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

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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.

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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 geolocator. 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).

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Data processing

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

Raw data were downloaded, viewed and preliminarily cleaned using the BASTrack software suite (British Antarctic Survey, Cambridge, UK; see Fox 2010 for an overview of the following processes). We adjusted for clock drift, assuming that any drift was linear. We used the Transedit2 software that is part of the BASTrack software to view raw data as light curves over time. We used our minimum observed value of -2 to define sunrise. False twilight events due to shading from weather or 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   2nd 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

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

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

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

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

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

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

Major stop-overs were significantly longer after a migration leg over the Sahara (8.9 days) or the Sahara immediately followed by the Mediterranean Sea (8.9 days) compared with after a leg over just the Mediterranean Sea (2.2 days), land (2.4 days, continental Europe or Africa outwith the Sahara), or the Mediterranean Sea immediately followed by continental Europe (4.5 days). Continuous migration (without any major stop-overs of more than two days) crossing the Sahara and then the Mediterranean Sea and then continental Europe resulted in significantly longer major stop-over duration compared to 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 ± 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 ± 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 ± 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

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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

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

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

Conclusion

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

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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 28th. 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.

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	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	**0.006**
Wing length	-121.3	53.4	-121 to -111	71.6	-2.3	**0.026**
Year (2014)	-291.4	127.8	-335 to -264	71.6	-2.3	**0.026**
Migration start date	25.7	9.1	23 to 27	71.6	2.8	**0.0061**
Sea	-1606.2	237.6	-1595 to -1808	71.6	-6.8	**<0.001**
Land	-1465.7	145.0	-1445 to -1615	71.6	-10.1	**<0.001**
Sea + Land	-490.9	181.5	-717 to -491	71.6	-2.7	**0.009**
Sahara + Sea	835.0	245.7	532 to 914	71.6	3.4	**0.001**
Sahara + Sea + Land	2043.7	259.9	1741 to 2043	71.6	7.9	**<0.001**

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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 28th. 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	**0.046**
Land	-17.8	4.4	-20.7 to -17.1	69.9	-4.1	**<0.001**
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 28th. 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)

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	Estimate	se	df	t value	P 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	**0.008**
Land	-6.6	2.1	41.5	-3.1	**0.003**
Sea + Land	-4.4	1.3	35.6	-3.3	**0.002**
Sahara + Sea	-0.10	1.7	39.2	-0.06	0.95
Sahara + Sea + Land	6.5	2.1	37.9	3.1	**0.003**

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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

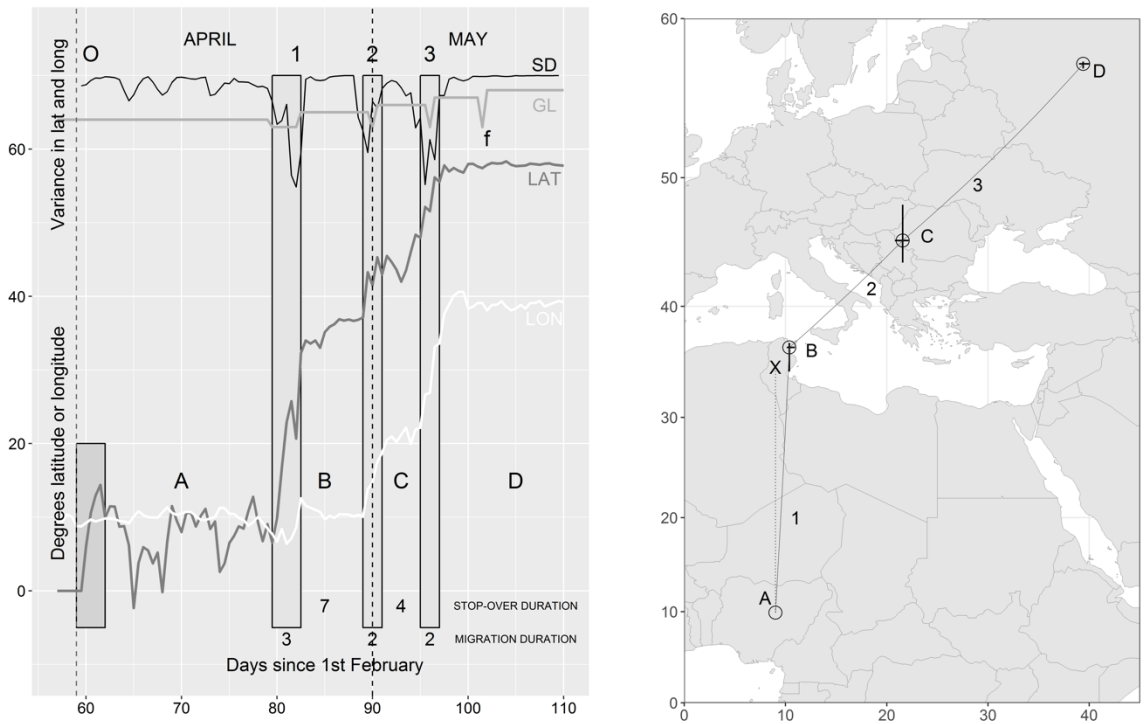764 opposite side of the Sahara for a Whinchat flying due north.

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).
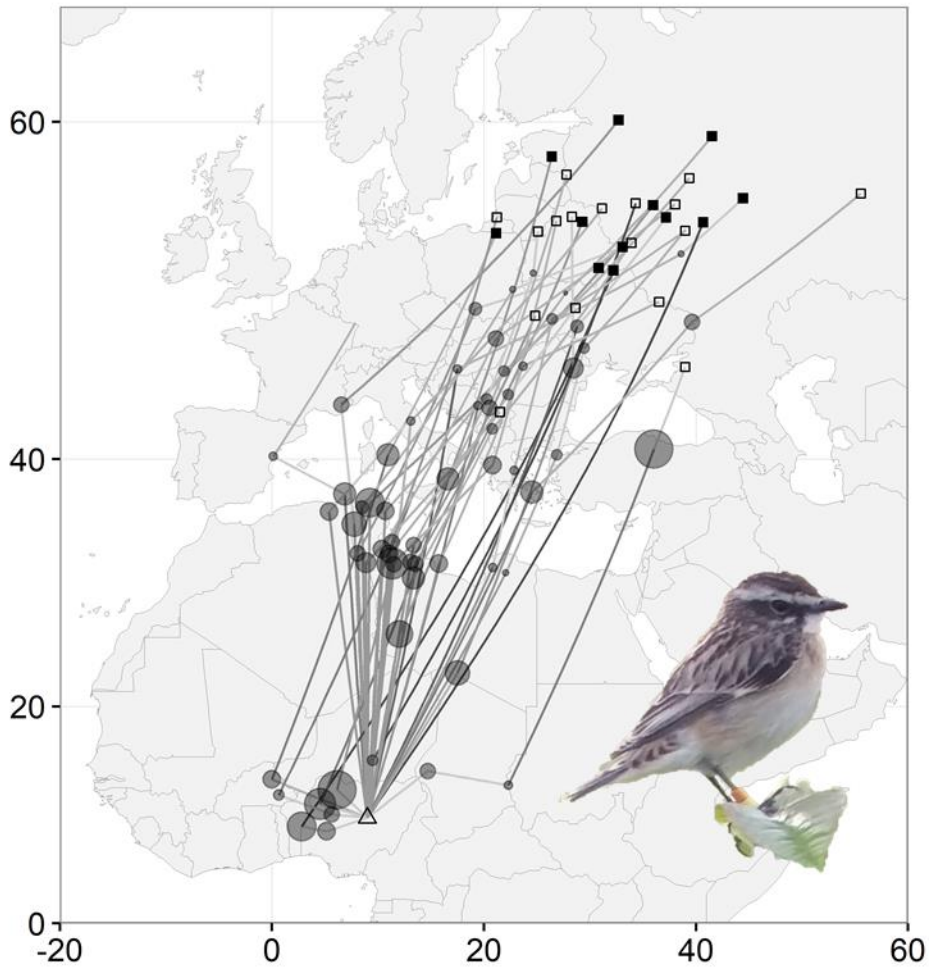
782   **Figure 4**. Variation in Whinchat stopover duration dependent on migration start date. Predicted values

783   from the model in Table 3 (but without barrier type included) are plotted (+/- 1 se), for an adult male of

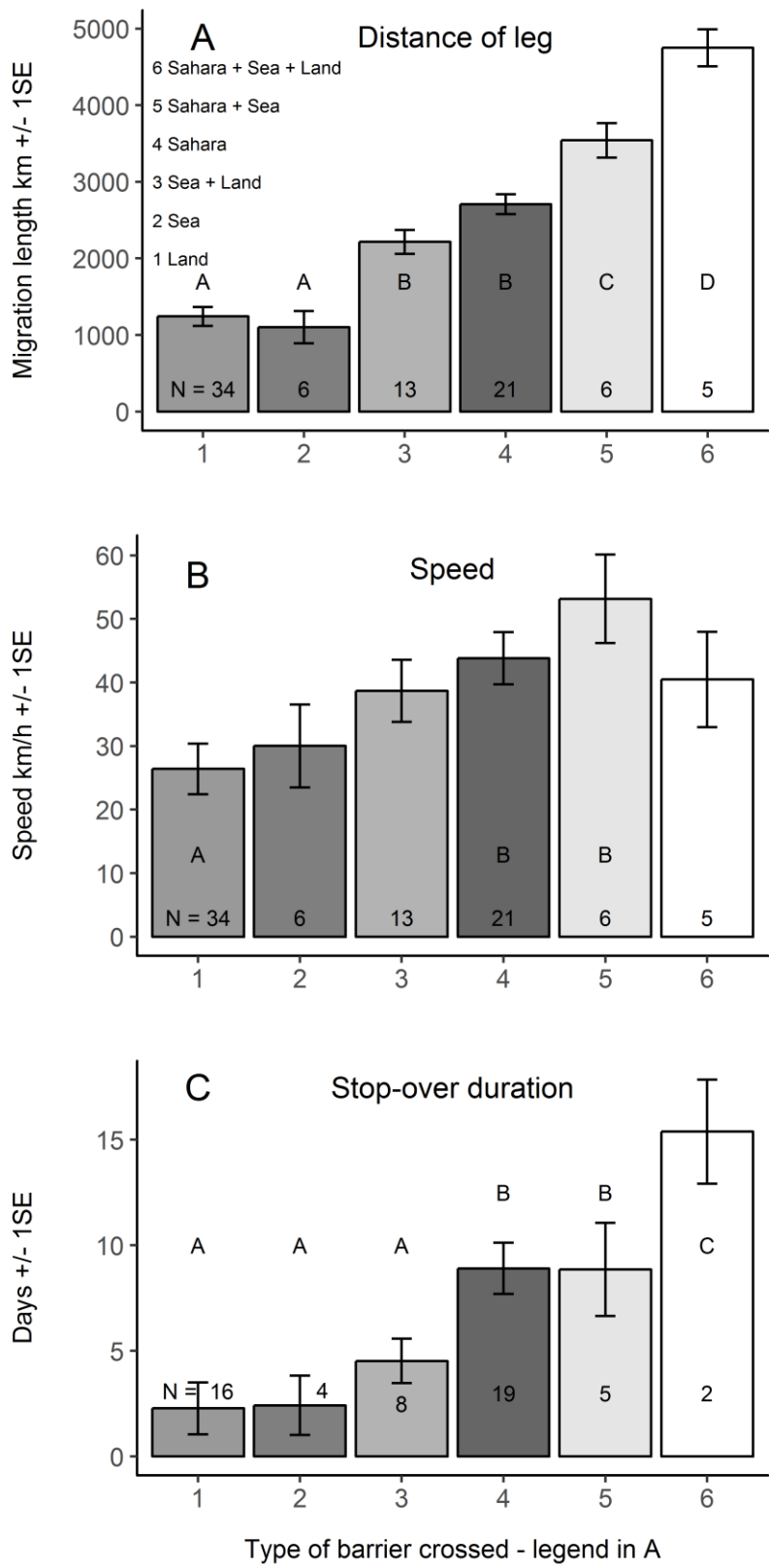784   mean wing length and median migration distance, in 2014.
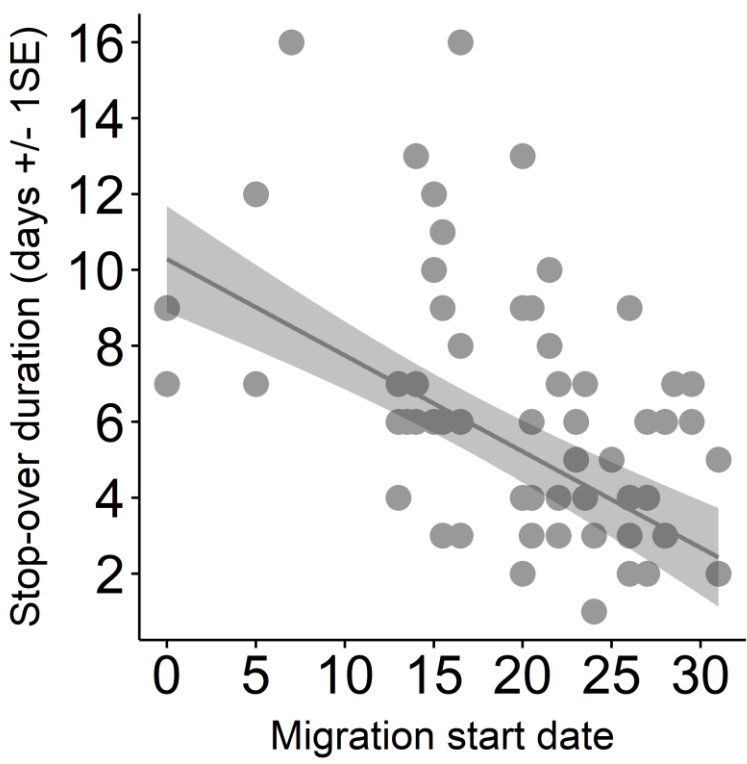
Figure 1:

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Figure 3:

Figure 4: