratory legs. Nevertheless, data from successful migrants with geolocators can  
76 still reveal constraints associated with barriers if there are particular migration behaviours associated  
77 with them.

78         Here, we define a migratory barrier as an area where stop-over options are decreased, but  
79 barriers are not absolute and their biological effect will depend on their width (Henningsson & Alerstam  
80 2005), the degree of wind-assistance during crossing (Gill *et al.* 2009), plus the number and quality of  
81 suitable stop-overs both within barriers and before and after them. Passerine migrants are assumed to  
82 migrate nocturnally and then to rest and refuel if possible during the following day, even when crossing  
83 a desert (Bairlein 1988, Backman *et al.* 2017), but where there are few or no suitable areas available  
84 for refuelling we might expect an increasing proportion of the day spent flying, and even continuous 24  
85 hour migration (Biebach 1995, Schmaljohann *et al.* 2007, Adamik *et al.* 2016). Furthermore, it is unlikely  
86 that short stopovers in inhospitable areas will provide adequate fuelling opportunities for significant  
87 onward migration. If areas such as the Sahara and the Mediterranean do represent a barrier - a  
88 constraint for migration selecting for enhanced migratory capability - we might then expect three  
89 migratory characteristics to be associated with them: 1) We expect maximum flight distance of  
90 individuals to match or exceed barrier widths, and to be greater than flight range in areas where major  
91 stop-overs are possible, such as Continental Europe; 2) We expect rapid crossings at maximum flight  
92 speed over barriers because stop-overs of any duration are limited (over the Sahara) or not possible  
93 (over the sea); and, 3) We then consequently expect stop-overs after crossing the Sahara or the sea to  
94 be longer, reflecting the increased fuel use during extended and rapid barrier crossing (Hedenstrom &  
95 Alerstam 1997, Schmaljohann & Eikenaar 2017).

96         We might also expect variation according to age and experience (Cresswell 2014, e.g. see  
97 Perdeck 1967, Thorup *et al.* 2007, Rotics *et al.* 2016): those individuals that have previously migrated  
98 in spring could have some knowledge of prevailing winds, routes and stop-overs resulting in differences  
99 in the distances, speed during a migration leg and duration of stop-overs compared to first year birds.  
100 We also then might expect that: 4) first year birds will show shorter and slower migration legs and have  
101 longer stop-over periods after crossing barriers compared to adults.

102 Here, we test these four predictions by comparing flight distance, speed, and duration of major  
103 stop-overs (more than two days), and how this varied with age, for migratory legs across the Sahara,  
104 Mediterranean Sea and Continental Europe, in Whinchats *Saxicola rubetra* tagged with geolocators,  
105 migrating from West Africa to Eastern Europe during two spring migrations.

106

## 107 **METHODS**

108

### 109 **Study system**

110 The study took place between February 2013 and November 2013 (Year 1) and February 2014 until  
111 April 2015 (Year 2) on the Jos Plateau in the guinea savannah zone of central Nigeria, West Africa  
112 (N09°53', E08°59', approximately 1250 m altitude). Whinchats were captured within an area of  
113 approximately 5 x 8 km; full site details are described in Blackburn and Cresswell (2016b). Capture  
114 areas were principally open scrubland with varying degrees of habitat degradation from human  
115 habitation, arable farming and livestock grazing, the latter increasing in intensity over the dry season  
116 (see Hulme & Cresswell 2012, Blackburn & Cresswell 2015). The study area represents typical non-  
117 breeding habitat for this species in the region (open savannah) and has a high density of Whinchats.  
118 Whinchats in this study were caught with spring traps and mist nets in late February and March in 2013  
119 or 2014 (birds in 2014 were on average tagged  $10.3 \pm 3.3$  se days earlier than in 2013,  $F_{1,27} = -3.2$ ,  $P$   
120  $= 0.004$ ). Birds were aged and sexed (Jenni & Winkler 1994), ringed with unique combinations of colour-  
121 rings, and fitted with a geocator. We deployed 49 and 130 geolocators, in Year 1 and Year 2  
122 respectively, fitted using leg-loop 'Rappole-Tipton' (also called backpack) harnesses. Full details of tag  
123 and harness design are given in Blackburn *et al.* (2016). Tags weighed on average 0.63 g (0.01 se),  
124 representing 4.1 % of average body mass, and had no effect on survival (Blackburn *et al.* 2016).  
125 Attempts were made to recapture any returning tagged bird resighted in the following winter. Upon  
126 recapture, geolocators were removed by cutting the harness and birds were released unharmed after  
127 briefly assessing body condition (see Blackburn *et al.* 2016). Only one spring migration was recorded  
128 for each individual (i.e. no repeated tracks).

129

130

131 **Data processing**

132 Whinchat location data (and so their speed and duration of migration) were obtained from geolocators,  
133 which record the time of sunrise and sunset so allowing location to be determined on a scale of about  
134 100 – 500 km, subject to assumptions of the sun elevation angle and to imprecision due to shading  
135 (Fudickar *et al.* 2012, McKinnon *et al.* 2012). Sun elevation angle is unknown unless location is known  
136 (and vice versa), but a sun elevation angle must be used to calculate latitude (to determine effective  
137 sunrise). Here, we take the approach of using the best information possible to estimate sun elevation  
138 angle (see below), but also use single mid-values of sun elevation angle applied to all birds. This uses  
139 the logic that although we may not know the correct sun elevation angle for a single bird, we assume  
140 any individual has an equal chance of having a lower or higher sun elevation value than the chosen  
141 one, and so that errors are normally distributed. The minimum sun elevation angle we observed was  
142 close to -2, and the distribution of sun elevation angles calculated from the wintering ground, from the  
143 known location where each individual was tagged, was approximately normal, Shapiro-Wilk normality  
144 test,  $n = 35$ , mean =  $-4.55 \pm 0.10$  se,  $W = 0.96$ ,  $P = 0.26$ ). If errors are normally distributed, the use of  
145 a single sun elevation angle assumption prevents systematic bias, so that averaging across individuals  
146 should give true means with respect to distance travelled and speed, even if there is uncertainty about  
147 where any individual started or finished its migration leg. We then also varied the mean value of SEA  
148 used to investigate how sensitive the results are to which single average we use for all individuals (see  
149 below). Furthermore, our data uniquely comes from birds tagged initially on their non-breeding ground  
150 in West Africa, about 500 kilometres south of the Sahara, just before spring migration, so greatly  
151 reducing the uncertainty about their starting place and time with respect to crossing the Sahara, as well  
152 as precision of geolocator locations (McKinnon *et al.* 2012). We concentrate on spring migration only  
153 because this provides the most certain data to assess barrier crossing and because most autumn tracks  
154 occur during the equinox period when latitude cannot be calculated.

155         Raw data were downloaded, viewed and preliminarily cleaned using the BASTrack software  
156 suite (British Antarctic Survey, Cambridge, UK; see Fox 2010 for an overview of the following  
157 processes). We adjusted for clock drift, assuming that any drift was linear. We used the Transedit2  
158 software that is part of the BASTrack software to view raw data as light curves over time. We used our  
159 minimum observed value of -2 to define sunrise. False twilight events due to shading from weather or  
160 vegetation were identified and removed with the 'minimum dark period' filter (we used 4 hours), which

161 removes any impossible sunrise and sunset events (for a review and exploration of the effects of  
162 enviromental factors on geolocator data, see Lisovski *et al.* 2012). Data were then visually inspected to  
163 ensure that only one sunrise and sunset occurred within any 24-hour period.

164 Further analyses were then carried out using R 3.2.3 (R Development Core Team 2014). We  
165 used the LoessFilter in the R package 'GeoLight' (Lisovski & Hahn 2012) to validate twilight events and  
166 identify those influenced by shading events at dawn and dusk: a polynomial regression of twilight events  
167 identified residuals that were greater than three times the interquartile range and are therefore likely to  
168 be erroneous (Lisovski & Hahn 2012). Identified outliers were checked within the original data and were  
169 retained because large movements resulting from migration were often incorrectly identified as outliers.

170 Because conditions away from the wintering grounds are unknown, we used four different  
171 values of sun elevation angle (SEA value) to calculate latitude: note results do not change depending  
172 on which set of SEA values we used. First, we used a sun elevation angle of -4.5 for all loggers in both  
173 years. This is a reasonable median value and was chosen because this gave the most biologically  
174 sensible plots of locations immediately after crossing the Sahara (i.e. all locations were on land in North  
175 Africa or Europe rather than in the Mediterranean Sea, within 2 standard errors of the mean of latitude  
176 for the stop-over period). Second, we used the mean location calculated for each bird for sun elevation  
177 angles -2 to -6 at 0.5 increments (i.e. 9 mean locations), then averaged across these 9 locations, applied  
178 to all birds regardless of year. Third, we used the sun elevation angle for each individual that best  
179 reflected their known wintering location on tagging (range of values -3.5 to -5.9, mean -4.6); we used  
180 the LocatorAid software from the BASTrack software suite, which uses known residency times and  
181 wintering location to calculate the corresponding wintering ground SEA value. Fourth, we attempted to  
182 find the correct summer angle using the Hill-Ekstrom (H-E) calibration method (Hill & Braun 2001,  
183 Ekstrom 2004, see Tottrup *et al.* 2012) in which we selected the SEA value that gave the least amount  
184 of variation in latitude during the first two weeks in June when all individuals were very likely to be  
185 stationary on their breeding grounds (see Blackburn *et al.* 2017 for further details and validation of this  
186 approach). If the calibration was not successful, we used the mean value for all the loggers for which  
187 the calibration had been successful, calculated for each year separately (range of values -2 to -4.5,  
188 mean -3.8). We used these SEA values to calculate noon and midnight locations derived from sunrise  
189 and sunset times using the 'coord' function in the Geolight package (Lisovski & Hahn 2012). Because  
190 of the uncertainty introduced by not knowing the SEA value for any stationary period, we analysed the

191 locations with each of the four different sets of SEA values. Results are biologically and statistically very  
192 similar in all cases. Here, we present the results in detail from the most reasonable assumption of SEA  
193 value (i.e. -4.5 for all birds), but also include the range of values obtained from the analyses using the  
194 other three sets of SEA values to demonstrate the similarity. Note that analyses using mean SEA values  
195 of -3 or -6 also gave results that are biologically and statistically similar.

196 Stationary periods (stop-overs of more than two days or breeding locations) were determined  
197 using Geolight (quantile = 0.95, day = 2) and confirmatory visual inspection of latitude and longitude  
198 changes with date. Data analysis to identify stationary periods was restricted to the spring migration  
199 period (i.e. late March to early June). All periods identified as migratory periods (through large daily  
200 changes in sunrise and sunset time) were confirmed first by checking how the product of 5-day moving  
201 average standard deviations for latitude and longitude also varied (all peaks were coincident with the  
202 periods identified by Geolight), and by manual visual inspection of latitude and longitude with date (as  
203 a bird migrates, longitude and latitude change suddenly, with the latter increasing very sharply,  
204 particularly for the onset of migration across the Sahara, see example trace for logger 072 in Fig. 1).  
205 Occasionally, the Geolight function indicated a non-stationary period after an individual was very likely  
206 to have reached the breeding ground (after the second week in May) and when there was no other  
207 supporting evidence for a migration. An analysis of variance to compare locations in periods either side  
208 of the Geolight non-stationary period confirmed whether locations had changed: when the mean  
209 locations were not significantly different, the Geolight identified migratory period was ignored. Stationary  
210 periods were then plotted as stop-over locations, with the final period in the first half of June as the  
211 breeding location (Figs 1 & 2). Maps were plotted using the raster, rgdal, rgeos and mapproj libraries in  
212 R; distances between locations were calculated using the distHaversine function in R. The duration of  
213 each migratory leg and each stop-over period between them were then calculated by from the start and  
214 end dates (to the nearest half day) of each stationary and migration period (Fig. 1).

215 Note that there is a degree of uncertainty in determining short stop-over periods from geolocator  
216 data because of daily shading variation at sunrise (e.g. cloud cover) introducing spurious variation in  
217 latitude, and where longitude may not be varying much regardless of whether a bird is migrating  
218 because they are heading north. Such errors should simply add noise (error) to the accuracy of a  
219 location. Hence our approach was to analyse averaged rather than single locations so that we should  
220 have a reasonable estimate of the mean, and variation with respect to the mean. If errors are biased,



221 these errors occur in all stages and ages etc. to the same degree, so that comparisons across stages  
222 should be biased to the same degree, so making differences valid. This is the same rationale for  
223 conventionally using long stationary periods when analyzing at the level of the individual – because we  
224 are measuring location on a daily basis at very poor resolution we use a longer period with more data  
225 points in order to calculate a true mean for an individual. But we also gain more data points by pooling  
226 observations across individuals and calculating means of individual means (a mixed model approach).  
227 So logically, when we pool data across individuals, we can then use shorter stationary periods that still  
228 result in a reasonable estimate of the mean.

229           We also chose two days as the minimum period where stability may be determined, because  
230 in many cases there were clear periods of relatively gradual change of sunrise and sunset times  
231 consistent only with seasonal change that could be observed over periods beyond 2 days' duration,  
232 particularly after crossing the Sahara when all birds gained a significant easterly component to their  
233 trajectory, which also changed longitude. These periods were then confirmed independently through  
234 the use of the Geolight and moving average analyses (e.g. Fig. 1); use of Geolight to identify stationary  
235 periods of short duration (< 4 days) increases the likelihood of incorrectly identifying a stationary period  
236 (Lisovski & Hahn 2012). Visual examination of traces (i.e. as in Fig. 1) during the migration period (April  
237 2<sup>nd</sup> until the middle of May) identified two birds where a stationary period was identified by Geolight but  
238 not supported by any other evidence, four birds where a stationary period was probably missed (no  
239 consistent change in latitude or longitude during a period), and 29 birds where all evidence for stationary  
240 periods coincided. Therefore, stationary periods identified here are reasonably clear and there was  
241 likely a low error rate in classification, without any substantial bias towards identifying false stationary  
242 periods when we used Geolight.

243

#### 244 **Data analysis**

245 Our aim was to identify how: 1) the distance a bird travelled; 2) its overall speed of travel; and, 3) the  
246 duration of stopover, for each leg during spring migration differed with respect to the type of barrier  
247 being crossed. To test this, we applied a final data set of 96 separate migratory legs from the 35  
248 individuals we could recapture with functioning loggers, but sample sizes differ according to analysis  
249 because some individuals made a continuous migration (i.e. had no major stop-overs) and others had  
250 tags that failed before the breeding ground was reached. Migration distances and speeds without

251 missing age and sex data were available for 85 legs and 31 individuals. Sample sizes were further  
252 reduced to 55 migration legs from 29 individuals for the analysis of stop-over durations. For each  
253 migratory leg, the following explanatory variables were added at the level of the individual bird: age,  
254 sex, wing length, year and migratory start date. Migration start and end times were rescaled so that the  
255 day the first Whinchat migrated was day 0 (28<sup>th</sup> March; first bird left on the night of the 28<sup>th</sup> March in  
256 2013, and the 8<sup>th</sup> April 2014); wing lengths were rescaled so that the mean wing length of 78.7mm was  
257 0. Each migratory leg was assigned to one of six different classes to reflect the potential barriers being  
258 crossed in all possible combinations: 1) land (Continental Europe or continental Africa outwith the  
259 Sahara); 2) sea (the Mediterranean Sea, including one leg over the Black Sea); 3) sea + land (as 2, but  
260 continuing on at least >100km over land); 4) Sahara (starting below 14 degrees latitude and continuing  
261 at least past 25 degrees latitude, although almost all (33/35) finished beyond the desert close to the  
262 North African coast); 5) Sahara + sea (as 4, but then followed by 2); and, 6) Sahara + sea + land (as 4,  
263 but then followed by 3, including 5 cases where an individual made an apparently 'continuous' migration  
264 over the Sahara then the Mediterranean Sea and then continental Europe, without major stop-over to  
265 its breeding site; see Figs 1 & 2).

266         These data were then analysed using General Linear Mixed Models in R assuming a normal  
267 distribution; residuals of all models were reasonably normally distributed. We ran three separate models  
268 to predict distance travelled, speed during a leg and duration of stopover. For all three models we  
269 included age, sex, wing length, migration start date, year, migratory leg class and Whinchat identity (as  
270 a random intercept using the library lme4) as explanatory variables. For models predicting duration of  
271 stopover, we additionally included the distance of the previous migratory leg because this may influence  
272 stopover duration, but because distance was inevitably a function of our migration leg classification, we  
273 also tested an alternative version where we replaced migratory leg class with duration of the leg and so  
274 a proxy of distance and speed of the leg. All models were tested for the significance of interactions  
275 between barrier\*age to test the fourth hypothesis, i.e. if any of the differences across barrier types were  
276 less for adults (that might be less constrained or more migratory-capable) compared to first years on  
277 their first spring migration. We also tested for interactions of sex\*barrier and wing length\*barrier to  
278 determine if any of the responses to different barriers also depended on sex or size, so potentially  
279 improving the robustness of models.

280 Any models that contained migration variables that involved location data (i.e. distance and  
281 speed) were affected by choice of SEA value used. In these cases, we ran each model four times to  
282 explore the effects of varying SEA values. For example, distance of migration assumed: (1) a SEA value  
283 of -4.5 (i.e. the minimum value – see above); (2) the average SEA value of -4; (3) the SEA value for the  
284 breeding location of -4.6; and, (4) the SEA value for the wintering location of -3.8. The analyses that  
285 involved stop-over duration rather than distance were not affected by choice of SEA value used.

286 Note that different individual Whinchats were fitted with slightly different tag designs, with  
287 variation in the length of the light stalk protruding from the tag (0, 5 and 10 mm see Blackburn *et al.*  
288 2016). Inclusion of light stalk as a factor (three way, 0, 5 and 10mm length) in all models resulted in no  
289 change in parameter estimates or statistical significance and so effects of tag design were not  
290 considered further.

291 Model fits were evaluated from diagnostic model plots, and assumptions were reasonably met  
292 in all models presented here (Crawley 2007). Mean values are presented with one standard error (se)  
293 in all cases;  $R^2$  values were adjusted in all cases.

294

## 295 **RESULTS**

296

### 297 **1. Migration legs were longer when crossing the Sahara but birds frequently flew much longer** 298 **distances**

299 The average distance of a migratory leg was significantly greater if the migration leg involved crossing  
300 the Sahara (2,707 km) compared to legs over Continental Africa before the Sahara or Europe (1,241  
301 km). Crossing the Mediterranean Sea only (1,101 km) involved similar distances to legs over land  
302 outwith the Sahara. But many migratory legs were similar in distance to crossing the Sahara, or greatly  
303 exceeded it, even when stop-overs were possible during them, for example, legs crossing the  
304 Mediterranean Sea followed by continued travel over Continental Europe (2,217 km), over the Sahara  
305 followed by the sea (3,542 km) or over the Sahara followed by the sea and then Continental Europe  
306 (4,751 km). Note distances are predicted values derived from the model in Table 1 for an adult male of  
307 mean wing length and median migration start date, in 2014 (Fig. 3B). Seventy-four percent and 34% of  
308 birds crossed the sea or the Sahara respectively, with migratory legs that exceeded the minimum  
309 distance necessary to cross these barriers (Fig. 2, Fig. 3A). Only nine of 34 individuals (26%) crossed

310 the Mediterranean Sea as a distinct leg, with major stop-overs directly before and after. Twenty-three  
311 of 35 individuals (66%) crossed the Sahara as a distinct leg, starting below 14 degrees latitude (although  
312 including 19 directly from the latitude of the study site, approximately 500 km south of the edge of the  
313 Sahara and a further one approximately 50 km further south still) and ending with a major stop-over  
314 within 250 km or less from the Mediterranean coast. Therefore, even distinctly Saharan crossing  
315 individuals probably travelled further than was necessary just to cross the Sahara. Age did not affect  
316 average migration distance of a leg, but males on average travelled greater distances per leg compared  
317 to females (480 km), longer winged individuals travelled shorter distances per leg (121 km less for every  
318 increase in wing length of 1 mm), and later migrating birds travelled greater distances per leg (26 km  
319 increase for every day later migration was started; Table 1).

320

## 321 **2. Migration speed during a leg was slowest crossing Continental Europe and fastest if crossing** 322 **the Sahara**

323 The hourly speed of migration during a leg was greatest when individuals crossed the Sahara followed  
324 immediately by the Mediterranean Sea (53.2 km/h); when crossing the Sahara only, speeds were slower  
325 but not significantly so (43.8 km/h). Speeds of migration during a leg when crossing the Sahara only  
326 were significantly faster than when crossing land in continental Europe or Africa outwith the Sahara  
327 (26.4 km/h) or when crossing the Mediterranean Sea (30.0 km/h). Note these speeds are predicted  
328 values derived from the model in Table 2 for an adult male of mean wing length and median migration  
329 start date, in 2014 (Fig. 3C). Age, sex, wing length and migration start date did not significantly affect  
330 speed (Table 2).

331

## 332 **3. Major stop-over duration was longer after migratory legs crossing the Sahara**

333 Major stop-overs were significantly longer after a migration leg over the Sahara (8.9 days) or the Sahara  
334 immediately followed by the Mediterranean Sea (8.9 days) compared with after a leg over just the  
335 Mediterranean Sea (2.2 days), land (2.4 days, continental Europe or Africa outwith the Sahara), or the  
336 Mediterranean Sea immediately followed by continental Europe (4.5 days). Continuous migration  
337 (without any major stop-overs of more than two days) crossing the Sahara and then the Mediterranean  
338 Sea and then continental Europe resulted in significantly longer major stop-over duration compared to  
339 all other barrier types (15.3 days). Note these stop-over durations are predicted values derived from the

340 model in Table 3 for an adult male of mean wing length, median migration start date, and median  
341 distance of migration leg, in 2014 (Fig. 3D). Within a barrier type, distance travelled was marginally  
342 significantly negatively correlated with stop-over duration (approximately 1 day shorter for each  
343 additional 500 km travelled: Table 3). Note that distance was correlated with barrier type (Figs 3A and  
344 3B), but removal of distance from the model did not affect the biological and statistical significance of  
345 the variation across barrier type.

346 If barrier type is removed from the model and replaced with duration of the migratory leg prior  
347 to the stop-over, distance becomes positively associated with stop-over duration: with every 1,000 km  
348 extra travelled, there was an extra day's stop-over ( $0.0010 \pm 0.0004$ ,  $t_{38.1} = 2.3$ ,  $P = 0.025$ ), but there  
349 was no significant effect of migration leg duration on subsequent stop-over duration (i.e. the effect of  
350 the speed travelled because distance is also in the model,  $-0.08 \pm 0.27$ ,  $t_{44.9} = -0.3$ ,  $P = 0.76$ ). Within  
351 this model, migration start date becomes significant (from marginal significance in the model above,  
352 Table 3), with the duration of stop-overs of more than 2 days decreasing by 0.25 days for every day  
353 later that migration was started ( $-0.25 \pm 0.08$ ,  $t_{21.4} = -3.1$ ,  $P = 0.006$ ;  $n = 54$  migration legs from  $n = 29$   
354 individuals; marginal  $R^2 = 0.27$ , random effects accounted for 0.25 additional variance; Fig. 3). Age,  
355 sex, and wing length did not significantly affect major stop-over duration (Table 3). Note that in a mixed  
356 model predicting duration of a migratory leg with its distance, and individual identity included as a  
357 random effect, only 12.4% of variation was accounted for by distance.

358

#### 359 **4. First year birds did not show any differences in response to barriers compared to adults**

360 None of the differences in distance travelled (Table 1), speed travelled during a leg (Table 2) or stop-  
361 over duration (Table 3) between the barrier types being crossed were dependent on age.

362

## 363 **DISCUSSION**

364

365 We tracked the spring migration of 35 Whinchats to examine whether migratory barriers are associated  
366 with distinct migratory behaviour. Key results were that migration legs including much more than the  
367 Sahara were common, migration was faster over the Sahara, major stop-over duration increased with  
368 distance travelled during a leg, and juveniles performed like adults. We found that Whinchats showed  
369 distinct migratory behaviour when crossing the Sahara, with longer flights, faster overall travel speed

370 and longer stop-over durations afterwards compared to when crossing continental Europe, providing  
371 some evidence for adaptive behaviours that act to shorten the period of time spent crossing inhospitable  
372 barriers (or as a response to not encountering suitable refuelling sites). These behaviours did not occur  
373 when crossing the Mediterranean Sea, which is much narrower than the Sahara. However, many  
374 individual Whinchats performed long flights, fast flights and had long stop-over durations during all  
375 stages of the spring migration. This was regardless of the barrier types being crossed, demonstrating  
376 substantial variation in migration strategy. Variation in migration strategy across individuals may confer  
377 resilience to future changes in barrier width, although we discuss that this may depend crucially on the  
378 presence of stop-over sites afterwards, and that this may not be true of first autumn migrations.

379 Migration legs were longer when crossing the Sahara, but Whinchats frequently flew much  
380 longer distances. This suggests that the Sahara does have fewer options for stop-overs, but also that  
381 Whinchats can and frequently do greatly exceed the current width of the Sahara in a single migratory  
382 leg. Migration speed during a leg was slowest crossing Continental Europe and fastest crossing the  
383 Sahara. This suggests fewer stop-over options are available in the Sahara. Migration speed averaging  
384 twice-daily locations across groups of individuals can only realistically measure speed of migration at  
385 the level of kilometres travelled per day, i.e. they include periods when a bird is migrating (probably at  
386 a speed of about 45 km/h without wind effects; Bruderer & Boldt 2001) and when a bird is resting or  
387 foraging. Therefore, slower speeds for legs over Continental Europe, for example, reflect longer daily  
388 periods of resting or foraging, and/or periods of headwind. Faster speeds for legs over the Sahara  
389 reflect shorter resting or foraging periods and/or the periods of tailwind. The average speed over the  
390 Sahara was of the order of continuous flight with no stop-overs at all, if there were no wind effects. This  
391 is theoretically possible, and such continuous migration over the whole 24-hour period or longer has  
392 probably been found in other small passerine species (DeLuca *et al.* 2015, Adamik *et al.* 2016,  
393 Ouwehand & Both 2016, Xenophontos *et al.* 2017).

394 Alternatively, Whinchats may well stop-over for rest periods when crossing the Sahara and only  
395 cross when they have favourable tailwinds which may increase ground speed considerably, allowing  
396 several hours each day for stop-overs (Erni *et al.* 2005, Liechti 2006). The fastest average speeds were  
397 recorded for Whinchats which crossed both the Sahara and the Mediterranean without a major stop-  
398 over. Even if flights were continuous in these cases, tailwinds were still very likely to be involved and,  
399 indeed, may be a factor in determining whether a Whinchat could continue migration over the

400 Mediterranean after crossing the Sahara. The slowest speeds were recorded during legs over land  
401 outwith the Sahara and the Mediterranean. This again may reflect daily stop-over periods to rest and  
402 refuel and, at least over land, probably reflects predominantly typical nocturnal migration (Bairlein 1988,  
403 Backman *et al.* 2017). When crossing the Mediterranean, this suggestion logically would then mean  
404 routes involving islands or through Italy, where stop-overs are possible. Alternatively, the slow speeds  
405 over the Mediterranean may reflect strong headwinds and again, if this was the case, this may have  
406 been a factor in determining whether a Whinchat stopped migration for a major stop-over after crossing  
407 the Mediterranean rather than continuing for a longer leg.

408 Major stop-over duration was longer after migratory legs crossing the Sahara, and in general  
409 flights of increasing duration or distance required longer major stop-overs afterwards, with major stop-  
410 over duration afterwards increasing by about a day for every 1000km travelled. However, when  
411 controlling for barrier type in a model, stop-over durations decreased slightly as the distance of the  
412 migratory leg increased, suggesting that longer migratory legs may well reflect easier conditions such  
413 as tailwinds or profitable daily refuelling stop-overs. Much stop-over variation may also be due to  
414 adaptive timing ensuring a Whinchat arrives at the breeding ground at the optimum time, rather than  
415 reflecting a constraint where stop-over duration is as long as it takes to refuel. Individual variation in  
416 speed and stop-over duration afterwards was high: approximately one third of the explained variation  
417 in speed and stop-over duration in the models was accounted for by the random effect of individual.  
418 Variation in the timing of migration initiation also exerted a strong effect in some models: the latest  
419 leaving individuals might have stop-overs 6 days less on average than the earliest leaving individuals.  
420 Other studies have shown that timing rather than routes primarily determines stop-over duration and so  
421 overall speed of migration (Fraser *et al.* 2013, Cohen *et al.* 2014, Loon *et al.* 2017). Adaptive shortening  
422 or even dropping of daily stop-overs may be a common strategy for faster migration (Schmaljohann &  
423 Both 2017).

424 First year birds did not show any differences in response to barriers compared to adults,  
425 suggesting that age and so experience did not affect key migration characteristics. Although timing of  
426 the start of migration varied with age, none of the other characteristics involved with crossing the Sahara  
427 (faster speed during a migratory leg and longer stop-overs) were different for first years (see also  
428 McKinnon *et al.* 2014). Furthermore, there were no differences in survival with sex and age within this  
429 cohort (Blackburn & Cresswell 2016a), suggesting that spring migration overall does not represent more

430 of a challenge for first years (see also Sillett & Holmes 2002). Again, although crossing the Sahara does  
431 result in a change in behaviour (faster migration) suggesting increased constraint, first year birds on  
432 their first spring migration responded to the barrier to the same degree as adults, and without additional  
433 survival costs.

434 It is however important to note that we do not consider autumn migration. Most studies of  
435 migrant passerines show much lower survival for first year birds compared to adults (Saether 1989,  
436 Donovan *et al.* 1995, Saether & Bakke 2000), and although some of this will reflect lower natal site  
437 philopatry for first years and reduced survival post fledging, it might also arise during autumn migration  
438 (Sillett & Holmes 2002, Matthew *et al.* 2013). Studies on non-passerines large enough to carry satellite  
439 tags also show higher mortality in naive juveniles on their first migration (e.g. Rotics *et al.* 2016,  
440 Vansteelant *et al.* 2017). The Mediterranean and Sahara may represent much wider barriers during the  
441 autumn because migrants arrive in Southern Europe and North Africa at the end of the summer when  
442 conditions for rapid refuelling may be poor because no significant rain will have fallen in these areas  
443 since April. Migration may also benefit from experience (Perdeck 1967, Thorup *et al.* 2007, Rotics *et al.*  
444 2016), although the lack of a difference in survival in Whinchats after the first migration (Blackburn &  
445 Cresswell 2016a) argues against this, as does the fact that spring migration routes and timing are  
446 usually different to autumn routes, as in this study (unpubl. data) and as shown in many others (e.g.  
447 Schmaljohann *et al.* 2012, Tottrup *et al.* 2012, Kristensen *et al.* 2013).

448

## 449 **Conclusion**

450 Our results overall may suggest that the width of the Sahara may not be the major limiting factor in  
451 determining migration characteristics. There may be a variety of successful ways to migrate between  
452 Africa and Europe in terms of distances of migratory legs, speed during a migratory leg and major stop-  
453 over duration, whether for more experienced adult birds or for first year birds carrying out their first  
454 spring migration. Whinchats can and often do employ migration legs that far exceed what is necessary  
455 to cross the Sahara. This is all likely related to the need for time-minimisation on spring migration  
456 (Hedenstrom & Alerstam 1997), to reach the breeding ground as quickly as possible to reduce risk  
457 associated with long stop-overs (Houston 1998), to ensure arriving early to be able to time breeding to  
458 match peaks of food availability (Both & te Marvelde 2007), and to gain or maintain the best territories  
459 (Kokko 1999). These selective pressures will have driven the evolution of the time-minimising migration



460 characteristics that pre-adapt migrants for barrier crossing. Put simply, Whinchats probably need to  
461 behave as if they are crossing real barriers during spring migration most of the time anyway. However,  
462 reducing short daily stop-overs (i.e. increasing daily distance travelled and so speed of migration) likely  
463 increases the need for major stop-overs or high quality stop-over sites afterwards (Bayly *et al.* 2012).  
464 This perhaps highlights the importance of stop-over site quality rather than presence of a barrier as the  
465 likely key component to successful migration (Hewson *et al.* 2016, Halupka *et al.* 2017, Schmaljohann  
466 *et al.* 2017).

467         Despite apparent flexibility in distance travelled and speed of a migratory leg, and stop-over  
468 duration afterwards with respect to the width of the barriers, crossing the Sahara or Mediterranean Sea  
469 may still represent a problem. Factors associated with areas such as the Sahara like storms and  
470 reduced stop-over habitat quality because of unpredictable environmental conditions may lower survival  
471 for migrants, and these events likely affect all migrants in a similar way regardless of their age,  
472 experience, migratory capability and even species (Newton 2006). It is perhaps possible that it is mostly  
473 unpredictable conditions that make migration difficult for birds, and the probability of encountering these  
474 increases with the width of a barrier and so the duration of the migratory leg. As unpredictable conditions  
475 increase through climate and anthropogenic habitat change, so we may observe population declines  
476 across migrant species regardless of their individual ecology (Sanderson *et al.* 2006). Many more data  
477 are needed to show when, where and how small passerine migrants die during migration, and how  
478 successful adult migration strategies arise through differential survival and/or experience.

479

480

481 The study was carried out in Nigeria where no licences are required for the procedures used.  
482 Nevertheless, this study was carried out under the ethical guidelines of the AP Leventis Ornithological  
483 Research Institute Scientific Committee (APLORI is the only ornithological research institute in Nigeria)  
484 based on the Association for the Study of Animal Behaviour guidelines and those of the British Trust  
485 for Ornithology's ringing scheme. All personnel involved in fieldwork – either catching, colour-ringing or  
486 tagging birds had BTO ringing licences. MB had been previously licensed to fit geolocators in the UK.  
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490 **REFERENCES**

491

492 Adamik, P., Emmenegger, T., Briedis, M., Gustafsson, L., Henshaw, I., Krist, M., Laaksonen, T., Liechti,  
493 F., Prochazka, P., Salewski, V. & Hahn, S. 2016. Barrier crossing in small avian migrants:  
494 individual tracking reveals prolonged nocturnal flights into the day as a common migratory  
495 strategy. *Scientific Reports*, **6**.

496 Alerstam, T., Hedenstrom, A. & Akesson, S. 2003. Long-distance migration: evolution and  
497 determinants. *Oikos*, **103**: 247-260.

498 Alerstam, T., Lindstrom, A. & Gwinner, E. 1990. Optimal bird migration: the relative importance of time,  
499 energy and safety. In *Bird Migration: physiology and ecophysiology*. (ed. E. Gwinner), pp. 331-  
500 351. Berlin: Springer-Verlag.

501 Backman, J., Andersson, A., Alerstam, T., Pedersen, L., Sjoberg, S., Thorup, K. & Tottrup, A. P. 2017.  
502 Activity and migratory flights of individual free-flying songbirds throughout the annual cycle:  
503 method and first case study. *Journal of Avian Biology*, **48**: 309-319.

504 Bairlein, F. 1988. How do migratory songbirds cross the Sahara? *Trends in Ecology & Evolution*, **3**:  
505 191-194.

506 Bayly, N., Atkinson, P. & Rumsey, S. 2012. Fuelling for the Sahara crossing: variation in site use and  
507 the onset and rate of spring mass gain by 38 Palearctic migrants in the western Sahel. *Journal*  
508 *of Ornithology*, **153**: 931-945.

509 Biebach, H. 1995. Stopover of migrants flying across the Mediterranean Sea and the Sahara. *Israel*  
510 *Journal of Zoology*, **41**: 387-392.

511 Blackburn, E., Burgess, M., Freeman, B., Risely, A., Izang, A., Ivande, S., Hewson, C. & Cresswell, W.  
512 2016. An experimental evaluation of the effects of geolocator design and attachment method  
513 on between-year survival on Whinchats *Saxicola rubetra*, a long distance migrant. *Journal of*  
514 *Avian Biology*, **47**: 530-539.

515 Blackburn, E., Burgess, M., Freeman, B., Risely, A., Izang, A., Ivande, S., Hewson, C. & Cresswell, W.  
516 2017. Low and annually variable migratory connectivity in a long distance migrant: Whinchats  
517 *Saxicola rubetra* may show a bet-hedging strategy. *Ibis*, **159**: 902-918.

518 Blackburn, E. & Cresswell, W. 2015. Fine-scale habitat use during the non-breeding season suggests  
519 that winter habitat does not limit breeding populations of a declining long-distance Palearctic  
520 migrant. *Journal of Avian Biology*, **46**: 622-633.

521 Blackburn, E. & Cresswell, W. 2016a. High overwinter and annual survival for a declining Palearctic  
522 migrant: evidence that wintering conditions may not limit migrant populations *Ibis*, **158**: 92-105.

523 Blackburn, E. & Cresswell, W. 2016b. High winter site fidelity in a long-distance migrant: implications  
524 for wintering ecology and survival estimates. *Journal of Ornithology*, **157**: 93-108.

525 Both, C., Bouwhuis, S., Lessells, C. M. & Visser, M. E. 2006. Climate change and population declines  
526 in a long-distance migratory bird. *Nature*, **441**: 81-83.

527 Both, C. & te Marvelde, L. 2007. Climate change and timing of avian breeding and migration throughout  
528 Europe. *Climate Research*, **35**: 93-105.

529 Bridge, E. S., Kelly, J. F., Contina, A., Gabrielson, R. M., MacCurdy, R. B. & Winkler, D. W. 2013.  
530 Advances in tracking small migratory birds: a technical review of light-level geolocation. *Journal*  
531 *of Field Ornithology*, **84**: 121-137.

532 Bruderer, B. & Boldt, A. 2001. Flight characteristics of birds: 1. radar measurements of speeds. *Ibis*,  
533 **143**: 178-204.

534 Chen, I. C., Hill, J. K., Ohlemuller, R., Roy, D. B. & Thomas, C. D. 2011. Rapid Range Shifts of Species  
535 Associated with High Levels of Climate Warming. *Science*, **333**: 1024-1026.

536 Cohen, E., Moore, F. & Fischer, R. 2014. Fuel stores, time of spring, and movement behavior influence  
537 stopover duration of Red-eyed Vireo *Vireo olivaceus*. *Journal of Ornithology*, **155**: 785-792.

538 Crawley, M. J. (2007) *The R Book*, Chichester: John Wiley & Sons Ltd.

539 Cresswell, W. 2014. Migratory connectivity of Palaeartic-African migratory birds and their responses  
540 to environmental change: the serial residency hypothesis. *Ibis*, **156**: 493-510.

541 DeLuca, W. V., Woodworth, B. K., Rimmer, C. C., Marra, P. P., Taylor, P. D., McFarland, K. P.,  
542 Mackenzie, S. A. & Norris, D. R. 2015. Transoceanic migration by a 12 g songbird. *Biology*  
543 *Letters*, **11**.

544 Donovan, T. M., Thompson, F. R., III, Faaborg, J. & Probst, J. R. 1995. Reproductive Success of  
545 Migratory Birds in Habitat Sources and Sinks. *Conservation Biology*, **9**: 1380-1395.

- 546 Doswald, N., Willis, S. G., Collingham, Y. C., Pain, D. J., Green, R. E. & Huntley, B. 2009. Potential  
547 impacts of climatic change on the breeding and non-breeding ranges and migration distance of  
548 European *Sylvia* warblers. *Journal of Biogeography*, **36**: 1194-1208.
- 549 Ekstrom, P. A. 2004. An advance in the geolocation by light. In *Memoirs of the National Institute of Polar*  
550 *Research, Special Issue*. (ed. Y. Naito), pp. 210-226. Tokyo: National Institute of Polar  
551 Research.
- 552 Erni, B., Liechti, F. & Bruderer, B. 2005. The role of wind in passerine autumn migration between Europe  
553 and Africa. *Behavioral Ecology*, **16**: 732-740.
- 554 Faaborg, J., Holmes, R. T., Anders, A. D., Bildstein, K. L., Dugger, K. M., Gauthreaux, S. A., Heglund,  
555 P., Hobson, K. A., Jahn, A. E., Johnson, D. H., Latta, S. C., Levey, D. J., Marra, P. P., Merkord,  
556 C. L., Nol, E., Rothstein, S. I., Sherry, T. W., Sillett, T. S., Thompson, F. R. & Warnock, N. 2010.  
557 Recent advances in understanding migration systems of New World land birds. *Ecological*  
558 *Monographs*, **80**: 3-48.
- 559 Fox, J. 2010. Geocator manual v8 (March 2010).  
560 [http://www.antarctica.ac.uk/engineering/geo\\_downloads/Geocator\\_manual\\_v8.pdf](http://www.antarctica.ac.uk/engineering/geo_downloads/Geocator_manual_v8.pdf).
- 561 Fraser, K. C., Stutchbury, B. J. M., Kramer, P., Silverio, C., Barrow, J., Newstead, D., Mickle, N.,  
562 Shaheen, T., Mammenga, P., Applegate, K., Bridge, E. & Tautin, J. 2013. Consistent range-  
563 wide pattern in fall migration strategy of Purple Martin (*Progne subis*), despite different  
564 migration routes at the Gulf of Mexico. *Auk*, **130**: 291-296.
- 565 Fudickar, A. M., Wikelski, M. & Partecke, J. 2012. Tracking migratory songbirds: accuracy of light-level  
566 loggers (geolocators) in forest habitats. *Methods in Ecology and Evolution*, **3**: 47-52.
- 567 Gill, R. E., Tibbitts, T. L., Douglas, D. C., Handel, C. M., Mulcahy, D. M., Gottschalck, J. C., Warnock,  
568 N., McCaffery, B. J., Battley, P. F. & Piersma, T. 2009. Extreme endurance flights by landbirds  
569 crossing the Pacific Ocean: ecological corridor rather than barrier? *Proceedings of the Royal*  
570 *Society B-Biological Sciences*, **276**: 447-458.
- 571 Hahn, S., Bauer, S. & Liechti, F. 2009. The natural link between Europe and Africa – 2.1 billion birds on  
572 migration. *Oikos*, **118**: 624-626.
- 573 Halupka, L., Wierucka, K., Sztwiertnia, H. & Klimczuk, E. 2017. Conditions at autumn stopover sites  
574 affect survival of a migratory passerine. *Journal of Ornithology*, **158**: 979-988.

575 Hedenstrom, A. & Alerstam, T. 1997. Optimum fuel loads in migratory birds: Distinguishing between  
576 time and energy minimization. *Journal of Theoretical Biology*, **189**: 227-234.

577 Henningsson, S. S. & Alerstam, T. 2005. Barriers and distances as determinants for the evolution of  
578 bird migration links: the arctic shorebird system. *Proceedings of the Royal Society B-Biological*  
579 *Sciences*, **272**: 2251-2258.

580 Hewson, C. M., Thorup, K., Pearce-Higgins, J. W. & Atkinson, P. W. 2016. Population decline is linked  
581 to migration route in the Common Cuckoo. *Nature Communications*, **7**.

582 Hill, R. D. & Braun, M. J. 2001. Geolocation by light level - the next step: Latitude. In *Electronic tagging*  
583 *and tracking in marine fisheries*. (eds. J. R. Silbert & J. L. Nielsen), pp. 315-330. Dordrecht:  
584 Kluwer Academic publishers.

585 Houston, A. I. 1998. Models of optimal avian migration: state, time and predation. *Journal of Avian*  
586 *Biology*, **29**: 395-404.

587 Hulme, M. F. & Cresswell, W. 2012. Density and behaviour of Whinchats *Saxicola rubetra* on African  
588 farmland suggest that winter habitat conditions do not limit European breeding populations.  
589 *Ibis*, **154**: 680-692.

590 Jenni, L. & Winkler, R. (1994) *Moult and ageing of European Passerines*, London: Academic Press.

591 Klaassen, R. H. G., Hake, M., Strandberg, R., Koks, B. J., Trierweiler, C., Exo, K.-M., Bairlein, F. &  
592 Alerstam, T. 2014. When and where does mortality occur in migratory birds? Direct evidence  
593 from long-term satellite tracking of raptors. *Journal of Animal Ecology*, **83**: 176-184.

594 Kokko, H. 1999. Competition for early arrival in migratory birds. *Journal of Animal Ecology*, **68**: 940-  
595 950.

596 Kristensen, M. W., Tottrup, A. P. & Thorup, K. 2013. Migration of the common redstart (*Phoenicurus*  
597 *phoenicurus*): a Eurasian songbird wintering in highly seasonal conditions in the West African  
598 Sahel. *Auk*, **130**: 258-264.

599 Liechti, F. 2006. Birds: blowin' by the wind? *Journal of Ornithology*, **147**: 202-211.

600 Lisovski, S. & Hahn, S. 2012. GeoLight-processing and analysing light-based geolocator data in R.  
601 *Methods in Ecology and Evolution*, **3**: 1055-1059.

602 Lisovski, S., Hewson, C. M., Klaassen, R. H. G., Korner-Nievergelt, F., Kristensen, M. W. & Hahn, S.  
603 2012. Geolocation by light: accuracy and precision affected by environmental factors. *Methods*  
604 *in Ecology and Evolution*, **3**: 603-612.

605 Lockwood, R., Swaddle, J. P. & Rayner, J. M. V. 1998. Avian wingtip shape reconsidered: wingtip shape  
606 indices and morphological adaptations to migration. *Journal of Avian Biology*, **29**: 273-292.

607 Lok, T., Overdijk, O. & Piersma, T. 2015. The cost of migration: spoonbills suffer higher mortality during  
608 trans-Saharan spring migrations only. *Biology Letters*, **11**: 20140944.

609 Loon, A. V., Ray, J. D., Savage, A., Mejeur, J., Moscar, L., Pearson, M., Pearman, M., Hvenegaard, G.  
610 T., Mickle, N., Applegate, K. & Fraser, K. C. 2017. Migratory stopover timing is predicted by  
611 breeding latitude, not habitat quality, in a long-distance migratory songbird. *Journal of*  
612 *Ornithology*, **158**: 745-752.

613 Matthew, I. M.-L., Jeffrey, P. H., Thomas, J. B. & Wendy, M. S. 2013. Juvenile survival in a neotropical  
614 migratory songbird is lower than expected. *PLoS ONE*, **8**.

615 McKinnon, E. A., Fraser, K. C., Stanley, C. Q. & Stutchbury, B. J. M. 2014. Tracking from the Tropics  
616 Reveals Behaviour of Juvenile Songbirds on Their First Spring Migration. *PLoS ONE*, **9**.

617 McKinnon, E. A., Stanley, C. Q., Fraser, K. C., MacPherson, M. M., Casbourn, G., Marra, P. P., Studds,  
618 C. E., Diggs, N. & Stutchbury, B. J. 2012. Estimating geolocator accuracy for a migratory  
619 songbird using live ground-truthing in tropical forest. *Animal Migration*, **1**: 31-38.

620 Mettke-Hofmann, C. & Greenberg, R. 2005. Behavioral and cognitive adaptations to long-distance  
621 migration. In *Birds of two worlds: the ecology and evolution of migration*. (eds. R. Greenberg &  
622 P. P. Marra), pp. 114-123. Baltimore, Maryland: John Hopkins University Press.

623 Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds?  
624 *Journal of Ornithology*, **147**: 146-166.

625 Newton, I. (2008) *The migration ecology of birds*, Oxford: Academic Press.

626 Oppel, S., Dobrev, V., Arkumarev, V., Saravia, V., Bounas, A., Kret, E., Veleviski, M., Stoychev, S. &  
627 Nikolov, S. C. 2015. High juvenile mortality during migration in a declining population of a long-  
628 distance migratory raptor. *Ibis*, **157**: 545-557.

629 Ouwehand, J. & Both, C. 2016. Alternate non-stop migration strategies of pied flycatchers to cross the  
630 Sahara desert. *Biology Letters*, **12**: 20151060.

631 Perdeck, A. C. 1967. Orientation of Starlings after displacement to Spain. *Ardea*, **55**: 93-104.

632 R Development Core Team. 2014. R: A Language and Environment for Statistical Computing. Vienna,  
633 Austria: R Foundation for Statistical Computing.

634 Rotics, S., Kaatz, M., Resheff, Y. S., Turjeman, S. F., Zurell, D., Sapir, N., Eggers, U., Flack, A., Fiedler,  
635 W., Jeltsch, F., Wikelski, M. & Nathan, R. 2016. The challenges of the first migration: movement  
636 and behaviour of juvenile vs. adult white storks with insights regarding juvenile mortality.  
637 *Journal of Animal Ecology*, **85**: 938-947.

638 Saether, B. E. 1989. Survival rates in relation to body-weight in European birds *Ornis Scandinavica*,  
639 **20**: 13-21.

640 Saether, B. E. & Bakke, O. 2000. Avian life history variation and contribution of demographic traits to  
641 the population growth rate. *Ecology*, **81**: 642-653.

642 Sanderson, F. J., Donald, P. F., Pain, D. J., Burfield, I. J. & van Bommel, F. P. J. 2006. Long-term  
643 population declines in Afro-Palearctic migrant birds. *Biological Conservation*, **131**: 93-105.

644 Schmaljohann, H. & Both, C. 2017. The limits of modifying migration speed to adjust to climate change.  
645 *Nature Clim. Change*, **7**: 573-576.

646 Schmaljohann, H., Buchmann, M., Fox, J. W. & Bairlein, F. 2012. Tracking migration routes and the  
647 annual cycle of a trans-Saharan songbird migrant. *Behavioral Ecology and Sociobiology*, **66**:  
648 915-922.

649 Schmaljohann, H. & Eikenaar, C. 2017. How do energy stores and changes in these affect departure  
650 decisions by migratory birds? A critical view on stopover ecology studies and some future  
651 perspectives. *Journal of Comparative Physiology a-Neuroethology Sensory Neural and*  
652 *Behavioral Physiology*, **203**: 411-429.

653 Schmaljohann, H., Liechti, F. & Bruderer, B. 2007. Songbird migration across the Sahara: the non-stop  
654 hypothesis rejected! *Proceedings of the Royal Society B-Biological Sciences*, **274**: 735-739.

655 Schmaljohann, H., Lisovski, S. & Bairlein, F. 2017. Flexible reaction norms to environmental variables  
656 along the migration route and the significance of stopover duration for total speed of migration  
657 in a songbird migrant. *Frontiers in Zoology*, **14**.

658 Sillett, T. S. & Holmes, R. T. 2002. Variation in survivorship of a migratory songbird throughout its annual  
659 cycle. *Journal of Animal Ecology*, **71**: 296-308.

660 Strandberg, R., Klaassen, R. H. G., Hake, M. & Alerstam, T. 2010. How hazardous is the Sahara Desert  
661 crossing for migratory birds? Indications from satellite tracking of raptors. *Biology Letters*, **6**:  
662 297-300.

663 Thorup, K., Bisson, I. A., Bowlin, M. S., Holland, R. A., Wingfield, J. C., Ramenofsky, M. & Wikelski, M.  
664 2007. Evidence for a navigational map stretching across the continental US in a migratory  
665 songbird. *Proceedings of the National Academy of Sciences of the United States of America*,  
666 **104**: 18115-18119.

667 Tottrup, A. P., Klaassen, R. H. G., Strandberg, R., Thorup, K., Kristensen, M. W., Jorgensen, P. S.,  
668 Fox, J., Afanasyev, V., Rahbek, C. & Alerstam, T. 2012. The annual cycle of a trans-equatorial  
669 Eurasian-African passerine migrant: different spatio-temporal strategies for autumn and spring  
670 migration. *Proceedings of the Royal Society B-Biological Sciences*, **279**: 1008-1016.

671 Vagasi, C. I., Pap, P. L., Vincze, O., Osvath, G., Erritzoe, J. & Moller, A. P. 2016. Morphological  
672 Adaptations to Migration in Birds. *Evolutionary Biology*, **43**: 48-59.

673 Vansteelant, W. M. G., Kekkonen, J. & Byholm, P. 2017. Wind conditions and geography shape the  
674 first outbound migration of juvenile honey buzzards and their distribution across sub-Saharan  
675 Africa. *Proceedings of the Royal Society B: Biological Sciences*, **284**.

676 Vickery, J. A., Ewing, S. R., Smith, K. W., Pain, D. J., Bairlein, F., Skorpilova, J. & Gregory, R. D. 2014.  
677 The decline of Afro-Palaeartic migrants and an assessment of potential causes. *Ibis*, **156**: 1-  
678 22.

679 Walther, G. R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T. J. C., Fromentin, J. M.,  
680 Hoegh-Guldberg, O. & Bairlein, F. 2002. Ecological responses to recent climate change.  
681 *Nature*, **416**: 389-395.

682 Xenophontos, M., Blackburn, E. & Cresswell, W. 2017. Cyprus wheatears *Oenanthe cyprica* likely  
683 reach sub-Saharan African wintering grounds in a single migratory flight. *Journal of Avian*  
684 *Biology*, **48**: 529-535.

685



686 **Table 1.** Results from a GLMM to test how distance travelled on a migration leg varied depending on  
687 the type of barrier crossed, controlling for age, sex, wing length, year and migration start date, with  
688 individual bird included as a random effect ( $n = 85$  migration legs from  $n = 31$  individuals; marginal  $R^2$   
689  $= 0.81$ , random effects accounted for no additional variance). Adult, female, 2013 and Sahara set as  
690 the intercept; wing length scaled relative to a mean of 78.66 mm and migration start date rescaled to 0  
691 for earliest day an individual started migration, March 28<sup>th</sup>. Interactions between barrier type and age  
692 ( $F_{5,59.5} = 1.0$ ,  $P = 0.46$ ), or sex ( $F_{5,59.5} = 2.1$ ,  $P = 0.074$ ) or wing length ( $F_{5,59.5} = 0.8$ ,  $P = 0.54$ ) were not  
693 significant when added to the model. The Estimate and se columns give the estimates and their  
694 standard errors for locations and so distance travelled between them calculated with a sun elevation  
695 angle (SEA value) of -4.5, which gives the most biologically sensible locations after crossing the Sahara.  
696 The range of estimates obtained using different values of SEA to calculate locations is given in the  
697 fourth column: estimates are biologically and statistically similar in significance in all analyses.  
698 Significant ( $P \leq 0.05$ ) effects are given in bold. Note that, although some distance differences by barrier  
699 type are inevitably larger because they combine barrier types, these increases are not simply additive,  
700 being much larger than necessary to cross the barrier.

701

	Estimate	se	Estimate variation dependent on			
			SEA value	df	t value	P value
(Intercept)	1991.5	306.6	1992 to 2174	71.6	6.5	<0.001
Age (First year)	-261.8	157.1	-261 to -241	71.6	-1.7	0.10
Sex (Male)	479.7	169.1	434 to 483	71.6	2.8	<b>0.006</b>
Wing length	-121.3	53.4	-121 to -111	71.6	-2.3	<b>0.026</b>
Year (2014)	-291.4	127.8	-335 to -264	71.6	-2.3	<b>0.026</b>
Migration start date	25.7	9.1	23 to 27	71.6	2.8	<b>0.0061</b>
Sea	-1606.2	237.6	-1595 to -1808	71.6	-6.8	<b>&lt;0.001</b>
Land	-1465.7	145.0	-1445 to -1615	71.6	-10.1	<b>&lt;0.001</b>
Sea + Land	-490.9	181.5	-717 to -491	71.6	-2.7	<b>0.009</b>
Sahara + Sea	835.0	245.7	532 to 914	71.6	3.4	<b>0.001</b>
Sahara + Sea + Land	2043.7	259.9	1741 to 2043	71.6	7.9	<b>&lt;0.001</b>

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703

704 **Table 2.** Results from a GLMM to test how speed (km/h) travelled on a migration leg varied depending  
705 on the type of barrier crossed, controlling for age, sex, wing length, year and migration start date, with  
706 individual bird included as a random effect ( $n = 85$  migration legs from  $n = 31$  individuals; marginal  $R^2$   
707  $= 0.28$ , random effects accounted for 0.10 additional variance). Adult, female, 2013 and Sahara set as  
708 the intercept; wing length scaled relative to a mean of 78.66 mm and migration start date rescaled to 0  
709 for earliest day an individual started migration, March 28<sup>th</sup>. Interactions between barrier type and age  
710 ( $F_{5,59.5} = 1.0$ ,  $P = 0.45$ ), or sex ( $F_{5,59.5} = 2.1$ ,  $P = 0.074$ ) or wing length ( $F_{5,59.5} = 0.8$ ,  $P = 0.54$ ) were not  
711 significant when added to the model. The Estimate and se columns give the estimates and their  
712 standard errors for locations calculated and so speed between them using a sun elevation angle (SEA  
713 value) of -4.5, which gives the most biologically sensible locations after crossing the Sahara. Significant  
714 ( $P \leq 0.05$ ) effects are given in bold. The range of estimates obtained using different values of SEA to  
715 calculate locations is given in the fourth column: estimates are biologically and statistically similar in  
716 significance in all analyses.

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	Estimate	se	Estimate variation dependent on SEA value	df	t value	P value
(Intercept)	32.4	10.4	32 to 46	27.8	3.1	<0.001
Age (First year)	4.3	5.4	2.5 to 5.4	24.5	0.8	0.44
Sex (Male)	-0.16	5.9	-2.6 to -0.2	22.3	-0.03	0.98
Wing length	1.1	1.8	0.6 to 1.5	24.6	0.6	0.57
Year (2014)	2.8	4.4	-104 to 3.5	26.2	0.6	0.53
Migration start date	0.43	0.32	0.3 to 0.4	23.7	1.4	0.18
Sea	-14.5	7.1	-18.0 to -13.8	68.3	-2.0	<b>0.046</b>
Land	-17.8	4.4	-20.7 to -17.1	69.9	-4.1	<b>&lt;0.001</b>
Sea + Land	-5.1	5.3	-11.8 to -5.1	58.4	-1.0	0.34
Sahara + Sea	8.8	7.5	2.3 to 10.1	73.2	1.2	0.24
Sahara + Sea + Land	-2.7	7.9	-10.5 to -2.7	73.6	-0.3	0.73

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722 **Table 3.** Results from a GLMM to test how duration of a stop-over after a migration leg varied depending  
723 on the type of barrier crossed, controlling for distance travelled, age, sex, wing length, year and  
724 migration start date, with individual bird included as a random effect ( $n = 54$  migration legs from  $n = 29$   
725 individuals; marginal  $R^2 = 0.45$ , random effects accounted for 0.21 additional variance). Adult, female,  
726 2013 and Sahara set as the intercept; wing length scaled relative to a mean of 78.66 mm and migration  
727 start date rescaled to 0 for earliest day an individual started migration, March 28<sup>th</sup>. Interactions between  
728 barrier type and age ( $F_{5,16.8} = 0.4$ ,  $P = 0.82$ ), or sex ( $F_{2,28.6} = 1.4$ ,  $P = 0.27$ ) or wing length ( $F_{4,19.5} = 0.1$ ,  
729  $P = 0.96$ ) were not significant when added to the model. Significant ( $P \leq 0.05$ ) effects are given in bold.  
730 Note that if barrier type is removed from the model and replaced with duration of the migratory leg prior  
731 to the stop-over, distance becomes positively associated with stop-over duration (see main text for this  
732 model analysis)

733

	Estimate	se	df	<i>t</i> value	<i>P</i> value
(Intercept)	15.2	3.3	36.1	4.6	<0.001
Distance	-0.0023	0.0012	41.7	-2.0	0.050
Age (First year)	1.1	1.2	21.6	0.9	0.40
Sex (Male)	1.7	1.4	20.9	1.3	0.22
Wing length	-0.44	0.42	24.8	-1.1	0.30
Year (2014)	-1.1	1.0	23.6	-1.0	0.31
Migration start date	-0.14	0.08	25.33	-1.8	0.09
Sea	-6.4	2.3	39.8	-2.8	<b>0.008</b>
Land	-6.6	2.1	41.5	-3.1	<b>0.003</b>
Sea + Land	-4.4	1.3	35.6	-3.3	<b>0.002</b>
Sahara + Sea	-0.10	1.7	39.2	-0.06	0.95
Sahara + Sea + Land	6.5	2.1	37.9	3.1	<b>0.003</b>

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738 **Figure legends**

739 **Figure 1.** Example data from one individual Whinchat tagged in 2014 (logger 072) to show how  
740 stationary periods, and migratory and stop-over periods were determined. The left hand graph shows  
741 location data and their variance. The light grey top line labelled GL shows the results of the Geolight  
742 analysis with dips in the line showing non-stationary periods as determined by a significant increase in  
743 variance in sunrise and sunset times; this was also confirmed by exploring how the product of 5-day  
744 moving average standard deviations for latitude and longitude varied, the black top line labelled SD,  
745 where dips in the line represent increased variation. The bottom two lines show the twice daily latitude  
746 (mid-grey line) and longitude (white line) locations calculated from the geolocator light records for a sun  
747 elevation value of -4.5. The right hand map plots median latitude and longitude for stationary periods B  
748 to D as open circles with interquartile ranges plotted as black asymmetric crosses, with the initial  
749 stationary period A being where the individual was resident on winter territory at the site of initial capture  
750 (and where marked with a darker grey rectangle, labelled O, observed on territory after tagging). Note  
751 migratory periods 1 to 3 (initially identified from Geolight) start and end points were ascertained by  
752 visual examination of latitude and longitude traces to determine the points of change; occasionally, as  
753 in this example marked f, Geolight indicated a non-stationary period when there was no other supporting  
754 evidence for a migration. An analysis of variance to compare periods either side of the Geolight non-  
755 stationary period confirmed whether locations had changed: where they were more or less identical as  
756 in this example, the migratory period was ignored. The duration of each migratory leg (1 to 3) and each  
757 stop-over period between them (B and C) were then calculated by from the start and end dates (to the  
758 nearest half day) of each period. Note that for this example, migratory leg 1 was classified as crossing  
759 the Sahara, leg 2 crossing the Mediterranean Sea + Land, and leg 3 crossing Land; if legs 1 and 2 had  
760 been continuous without stop-over B then the leg would have been classified as Sahara + Sea + Land;  
761 if leg 2 had stopped close to the 2 on the right hand map then the leg would have been classified as  
762 Sea; (i.e. these are the barrier types used in Fig. 2). The dotted line connecting A, the start point, with  
763 X represents a flight distance of 2,750 km which is the approximate distance from the study site to the  
764 opposite side of the Sahara for a Whinchat flying due north.

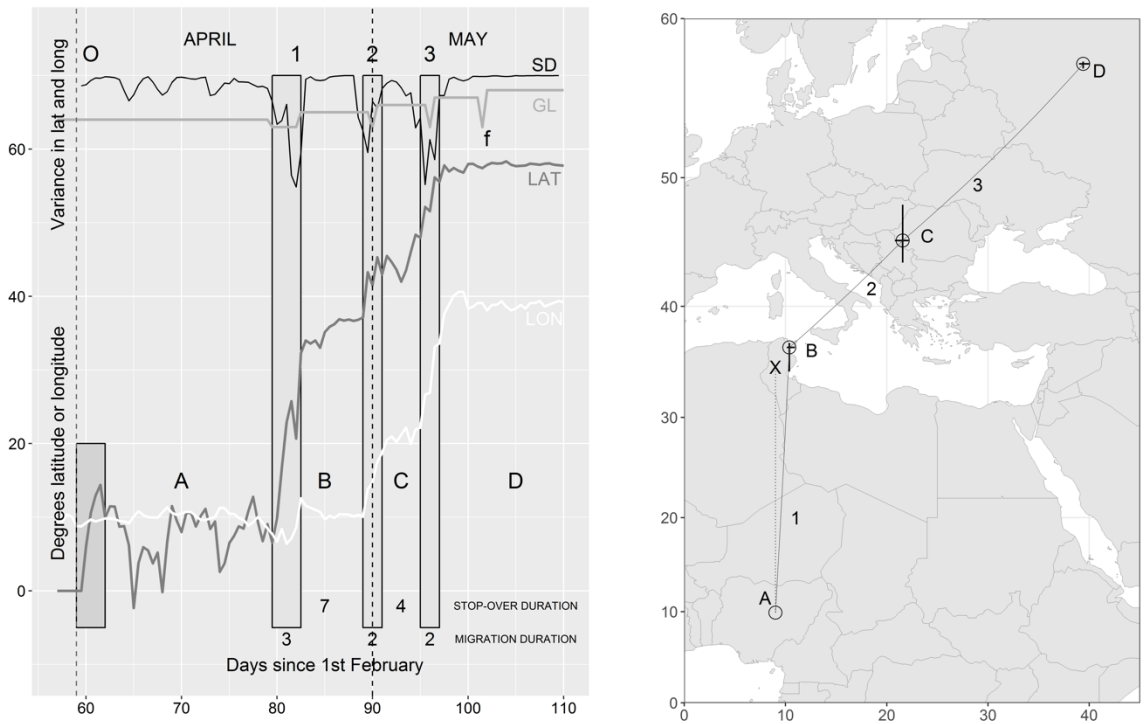
765 **Figure 2.** Stationary periods during spring migration for 35 Whinchats, plotted as grey circles with size  
766 scaled to stop-over duration (longer = larger), and connected by shortest distance migratory tracks, with  
767 length of track proportional to how dark the line is (longer = darker). Starting non-breeding and tagging

768 site shown as an open triangle in Nigeria; breeding locations for 2013 birds shown as filled squares for  
769 2013 and open squares for 2014.

770 **Figure 3.** A. Variation in migration stage distance dependent on barrier type: note that distances  
771 crossing the Sahara only were significantly different from all other barrier types apart from Sea + Land.  
772 B. Variation in hourly speed of migration dependent on barrier type; note that speeds crossing the  
773 Sahara, or the Sahara + Sea, were significantly different from crossing land. C. Variation in stopover  
774 duration dependent on the type of barrier crossed; note that stop-overs after continuous migration,  
775 crossing the Sahara + Sea + Land were significantly longer than almost all other barrier types. Predicted  
776 values from the model in Table 1 for A, Table 2 for B and Table 3 for C are plotted (+/- 1 se) for an adult  
777 male of mean wing length and median migration start date, in 2014, and also mean migration leg  
778 distance for C. Small letters associated with the bars indicate significant differences in pair-wise Tukey  
779 contrasts by barrier type; different letters are significantly different, and unlabelled bars were not  
780 significantly different in any pairwise tests. Numbers within the bars indicate the sample size of migration  
781 legs (overall n = 96 flights without stop-overs of greater than 2 days).

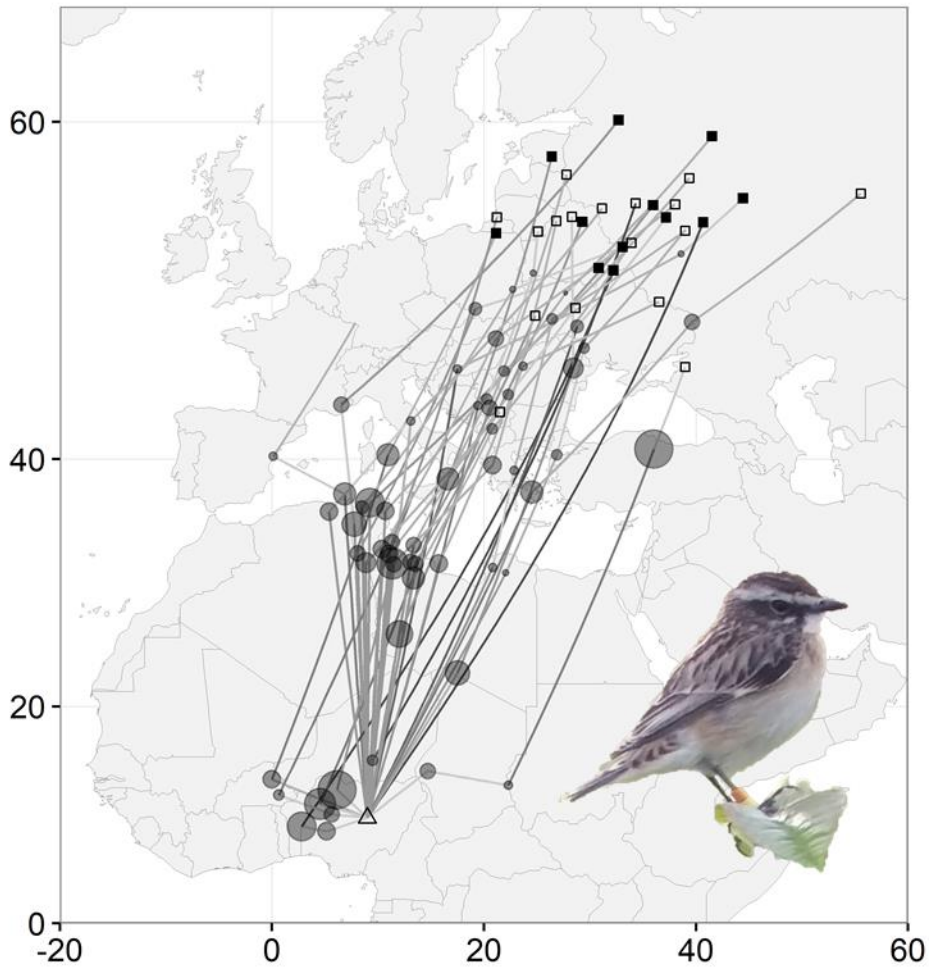
782 **Figure 4.** Variation in Whinchat stopover duration dependent on migration start date. Predicted values  
783 from the model in Table 3 (but without barrier type included) are plotted (+/- 1 se), for an adult male of  
784 mean wing length and median migration distance, in 2014.

785 Figure 1:  
786



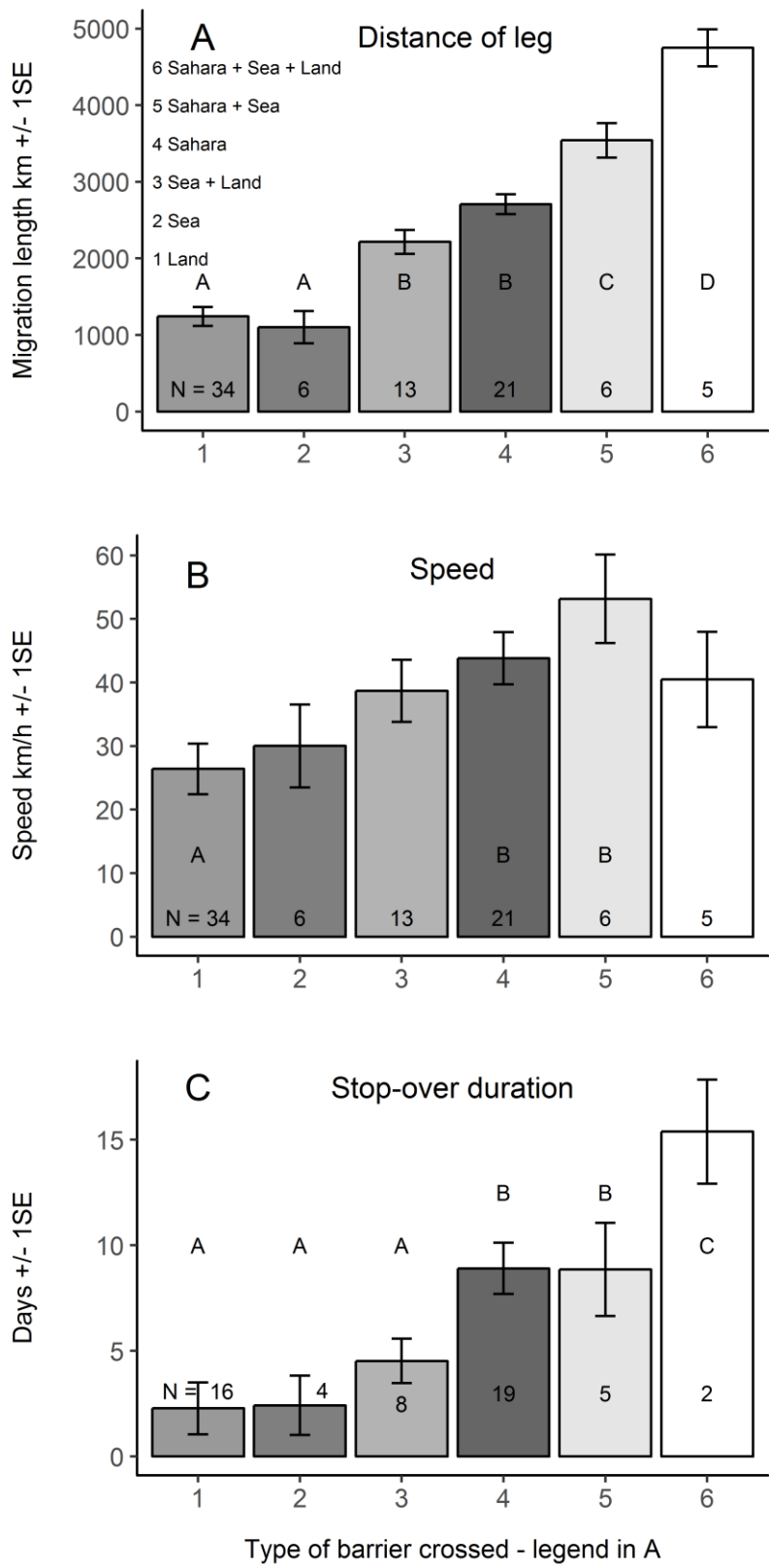
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789 Figure 2:



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792 Figure 3:  
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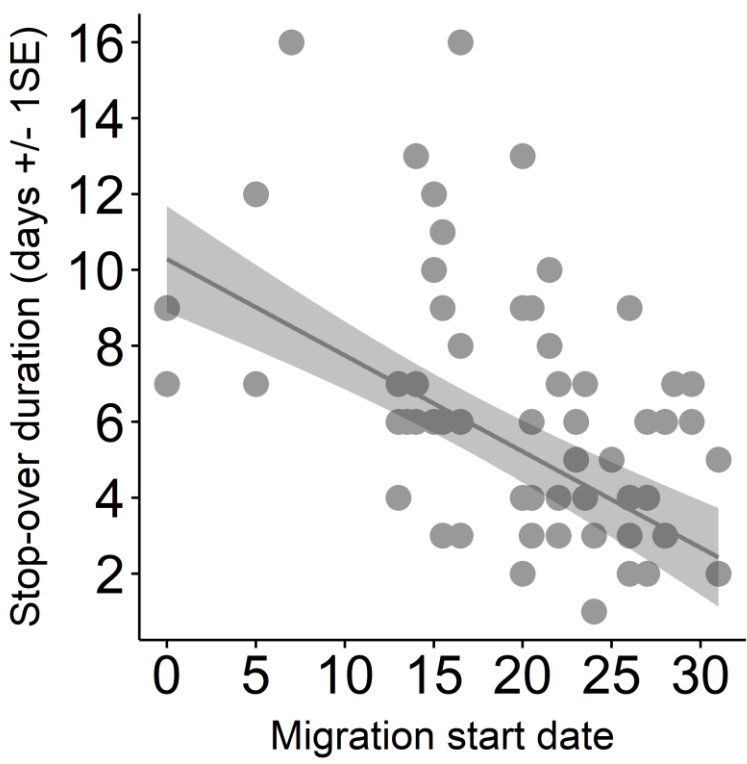


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Figure 4:



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