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2 **Patterns in departure phenology and mass gain on African non-breeding territories**  
3 **prior to the Sahara crossing for a long-distance migrant**

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14

## 15 Abstract

16 Afro-Palaeartic migrants are declining to a greater degree than other European species, suggesting  
17 that processes occurring in Africa or on migration may be driving these trends. Constraints in food  
18 availability on the wintering grounds may contribute to the declines but little is known about when  
19 and where these resource constraints may occur. Sufficient resources are particularly important prior  
20 to spring migration, when migrants must cross the Sahara desert. We examined mass gain and  
21 departure phenology in a long-distance Palaeartic passerine migrant to determine the degree to  
22 which pre-migratory fattening occurs in their long-term non-breeding territories in the Guinea  
23 Savannah region of Africa. We monitored 75 Whinchats *Saxicola rubetra* for departure from their non-  
24 breeding territories in one spring, and analysed mass data of 377 Whinchats collected over three non-  
25 breeding seasons plus 141 migrating Whinchats caught in April over eight years, all within the same  
26 few square kilometres of anthropogenically-modified Guinea Savannah in central Nigeria. Whinchats  
27 left their winter territories throughout April, with males departing on average eight days earlier than  
28 females. However, there was no evidence that time of departure from territory was linked to age,  
29 body size or mass at capture. Whinchats departed their territories with a predicted mass of  $16.8 \pm 0.3$   
30 g, which is much less than the  $\sim 24$  g required for the average Whinchat to cross the Sahara directly.  
31 Comparing departure dates with arrival dates in southern Europe shows a discrepancy of at least two  
32 weeks, suggesting that many Whinchats spend considerable time on pre-migratory fuelling outside of  
33 their territory prior to crossing the Sahara. Over-wintering birds gained mass slowly during February  
34 and March ( $0.03 \text{ g d}^{-1}$ ), and non-territorial or migrating birds at a much higher rate in April (at least  
35  $0.23 \text{ g d}^{-1}$ ), with up to 20% of migrating Whinchats in April potentially having sufficient fuel loads to  
36 cross the Sahara directly from central Nigeria. Our results suggest that most Whinchats leave their  
37 winter territories to fatten up locally or, possibly, by staging further north. Resource constraints are  
38 therefore likely to be particularly focussed in West Africa during mid-April and possibly at staging areas  
39 before the crossing of the Sahara desert.

## 40 Introduction

41 Pronounced declines of long-distance Afro-Palaeartic migrants in comparison to other European  
42 species point towards mechanisms operating on African wintering grounds as possible drivers  
43 (Bohning-Gaese & Bauer 1996, Sanderson *et al.* 2006, Heldbjerg & Fox 2008). Limited resources on  
44 the wintering grounds, especially prior to spring migration, may contribute to these declines (Baillie  
45 *et al.* 2008) by constraining spring fattening and delaying spring departure (Marra *et al.* 1998, Studds  
46 & Marra 2005, 2011). Additionally, migrants wintering in the Sahel region face one of the largest  
47 barriers in the world, the Sahara desert, and therefore availability of adequate resources to sustain a  
48 >2000 km flight during early spring is of critical importance.

49 There is some evidence, however, that food resources around the semi-arid Sahel or Guinea Savannah  
50 wintering grounds may not be a limiting factor for more generalist migrant species, which many long-  
51 distant migrants are thought to be (Cresswell 2014; see Ockendon *et al.* 2012 for species classifications  
52 and trends). For example, Ockenden *et al.* (2012) showed that generalist species are generally  
53 increasing in comparison to specialists, even those wintering in the African humid and southern  
54 bioclimatic regions associated with strong migrant population declines. Furthermore, Hulme &  
55 Cresswell (2012) found that typical human-modified habitat in the Guinea Savannah zone of West  
56 Africa may not limit Whinchat density, and this indicates that, where suitable habitat is present and  
57 species are not at carrying capacity, individuals may be fully capable of not only surviving but also  
58 fattening up in preparation for spring migration in these habitats. This is supported by the fact that  
59 energy requirements in the tropics and sub-tropics are relatively low (Wikelski *et al.* 2003); for  
60 example, wintering Whinchats spend only 11% of their time foraging (Barshep *et al.* 2012), and the  
61 process of meeting energy budgets outwith of migration in sub-tropical savannahs may only require a  
62 few hours foraging a day (Brandt & Cresswell 2009). If this is the case, then overwintering migrants in  
63 the Sahel and Guinea Savannah regions may be able to gain sufficient mass for the first major leg of  
64 their spring migration - the crossing of the Sahara - without leaving their territory or home range. This  
65 strategy would have the advantage of minimizing the risk involved in searching for food in potentially

66 unknown areas (Cresswell 2014), plus reduce the number of staging locations, a factor hypothesised  
67 to be relatively important during spring migration when time schedules are tighter than in autumn  
68 (Hedenström & Alerstam 1997, Weber & Houston 1997; but see McKinnon *et al.* 2013).

69 This study aimed to explore spring departure phenology from African wintering territories in a long-  
70 distance migrant, the Whinchat *Saxicola rubetra*, and link this to patterns in mass gain over the  
71 wintering period in order to infer to what extent pre-migratory fattening occurs on territory. We also  
72 compared departure dates from territory to phenology data from stopover sites in southern Europe  
73 to further determine whether there was time available between departure and arrival in Europe for  
74 additional pre-migratory fuelling.

75 The Whinchat is an Afro-Palaeartic migrant that breeds from western Europe east to Siberia, and  
76 winters in eastern central Africa and south of the Sahel in open landscapes and farmland (Cramp  
77 1988). Although widespread, Whinchats have undergone significant declines over much of their range  
78 over the last 20 years (BirdLife International 2004, Henderson *et al.* 2004). This is thought particularly  
79 to be due to changes in land use on their European breeding grounds affecting breeding success rather  
80 than their wintering grounds (Müller *et al.* 2005; Gruebler *et al.* 2008); nevertheless, ecological  
81 interactions on the non-breeding grounds will be important for any migratory species. Individuals  
82 hold small, distinct territories during the winter (Barshep *et al.* 2012, Blackburn & Cresswell 2015a),  
83 and their preference for open habitat and tendency to perch on low shrubs make them highly  
84 detectable (Hulme & Cresswell 2012).

85 We monitored individually marked Whinchats on a daily basis for departure from their long-term  
86 territories over several neighbouring sites (within the same 40 km<sup>2</sup> location) in central Nigeria  
87 (hereafter referred to as 'resident' Whinchats) to study departure patterns. We used mass data from  
88 the same resident population collected over three non-breeding seasons, combined with mass data  
89 from migrating individuals of unknown origin, but caught in an area within the same location but

90 where Whinchats do not hold territories (i.e. 'non-resident') in April, to analyse temporal patterns in  
91 mass gain on and off territory within the same location prior to the crossing of the Sahara.

92 If birds depart on migration straight from their wintering territories then a series of predictions  
93 regarding departure timing and mass can be made:

94 1) Departure timing from territory for the population should match arrival times in southern Europe  
95 (arrival times on the Italian island of Capri: late-April – mid-May; Jonzen *et al.* 2006) with an estimated  
96 lag time of around a week to cross the Sahara (a conservative estimate based on birds crossing 2500  
97 km at 36 km/hour for 12 hours per day = 5.8 days; Pilastro & Spina 1997, Schmaljohann *et al.* 2007,  
98 Delingat *et al.* 2008). We focus on southern Europe rather than eventual breeding grounds as these  
99 areas represent likely first refuelling stopover sites after the Sahara crossing.

100 2) Individuals will depart when they reach a mass that allows them to cross the Sahara. The Sahara  
101 border is 400 km north of the study site (an 11 hour flight for a small passerine), and the crossing from  
102 central Nigeria is a minimum journey of 2500 km, which is calculated to require 100% fuel load for a  
103 Whinchat (see Delingat *et al.* 2008). This is equivalent to a mass of approximately 24 g. Alternatively,  
104 if masses on departure are lower than these levels this would suggest that Whinchats add mass  
105 outside of their winter territories. If subsequent fattening can occur in the same area (i.e. within a few  
106 kilometres of the territory) then we would expect that Whinchats caught outside of their territories  
107 but still in the local area to show levels of mass that will allow them to cross the Sahara.

108 3) Birds may depart with a mass dependent on their dominance status (age) because territory quality  
109 is likely to correlate with dominance status (Piper 1997). Sub-dominant birds in their first winter  
110 (controlling for sex because males may inherently leave earlier than females to re-establish breeding  
111 territories; Maggini & Bairlein 2012) may depart later or with lower mass than birds of greater age and  
112 experience because they occupy lower quality territories.

113

## 114 Methods

### 115 *Study system*

116 The study took place over three non-breeding seasons (September - April) between 2012 and 2014 on  
117 the Jos Plateau in the Guinea Savannah zone of Nigeria, West Africa (09°53'N, 08°59'E) where many  
118 Afro-Palaeartic migrants winter (Fig. 1). We studied six sites over a 4000 ha area east of Jos  
119 containing typical overwintering habitat for Whinchats. Sites consisted of degraded Guinea Savannah:  
120 open scrub with moderate levels of grazing and small subsistence farming. Sites were selected on the  
121 basis of containing suitable Whinchat habitat and for logistical reasons, and did not differ significantly  
122 in habitat characteristics (Blackburn & Cresswell 2015a). Sites ranged from 50 to 200 ha in size, were  
123 no more than 2 km apart, and were surrounded by similar areas of habitat. Whinchats were common  
124 at a much larger scale around the whole study location (see Hulme & Cresswell 2012).

125 Whinchats were caught with spring traps with live bait and mist nets, both using a playback lure. All  
126 captured birds were uniquely colour-ringed. Most individuals were either captured in the winter of  
127 2014 or had returned to territories occupied in previous winters, resulting in a population of  
128 individually recognisable resident birds for departure study in April 2014. We fitted geolocator devices  
129 (~0.65 g; see Appendix A for permit information) to approximately half of the birds as part of a tracking  
130 study not considered here, but the opportunity was used to examine the effects of experimental  
131 application of additional mass on departure dates. Data from non-resident Whinchats of unknown  
132 origin (either migrants passing through or local birds off their territories) were collected as part of a  
133 Constant Effort Ringing Scheme (CES; see Stevens *et al.* 2013 for details) during April from 2002 to  
134 2013 inclusive, in an area adjacent to the territorial study areas where few whinchats hold territories  
135 (Fig. 1).

136 Flattened wing chord length (to the nearest 0.5 mm), tarsus length (to 0.1 mm), body mass (to 0.1 g  
137 using digital scales) and moult score were measured following Svensson (1992). Whinchats were sexed  
138 and aged as either first-winter (hatched the previous year; EURING code 5) or adult (hatched before

139 the previous year; EURING code 6), using a combination of features described by Svensson (1992) and  
140 Jenni & Winkler (1994). Detailed photographs were taken of all birds, and age and sex were  
141 independently corroborated by both A.R. and E.B.

#### 142 ***Estimating departure dates***

143 Mapping of marked individuals was carried out at all six sites from 3<sup>rd</sup> March 2014 by systematically  
144 walking each site every two to four days using binoculars and a telescope. Whinchats characteristically  
145 spend 80% of their time perching on the top of small bushes in open habitat (Barshep *et al.* 2012),  
146 therefore we could accurately identify the majority of individuals present during any visit. From 2<sup>nd</sup>  
147 April, known territories of marked birds at three of the six sites (for purposes of practicality) were  
148 visited almost daily to monitor for departure (mean number of visits over 24 days per individual = 20.1  
149  $\pm$  3.4 SE, n = 1509 total visits; including a decrease in territory visit frequency once an individual was  
150 not seen for five consecutive visits). If an individual was not resighted after five consecutive visits then  
151 it was assumed departed from its winter territory. All territories were visited at least every two-three  
152 days over the entire monitoring period to confirm absence and detect whether individuals were  
153 moving over a larger local scale than their winter territory just prior to departure. Territorial birds are  
154 extremely site-faithful: only one bird was recorded moving ~500 m from original territory prior to  
155 departure after unusual weather conditions and no others were seen outside their territories during  
156 departure monitoring.

157 Departure was measured as relative days after the first bird departed (day zero; 1<sup>st</sup> April). Only  
158 individuals which were consistently seen on territory (i.e. resident in the study area over winter) were  
159 included in analyses (n = 75). Birds visited four times or less during April before they departed were  
160 only included if they had been resighted regularly on territory prior to daily departure monitoring  
161 beginning (n = 5). These birds departed between 25<sup>th</sup> March and 1<sup>st</sup> April and were assigned a  
162 departure date of day zero (1<sup>st</sup> April) because their exact departure date was unknown. Although error  
163 in departure is higher for these individuals than the rest, excluding them from analyses did not

164 significantly change any results, therefore they were retained in analyses. Additionally, assuming these  
165 five birds departed the day after they were last resighted as opposed to 1<sup>st</sup> April did not significantly  
166 affect mean or standard deviation of departure date across the monitored population ( $13.0 \pm 8.1$  SD  
167 and  $13.4 \pm 7.25$  SD days after 1<sup>st</sup> April respectively). Error in departure was calculated to be  $1.4 \pm 1.1$   
168 SE days after last resighting ( $n = 70$ ; Appendix B).

## 169 ***Analysis***

### 170 *Modelling departure*

171 Model selection for all analyses was carried out using the information-theoretic approach based on  
172 Akaike's Information Criterion (AIC; Burnham & Anderson 2002). Candidate general linear models  
173 (LM) were first constructed using the subset of the birds captured in 2014 which had biometric and  
174 mass data collected within 3 months of departure ( $n = 57$ ). Age, sex, wing length, tarsus length, mass  
175 and time of day were included as main effects. Site and attachment of geolocator were also included  
176 as fixed factors to control for any confounding effect they may have had. Replacing tarsus and wing  
177 length with a single principal component that summarised 53% of the variation did not change any of  
178 the models in terms of biological or statistical significance. Component models were compared using  
179 AIC, and where there was no clear optimum model, model averaging was applied (including candidate  
180 models with  $\Delta AIC < 4$ ) and variable estimates and importance are presented. Because we lacked  
181 recent body size data for 18 individuals, candidate models were constructed again for all birds but  
182 excluding mass, wing and tarsus lengths to maximise sample sizes, and model selection repeated as  
183 above. Where individuals had been captured multiple times in 2014, we used the most recent capture  
184 event data to avoid pseudo-replication and to apply the mass nearest to departure. Using first  
185 captures instead makes no difference to model selection outcome. Repeating analyses with all  
186 captures and recaptures, and including individual and site as random effects in a linear mixed model  
187 (LMM; lme4 package, Bates *et al.* 2014), did not affect statistical or biological results, therefore we  
188 presented the simpler fixed effect models. There were no significant quadratic effects in any model.



189 *Predicting mass at departure*

190 In order to predict mass at departure, we modelled mass at capture against days until departure (from  
191 capture) using a general linear model for all resident birds sampled, controlling for tarsus length, age,  
192 sex and time by including these as predictor effects and comparing candidate models using AIC. The  
193 best model included only mass (days until departure  $\sim$  mass; see results), indicating that mass at  
194 capture is related to when the individual will depart from that date. Because the intercept of the  
195 model (mass at 0 days = departure) is an extrapolation as we lacked samples from birds less than 6  
196 days before departure, fitting a linear relationship including any time prior to the commencement of  
197 mass gain would bias our estimate of departure mass downwards. Therefore we carried out a  
198 sensitivity analysis (reported in the results), reducing the sampling period to samples less than 70 days  
199 from departure, then to samples less than 60 days from departure, and so on, to ascertain any change  
200 in rate of mass gain prior to departure.

201 *Mass patterns over non-breeding season*

202 Patterns in mass gain were analysed using birds with complete biometric data captured over the three  
203 non-breeding seasons of the study to increase sample sizes and to allow description of mass over the  
204 entire winter period as well as departure ( $n = 377$ ). Where birds were caught more than once, the  
205 first capture event data was used, unless any data was missing for first capture or there was a capture  
206 available in March or early-April, when this single capture was used instead to balance sample sizes,  
207 because there were many fewer captures during March and April during the study.

208 We split the wintering season into two periods (before and after 1<sup>st</sup> January) to explore strategies of  
209 mass gain over the winter: a model containing all data showed a significant interaction between these  
210 two periods and mass gain trajectory so justifying this split (see results). Candidate models predicting  
211 mass were constructed using sex, age, tarsus, wing, date, time, season, site and stage of pre-breeding  
212 partial moult (moulting/not-moulting as a 2-way factor) as main effects, and compared using AIC as  
213 above.

214 We estimated mass gain for non-resident Whinchats using the CES April mass data. An LM model was  
215 constructed with mass as dependent variable and date, sex, time, wing, year and site as predictors,  
216 using as similar models as possible to that found for the resident birds in the second half of winter  
217 (described above and in the results below) so that mass patterns would be as comparable as possible.  
218 As most birds had finished moulting by April we did not include moult stage. We compared predicted  
219 mass gain between the two models (i.e. February and March period against April) by comparing the  
220 confidence intervals of the parameter estimates for date. We did not model all the data together  
221 because they were collected at different sites, and the CES data was missing a reliable estimate of age  
222 and tarsus for most individuals. We used these CES data only to test whether fuelling rates  
223 (acknowledging that any estimate will be an underestimate; Minias & Kaczmarek 2013) were different  
224 for birds that were not on winter territories or on passage.

#### 225 *Calculating flight ranges*

226 Flight ranges were calculated in the following way: to calculate the average fuel load ( $f$ ), the following  
227 equation was used:  $f = [(m - m_i) / m_i]$ , where  $m$  = actual mass and  $m_i$  = lean body mass (LBM) (Delingat  
228 *et al.* 2008). An average lean body mass of 12.8 g was used, based on the average mass of Whinchats  
229 captured after crossing the Sahara with fat and muscle scores of zero (Pilastro & Spina 1997). A lower  
230 average lean body mass of 11.6 g was identified by Salewski *et al.* (2010), and although using this value  
231 did not alter final conclusions, we include ranges calculated from this value in the text as an example  
232 of what is possible for a Whinchat if it utilizes all possible energy reserves (including muscle mass).  
233 These two values were used because very few Whinchats were recorded in this study in poor condition  
234 (i.e. very low fat and muscle scores); therefore we suggest they did not accurately represent lean body  
235 mass. The 12.8 g value was similar to the lightest Whinchats recorded on our site, with 25% of captures  
236 under 14 g. Applying parameters higher than 12.8 g resulted in very high expected departure mass,  
237 which have not been recorded in sub-Saharan Africa, supporting the use of these chosen LBM  
238 parameters. Flight range in km ( $Y$ ) from estimated fuel load at departure was calculated using the

239 method according to Delingat *et al.* (2008):  $Y = 100 \times U \times \ln(1 + f)$ , where  $U$  = ground speed and  $f$  = fuel  
240 load. We used the air speed of 36 km h<sup>-1</sup> reported for small passerines (Bruderer & Boldt 2008).

241 Analyses were carried out in R software version 3.1.1 (R Core Team 2014). All means are given  $\pm$  1  
242 standard error (SE) unless otherwise stated.

## 243 Results

### 244 *Phenology of departure*

245 In total, 75 individually marked Whinchats were monitored for departure over April 2014 in central  
246 Nigeria. Birds departed over a four-week period between 25<sup>th</sup> March and 24<sup>th</sup> April 2014 (mean = 14<sup>th</sup>  
247 April  $\pm$  7.3 SD days; Fig. 2).

248 Sex was retained in all top models predicting departure for individuals with recent mass and biometric  
249 data (captured in February and March 2014,  $n = 57$ ), and was the only factor retained in the top model  
250 (Table 1a). Model averaging of all models with  $\Delta AIC < 4$  also resulted in sex being the only significant  
251 factor influencing departure date (Table 2a).

252 Repeating the analysis with all birds ( $n = 75$ , Table 1b) confirmed that sex was still the only significant  
253 factor: although site was retained in the top model, model averaging indicated that site was not a  
254 significant predictor (Table 2b). The optimal model to predict departure timing therefore contained  
255 sex only ( $F_{1,75} = 31.5$ ,  $R^2 = 0.30$ ,  $p < 0.0001$ ), with males leaving on average 8 days before females (Fig  
256 2). Departure was not significantly related to age, although statistical power for males was low due  
257 to low numbers of first winter males (adults:  $n = 21$ ; first-winter:  $n = 9$ ). However, there was clearer  
258 evidence that there was no difference in departure timing between adult and first-winter females  
259 (adults:  $n = 26$ , first-winter:  $n = 19$ ; Fig 2). Whether a bird had been fitted with a geolocator was  
260 retained in some of the top models when all birds were included, although it was not a significant  
261 factor when averaged out across top models, nor was it statistically significant in the models in which

262 it was retained. These models in any case predict a very small biological effect: birds with a geolocator  
263 left on average  $1.4 \pm 4.3$  days earlier than birds without geolocators (Table 2b).

#### 264 ***Mass gain at departure***

265 Days until departure from time of capture significantly predicted mass with an intercept (i.e. predicted  
266 mass on departure) of  $16.8 \pm 0.3$  g, using all data from less than 80 days before departure (Fig. 3).  
267 Rates of mass gain over the period sampled (6 – 77 days before departure) were  $0.03 \pm 0.007$  g per  
268 day (Fig. 3). The value of the intercept did not change significantly between periods sampled (birds  
269 captured within 80 days from departure as above,  $n = 57$ ; <70 days, intercept =  $16.8 \pm 0.3$  g,  $n = 55$ ;  
270 <60 days,  $16.5 \pm 0.4$  g,  $n = 45$ ; <50 days  $16.2 \pm 0.4$ ,  $n = 36$ ; <40 days,  $16.5 \pm 0.5$ ,  $n = 25$ ; <30 days,  $16.9$   
271  $\pm 0.6$ ,  $n = 21$ : see Fig. 3) suggesting that the intercept calculated using all of the available data was  
272 robust for the period up until 6 days before departure.

#### 273 ***Comparing phenology with southern Europe***

274 Whinchats pass through the Italian island of Capri between 22<sup>nd</sup> April (mean of earliest 10<sup>th</sup> percentile)  
275 and 12<sup>th</sup> May (mean of the latest 10<sup>th</sup> percentile; Jonzen *et. al* 2006 supplementary material): note  
276 that there are almost no ringing recoveries of Whinchats in Africa and so limited data to support this  
277 route except for a single Whinchat ringed on the study site recovered on spring passage in Northern  
278 Italy (unpublished data) and our own preliminary geolocator data which shows this route is common  
279 (unpublished data). This range of 20 days is similar to the departure range in our population study,  
280 and indicates that there is a three-week period between birds departing territory and arriving in  
281 southern Europe.

#### 282 ***Seasonal mass gain patterns***

283 An overall model using mass data of 377 resident colour-ringed Whinchats showed that the  
284 relationship between mass and date was significantly dependent upon whether a Whinchat was  
285 captured before December or after January (period \* date, additional mass gained in the second

286 period with date =  $0.026 + 0.01 \text{ g}$ ,  $t = 3.7$ ,  $P < 0.001$ ; full model including all variables in Table 3, overall  
287 adjusted  $R^2 = 0.34$ ,  $F_{16, 360} = 13.3$ ,  $P < 0.0001$ ; Fig. 4). Models predicting mass in the first half of the non-  
288 breeding season show that only tarsus length, wing length and year of capture were retained in the  
289 top models (Table 3a), and also had high importance when averaged out across top models (Table 4).  
290 Birds caught in 2013 were slightly heavier than those caught in 2012. Sex, age, date of capture, site  
291 and time of day were rarely retained in top models and model averaging across top models confirmed  
292 that these variables had low importance: during early winter mass remained uniformly low (Fig. 4). In  
293 contrast, model comparison for the second half of the wintering period presented a clear optimum  
294 model which retained tarsus length, sex, age, date of capture, time of day, stage of moult and site as  
295 predictors of mass (Table 3b; full model coefficients in Table 5). The Akaike weight of this model shows  
296 that it was 2.3 times more likely than the next ranking model ( $\omega = 0.57$  versus 0.25) which additionally  
297 retained wing length. This model predicted that mass in the second half of the wintering season  
298 increased with date, tarsus length, time of day, moult stage and that males were heavier than females  
299 (Fig. 4) and adults were heavier than birds in their first winter (Table 5).

300 There were 141 captures (no recaptures) in April from the CES (constant effort ringing; 5 in 2002, 30  
301 in 2003, 16 in 2004, 18 in 2007, 7 in 2008, 14 in 2010, 10 in 2011 and 41 in 2013) from non-resident  
302 birds. Mass increased significantly with date in April ( $0.228 \pm 0.063 \text{ g/day}$ ,  $t_{1,127} = 3.6$ ,  $P = 0.0005$ ; Fig.  
303 4) controlling for year, time of day, location, wing length and sex, and the confidence limits of this rate  
304 of change did not overlap with the confidence limits of the much lower rate of change during January  
305 to March ( $0.031 \pm 0.009 \text{ g/day}$ ; note the coefficient differs slightly from this value given above because  
306 a slightly different model structure was used to allow the most similar comparison possible between  
307 resident bird data and that from the CES transient birds, due to tarsus length and age not being  
308 available for CES data). Males were also heavier than females throughout April ( $1.4 \pm 0.5 \text{ g heavier}$ ,  $t_{1,127} = 2.9$ ,  $P = 0.008$ ; Fig. 4).

### 310 **Flight ranges**

311 A fuel load of 100% LBM was calculated to be required to cross the Sahara from the study site in  
312 central Nigeria (~2500 km), and 74% LBM from the Saharan border (~2000 km). A mass of 16.8 g –  
313 the predicted departure mass from territory for the resident birds in 2014 – was calculated to be  
314 between 31% or 45% of lean body mass, which allows an estimated flight range of 979 km or 1333 km  
315 (depending on whether the higher or lower LBM was used, respectively; Fig. 5). If we use the range of  
316 observed body masses (n = 141) from April CES non-resident birds then predicted ranges vary  
317 considerably. Assuming a higher lean body mass then c. 5% of Whinchats in April could cross the  
318 Sahara directly from the study site at Jos without a stopover, and assuming the lower lean body mass  
319 then 20% of Whinchats could directly cross the Sahara (Fig. 5).

## 320 Discussion

321 Whinchats departed their wintering territories in central Nigeria between late March and late April,  
322 with males departing earlier than females on average; however, no patterns relating to age, body size  
323 or condition at capture were found. Departures were unlikely to have been confounded by mortality  
324 because winter survival rates for Whinchats are extremely high, with probability of return the  
325 following year being unrelated to the timing of departure (Blackburn & Cresswell; unpublished data).  
326 Whinchats were predicted to depart from territory with an average mass of 16.8 g, 31 - 45% of lean  
327 body mass (LBM). This suggests that most Whinchats do not have sufficient fuel loads for a direct 2500  
328 km minimum crossing of the Sahara (i.e. without further fattening) when they leave their primary  
329 winter territories, a journey which is calculated to require 100% LBM (23.2 – 25.6 g) from central  
330 Nigeria. Moreover, it suggests that Whinchats at most only start to fatten up on their winter  
331 territories, and then depart with relatively low fuel reserves to fatten up elsewhere, possibly further  
332 north. The small and gradual amount of mass gain from January to March is perhaps more consistent  
333 with physiological changes, including increased reserves to deal with the cost of moulting (see Lind &  
334 Gustin 2004, Bauchinger & Biebach 2006, Fox & King 2013) and increased fat reserves associated with  
335 increasing foraging unpredictability as the dry season progresses (McNamara & Houston 1990,

336 Houston & McNamara 1993). Although it is possible that many individuals could potentially have  
337 gained more mass on territory between capture and departure from their territory, it is very unlikely  
338 that the individuals captured within two weeks of departure ( $n = 8$ ) had enough time to gain enough  
339 mass on territory, and probably impossible for those caught within a week of departure ( $n = 4$ ).  
340 Maximum fuel deposition rates found in comparably sized species Common Redstart *Phoenicurus*  
341 *phoenicurus* and Common Whitethroat *Sylvia communis* on stopover in Senegal during spring  
342 migration were found to be between  $2.6 \pm 2.2$  and  $3.5 \pm 2.6\%$  LBM/day, respectively (Bayly *et al.* 2012;  
343 no information on the Whinchat available), which translates to a mass gain of 0.3 - 0.5 g per day for  
344 the average Whinchat. It is therefore unlikely that many of the sampled resident Whinchats, even if  
345 they were indeed fattening up at a faster rate just prior to departure from their territory, would be  
346 fuelling at a sufficient rate to reach a mass sufficient to cross the Sahara.

347 Comparing departure dates from territory to arrival timing in southern Europe also provides evidence  
348 that pre-migratory fattening occurs after departure from territory. Whinchats pass through the Italian  
349 island of Capri (likely to be one of the first stops for many migrants after the Sahara) three weeks after  
350 departing territories in Nigeria. This period is much longer than expected if birds were leaving directly  
351 from their wintering territories if it takes only 2 – 6 days to cross the Sahara (Schmaljohann *et al.* 2007,  
352 Delingat *et al.* 2008). Our unpublished geolocator data shows that Whinchats cross the Sahara directly  
353 without stopping and then refuel in North Africa for several days (Blackburn *et al.* unpublished data).

354 There are three non-mutually exclusive possible explanations for why birds may not reach maximum  
355 fuel load on winter territory: 1) limited resources on a small territory do not allow sufficient fuel  
356 loading to cross the Sahara, and therefore birds abandon their territory to search for better quality  
357 habitat locally; 2) habitat quality in the area is not sufficient for migratory fuelling and therefore birds  
358 abandon their territory and move out of the local area to find better quality habitat regionally; or 3)  
359 resources on territory or locally are not limiting but birds move north as a strategy to reach maximum  
360 fuel loads closer to the Sahara desert, the border of which begins roughly 400-500 km further north,

361 even though fattening on territory (and/or locally) is possible. Our results suggest that habitat quality  
362 in the area generally is not a limiting factor, with 5 - 20% of transient individuals caught locally  
363 potentially able to cross the Sahara at the time of capture, although it cannot be ruled out that these  
364 birds fattened up further south. However, there was little evidence that birds were staying in the local  
365 area encompassed by the study sites to fatten up because no colour-ringed birds were resighted  
366 between sites in April or were caught nearby at the CES site over the three-year study period.  
367 Therefore the most likely explanation may be that birds are moving further north to fatten up as close  
368 to the desert barrier as possible. Although individuals with sufficient fuel loads to cross the Sahara  
369 are captured in the region, the average mass in April is around  $20.0 \pm 3.3$  g (see also Smith 1966 which  
370 reports almost identical masses at a nearby site in central Nigeria), indicating that most Whinchats  
371 reach some level of migratory condition in this region, but may delay depositing the maximum fuel  
372 load until further north. Although very few data exist for Whinchats in northern Nigeria, Fry (1969)  
373 found slightly lower masses (19.2 g [SD not reported],  $n = 11$ ), which would be consistent with birds  
374 requiring lower fuel loads to cross a shorter distance, although more data is needed to confirm this.  
375 Agriculture and vegetation extends another 400 km north to the edge of the desert from Jos, and  
376 important wetlands such as Hdejia-Nguru and Lake Chad lie 350 and 600 km to the northeast  
377 respectively. Although Whinchats are unlikely to be found in typical wetland habitat in the non-  
378 breeding season (e.g. Bayly *et al.* 2012), the surrounding vegetation and farmland may provide crucial  
379 resources in gaining sufficient fat for the >2000 km desert crossing from the desert border.

380 The hypothesis of moving north to fatten up is consistent with other studies which have shown that  
381 passerines tend to delay depositing large fuel loads during migration until reaching a major ecological  
382 barrier, such as the Sahara (Schaub & Jenni 2000, Ottosson *et al.* 2005), and that timing of maximum  
383 fuel loading is inherently linked to the latitude of these barriers (Fransson *et al.* 2001). Depositing  
384 maximum fat loads as late as possible avoids the increased predation risk associated with high fuel  
385 loads (Kullberg *et al.* 1996, Dierschke 2003) and the maintenance of high body mass (Alerstam &  
386 Lindström 1990, Klaassen & Lindström 1996). Departing from 400 km further north at the desert



387 border reduces the required fuel load to cross the Sahara by at least 25%, which may outweigh the  
388 advantages of remaining on territory or in central Nigeria. However, Ottosson *et al.* (2005) found  
389 evidence that many Garden Warblers (*Sylvia borin*) had sufficient mass to depart directly from this  
390 zone in the spring, rather than moving north, suggesting that other species may have different  
391 strategies, or their “barrier” starts at a lower latitude or that the best fattening area is in the Guinea  
392 Savannah. An alternative hypothesis, of course, is that migrants can refuel during stopovers in the  
393 Sahara: whether this is strategy at all for Whinchats requires further study.

394 Although we cannot measure mass gain immediately prior to departure, if mass at departure was an  
395 important driver of departure then patterns in mass gain over the non-breeding period may indirectly  
396 affect departure timing, for example, via processes such as dominance-based habitat segregation  
397 whereby dominant birds (e.g. males and adults) have access to the best resources (Marra & Holmes  
398 2001, Arizaga & Bairlein 2011). However, although mass in the latter part of the non-breeding season  
399 differs between sexes, ages and sites – potentially indicating dominance-based access to resources –  
400 this is not reflected in departure patterns, suggesting that mass is not a key driver of departure from  
401 territory. Sex was the strongest predictor of departure, with males departing territories on average  
402 eight days before females, reflecting patterns observed on arrival at the breeding grounds in  
403 Whinchats (Tøttrup & Thorup 2008) and other migratory species (Francis & Cooke 1986, Cooper *et al.*  
404 2009). However, neither age nor body size appeared to have any relationship with timing of  
405 departure, although segregation by these traits is sometimes reported on arrival at the breeding  
406 grounds (Stewart *et al.* 2002, Cooper *et al.* 2009, Risely *et al.* 2013).

407 In order to understand the mechanisms behind patterns in departure and mass, it should be noted  
408 that migratory timing is controlled by both endogenous (e.g. circannual rhythm) and by exogenous  
409 (e.g. resource availability) mechanisms (Gwinner 1986, Studds & Marra 2005, 2011, Maggini & Bairlein  
410 2012). Resource availability and its relationship with condition has been identified as a significant  
411 limiting factor during spring departure in the Neotropics, with American Redstarts *Setophaga ruticilla*

412 occupying better quality habitat reaching migratory condition and departing earlier on spring  
413 migration than those occupying poorer quality habitat (Marra *et al.* 1998, Studds & Marra 2005). This  
414 may not be the case in the Old World, however, where suitable wintering habitat may be more  
415 abundant (see Newton 2008), and differences in quality between habitats are not so well defined  
416 (Cresswell 2014). Indeed, there is no evidence of sex or age based habitat occupancy for wintering  
417 Whinchats over the study area based on fine-scale habitat characteristics (Blackburn & Cresswell  
418 2015a, 2015b), although it is possible these habitat characteristics do not necessarily reflect prey  
419 abundance. A lack of segregation would be expected in an area with low competition (Whinchats are  
420 not at carrying capacity in this area; Hulme & Cresswell 2012) and where energy costs are low  
421 (Whinchats spend only 11% of the day foraging; Barshep *et al.* 2012), indicating that differences in  
422 territory quality are probably not important for overwinter survival. In this system, patterns in  
423 departure phenology may more closely reflect differences in endogenous triggers rather than  
424 resource constraints. Studies on captive birds have shown that there are differences in endogenous  
425 timing of migration between populations (Maggini & Bairlein 2010) and sexes (Coppack & Pulido 2009,  
426 Maggini & Bairlein 2012), with males preparing for departure earlier than females independent of  
427 external factors; however, this has not been shown to be linked to age, although experimental  
428 evidence for this is lacking due to the difficulty is keeping individual birds captive over many years (but  
429 see Sergio *et al.* 2014 for age effects in a free-living raptor species). Therefore the pattern of departure  
430 we observed could be expected if departure timing from territory was triggered by endogenous  
431 mechanisms and relatively unconstrained by resource limitations. If Whinchats mostly fatten up  
432 outside of their territories, then territory quality cannot be a constraining factor, and therefore  
433 unlikely to have a strong effect on departure timing. Resource availability and dominance-related  
434 differences in access to resources may, however, become a constraining factor during migration,  
435 especially prior to the Sahara crossing when individuals need to deposit larger reserves of fat to fuel  
436 the desert crossing (Biebach 1992).

437 Overall, this study suggests that although this population of Whinchats may reach some level of  
438 migratory condition on territory (particularly if fuel deposition rate increased a few days just before  
439 territory departure), it seems more likely that most do not fatten up within their wintering territories.  
440 It is unknown whether they then reach maximum mass locally or move further north to fatten up  
441 closer to the Sahara, where they would require a smaller fuel load due to the shorter distance to travel.  
442 Indeed, many Palaearctic migrants, including Whinchats, have been captured in April on stopover near  
443 Lake Chad in north-east Nigeria (Fry 1969), although these areas have not been systematically studied.  
444 This is, however, a risky strategy if resources are not limiting on territory, because it involves  
445 expending energy searching for plentiful resources in unknown areas for first years on their first return  
446 migration. Further research is needed to determine whether this is an inherent strategy, which might  
447 in any case be expected for other wintering populations which winter further south in Kenya, Tanzania  
448 and Zambia, rather than close to the Sahara border. Additionally, these calculations are based on the  
449 assumption that Whinchats (and other generalist species) do not deliberately stopover in the desert  
450 to feed as a strategy. Stopovers seem unlikely if migrants have sufficient resources prior to the desert  
451 crossing, which many do even from local fattening as demonstrated in this study, as relying on finding  
452 suitable stopover sites in the desert must be extremely risky. Additionally, Whinchats have not been  
453 documented in any numbers refuelling in Saharan vegetation (Jenni-Eiermann *et al.* 2011) although  
454 this is absence of evidence rather than evidence of absence.

455 In conclusion, if territorial overwintering migrants largely leave their territories to fuel up elsewhere  
456 then initial winter territory selection may not be influential for Palaearctic passerine migrants because  
457 low quality territories may suffice in terms of over-winter survival (Cresswell 2014). However, the  
458 quality of staging sites (i.e. their potential to provide sufficient resources for large and rapid mass gain)  
459 in the spring prior to major barriers may be critical for some, if not all, of the population, determining  
460 phenology and likely survival, and so ultimately population dynamics. Further research is needed to  
461 determine how habitat quality further north in the northern Guinea savannah and in the Sahel  
462 constrains migration ecology in sub-Saharan Africa.

463

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471

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## 610 **Appendices**

### 611 **Appendix A**

#### 612 **Permits**

613 Note that no permits are required in Nigeria to trap, colour-ring or to place geolocators on birds.  
614 Nevertheless all people in this study involved in ringing and deployment of geolocators had been  
615 licenced to do this within Europe for other studies and all ethical criteria and animal handling and  
616 welfare procedures used were those that would have been acceptable for an equivalent study based  
617 within Europe.

### 618 **Appendix B**

#### 619 **Error in departure estimates**

620 Across monitored individuals (excluding early departing birds which were visited less than four times  
621 after 2<sup>nd</sup> April, because averaging over so few visits is less meaningful), the probability of resighting an  
622 individual during a territory visit before departure was  $81 \pm 14\%$  ( $n = 68$  individuals; measured simply  
623 by dividing number of detections by total number of visits for each individual). There was a 96%  
624 probability of detecting an individual after only two visits and a >99% probability of detection after  
625 three visits. Therefore our power of observing real departures from territory rather than non-  
626 detections was high and on the scale of a few days. In effect our probability of detecting a real  
627 departure was likely to be much higher, because on average approximately 5-10 minutes were spent

628 looking for each missing individual initially, and then effort was increased if a bird had not been  
629 detected for two consecutive visits.

630 Errors in departure date were not accounted for during analyses due to the high consistency of  
631 resighting and therefore detection probability, as outlined above. Excluding birds which departed  
632 prior to 2<sup>nd</sup> April (n = 5), the maximum number of consecutive days a bird was not detected when it  
633 was known to be present over the monitoring period was  $1.4 \pm 1.1$  days after last resighting (n = 70  
634 individuals). Therefore variation in error of departure date for 95% of individuals would be 0 – 2.2  
635 days after a bird was detected for the last time. This variation is small (9% of total variation in  
636 departure range) compared to the total duration of the departure period (24 days) and therefore  
637 unlikely to affect analyses.

638 Table 1. Top 10 competing candidate models to explain departure timing from wintering territory for  
 639 a) birds caught in 2014 (biometric data included; n = 57) and b) all birds (biometric data not included;  
 640 n = 75). Retained parameters in the models are indicated by + signs if categorical or the parameter  
 641 estimate if continuous; details are given in Table 2. Grey areas indicate where the variables were not  
 642 included a priori in any model. Geo = presence of geolocator tag. Date and winter of capture are not  
 643 included as they were not retained in any of the top models.

a)	Sex	Age	Site	Geo	Mass	Tarsus	Time	Wing	adj R <sup>2</sup>	F	df	logLik	ΔAICc	Weight ω
1	+								0.18	13.5	3	-186.5	0 (379.4)	0.08
2	+		+						0.22	6.1	5	-184.2	0.2	0.07
3	+		+			1.33			0.23	5.1	6	-183.3	0.9	0.05
4	+							-0.01	0.18	7.4	4	-185.9	1.1	0.05
5	+		+					-0.01	0.22	4.9	6	-183.6	1.5	0.04
6	+	+							0.18	7.0	4	-186.2	1.7	0.03
7	+		+	+					0.21	4.8	6	-183.8	1.8	0.03
8	+			+					0.17	6.9	4	-186.3	1.9	0.03
9	+					0.57			0.17	6.8	4	-186.3	2.0	0.03
10	+		+		0.66				0.21	4.7	6	-183.9	2.0	0.03
b)														
1	+		+						0.30	11.8	5	-239.4	0 (489.8)	0.3
2	+		+	+					0.31	9.3	6	-238.6	0.6	0.2
3	+			+					0.28	15.1	4	-241.4	1.7	0.1
4	+	+	+						0.29	8.7	6	-239.4	2.3	0.1
5	+								0.26	26.8	3	-242.9	2.3	0.1
6	+	+	+	+					0.30	7.4	7	-238.5	2.9	0.1
7	+	+		+					0.27	10.2	5	-241.1	3.4	0.1
8	+	+							0.25	13.2	4	-242.9	4.5	0
9		+		+					0.08	4.2	4	-250.4	19.7	0
10		+	+	+					0.10	3.1	6	-248.5	20.5	0

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649 Table 2. Relative importance and estimates of variables hypothesized to influence departure timing  
 650 in Whinchats for a) birds caught in 2014 (n = 57) and b) all birds (n = 75) for candidate models (see  
 651 Table 1) within  $\Delta AICc < 4$  of the top model (number of candidate models: a, n = 27; b, n = 7). Significant  
 652 variables are in bold.

	a)				b)			
	Relative Importance	Estimate	2.50%	97.50%	Importance	Estimate	2.50%	97.50%
<b>Sex (♀)</b>	1.00	6.18	<b>2.62</b>	<b>9.75</b>	1.00	7.23	<b>4.31</b>	<b>10.16</b>
Site 1	0.5				0.71			
2		2.8	-1.40	7.01		1.67	-0.76	5.43
3		-2.3	-6.92	2.29		-1.79	-6.80	1.78
Geolocator (none)	0.18	1.56	-2.52	5.63	0.49	1.09	-0.90	5.34
Age (1 <sup>st</sup> winter)	0.17	1.38	-2.56	5.32	0.23	0.09	-3.20	3.95
Tarsus	0.26	1.08	-1.22	3.39	–	–	–	–
Mass	0.19	0.20	-1.67	2.08	–	–	–	–
Wing	0.26	-0.01	-0.03	0.01	–	–	–	–
Time	0.04	-0.35	-0.96	0.26				

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664 Table 3. Top 10 candidate LM models predicting Whinchat mass during a) September – December  
 665 (period 1; n = 176) and b) January – March (period 2; n = 164). Parameters retained in the model are  
 666 indicated by + if categorical or the parameter estimate if continuous. Details are given in Table 4.

a)	Tarsus	Wing	Sex	Age	Moult	Site	Year	Date	Time	Adj R <sup>2</sup>	F	df	logLik	ΔAICc	Weight ω
1	0.37	0.09					+			0.21	17.1	5	-212.0	0(434.4)	0.09
2	0.38	0.09					+	-0.01		0.21	13.2	6	-211.3	0.7	0.06
3	0.37	0.07	+				+			0.21	13.2	6	-211.4	0.8	0.06
4	0.38	0.10					+		0.04	0.21	13.1	6	-211.4	0.9	0.06
5	0.37	0.09			-0.13		+			0.21	12.9	6	-211.7	1.5	0.04
6	0.39	0.10					+	-0.01	0.04	0.21	10.8	7	-210.6	1.5	0.04
7	0.38	0.08	+				+		0.04	0.21	10.8	7	-210.7	1.6	0.04
8	0.38	0.08	+				+	-0.01		0.21	10.8	7	-210.8	1.8	0.04
9	0.37	0.09		+			+			0.21	12.8	6	-212.0	2.1	0.03
10	0.37	0.07	+		-0.13		+			0.21	10.6	7	-211.0	2.3	0.03
<b>b)</b>															
1	0.40		+	+	0.17	+		0.03	0.07	0.44	15.1	13	-241.4	0(510.9)	0.57
2	0.41	0.00	+	+	0.18	+		0.03	0.07	0.44	13.8	14	-241.1	1.7	0.25
3	0.41		+	+	0.17	+	+	0.03	0.07	0.44	12.6	15	-241.3	4.5	0.06
4	0.42	0.00	+	+	0.17	+	+	0.03	0.07	0.44	11.8	16	-241.0	6.1	0.03
5	0.45		+	+	0.14			0.03	0.07	0.41	23.2	8	-250.4	6.6	0.02
6	0.46	0.00	+	+	0.15			0.03	0.07	0.41	20.2	9	-249.5	7.0	0.02
7	0.41		+	+	0.16	+		0.02		0.42	14.9	12	-246.5	7.8	0.01
8	0.40		+		0.15	+		0.03	0.07	0.41	14.7	12	-246.9	8.7	0.01
9	0.41		+	+		+		0.03	0.07	0.41	14.7	12	-247.2	9.2	0.01
10	0.42	0.00	+	+	0.163	+		0.02		0.41	13.6	13	-246.2	9.5	0.00

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674 Table 4. Relative importance and coefficient estimates of variables predicting mass in Whinchats  
 675 during the first half of the non-breeding season (September – December) for 24 candidate models  
 676 with  $\Delta AICc < 4$  (see Table 3a). Significant variables are in bold.

Variable	Importance	Estimate	95% CI	
			Lower	Upper
<b>Tarsus</b>	1.00	0.37	<b>0.20</b>	<b>0.56</b>
<b>Season</b>	1.00	0.59	<b>0.23</b>	<b>0.96</b>
<b>Wing</b>	0.97	0.09	<b>0.02</b>	<b>0.16</b>
Sex (♀)	0.39	-0.16	-0.43	0.11
Time	0.37	0.04	-0.03	0.12
Date	0.36	0.00	-0.02	0.00
Moult	0.25	-0.12	-0.44	0.20
Age (1 <sup>st</sup> winter)	0.19	0.02	-0.27	0.23
Site	0	0	0	0

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679 Table 5. Optimal general linear model identified by AICc (Table 3) identifying variables predicting mass  
 680 for 196 Whinchats caught in the second half of the non-breeding period in Nigeria. Significant variables  
 681 are in bold. Full model statistics: adjusted  $R^2 = 0.44$ ,  $F_{11,184} = 15.1$ ,  $p < 0.0001$ .

Variable	Estimate	95% CI		
		Lower	Upper	
<b>Tarsus</b>	0.40	<b>0.22</b>	<b>0.58</b>	
<b>Date</b>	0.03	<b>0.02</b>	<b>0.04</b>	
<b>Sex (♀)</b>	-0.49	<b>-0.75</b>	<b>-0.23</b>	
<b>Age (1<sup>st</sup> winter)</b>	-0.41	<b>-0.66</b>	<b>-0.16</b>	
<b>Moult</b>	0.17	<b>0.07</b>	<b>0.27</b>	
<b>Time</b>	0.07	<b>0.03</b>	<b>0.12</b>	
<b>Site</b>				
	2	-0.41	<b>-0.81</b>	<b>-0.01</b>
	3	-0.44	-0.93	0.05
	4	-0.44	<b>-0.85</b>	<b>-0.02</b>
	5	-0.87	<b>-1.30</b>	<b>-0.44</b>
	6	-0.91	<b>-1.69</b>	<b>-0.13</b>

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686 **Figure Legends:**

687 Figure 1: Map of the 6 sites used in the study (see methods for details). Departure monitoring from  
688 2<sup>nd</sup> April was focussed on sites 1-3, shown numbered in bold. The CES site was located between (and  
689 outwith) sites 1 and 2.

690 Figure 2: Phenology of departure from territory for Whinchats in central Nigeria; a) top graph shows  
691 the cumulative percent of birds departing by a particular date – all birds had departed by the 24<sup>th</sup>  
692 April. The bottom histogram shows the frequency of departure on particular dates for both male and  
693 female; b) departure timing relative to the earliest departing individuals (day zero) from winter  
694 territory for adult and second year Whinchats of both sexes (n = 75). Note that sample size for  
695 second year males is low (n = 9). For full model statistics see Tables 1 and 2.

696 Figure 3: The relationship between mass and days from departure to show predicted average mass  
697 on departure (day 0 – the vertical dotted line). The solid black line shows the predicted relationship  
698 using all data (<80 days from departure,  $R^2 = 0.23$ ,  $F_{1,55} = 16.1$ ,  $P = 0.0002$ ), and the dotted black line  
699 using <60 days from departure only ( $R^2 = 0.04$ ,  $F_{1,44} = 3.0$ ,  $P = 0.09$ ). The dotted grey lines show the  
700 predicted relationship using all data plus and minus two standard errors to demonstrate that all  
701 relationships fitted were statistically similar. Black-filled circles represent males and grey circles  
702 females.

703 Figure 4: Mass of 377 Whinchats captured over three non-breeding seasons in relation to date  
704 captured (intensive study data) for the period September to March inclusive, and mass of 141  
705 Whinchats captured over 8 years during April (CES ringing data): note different scales on all graphs.  
706 Predicted lines are plotted for males (light grey) and females (black) from the models predicting  
707 mass from date, winter season, time of day, wing length, minimum tarsus length, sex, age and  
708 location, except for CES data where age and minimum tarsus data were not available. All predicted  
709 lines are for an average sized bird, from the same ringing location, at 07:00, in 2013.

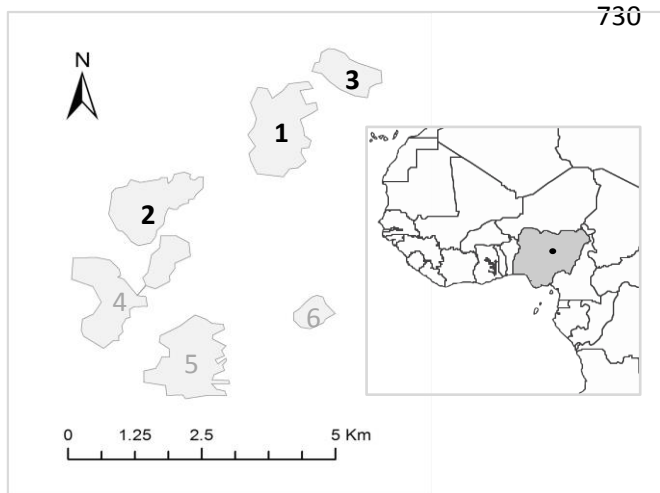
710 Figure 5: Estimated flight ranges of all Whinchats caught during April at Jos, the study site, and  
711 shown by a grey dot, with a map of West Africa (shaded area is the extent of the Sahara desert)  
712 scaled to the y axis and positioned with respect to the study site in the background. The grey 2,500  
713 km dashed line shows the approximate shortest distance to cross the Sahara from Jos; the grey  
714 2,800 dotted line the approximate distance to cross the Sahara to most northern part of Africa. The  
715 heavy solid increasing curve is the cumulative percent of birds with a respective flight range  
716 assuming a lean mass of 12.8 g – for example, all birds could migrate c. 400 km but only c. 5% could  
717 cross the shortest part of the Sahara if they left from the study site at Jos (i.e. the intersection of the  
718 dashed grey 2,500 km line with the 5% line). The dashed solid increasing curve is the cumulative  
719 percent of birds with a respective flight range assuming a minimum lean mass of 11.6 g – for  
720 example, all birds could migrate c. 600 km, c. 20% could cross the shortest part of the Sahara if they  
721 left from the study site at Jos (i.e. the intersection of the dashed grey 2,500 km line with the 20%  
722 line), and c. 5% could cross to the most northerly shore of Africa (i.e. the intersection of the dotted  
723 grey line with the 5% line). (A) & (B) show two potential flight ranges estimated from the observed  
724 average departure mass for resident birds, solid arrows (A) use an estimated lean mass of 12.8 g and  
725 dashed arrows (B) a lean mass of 11.6 g.

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728 Figure 1.

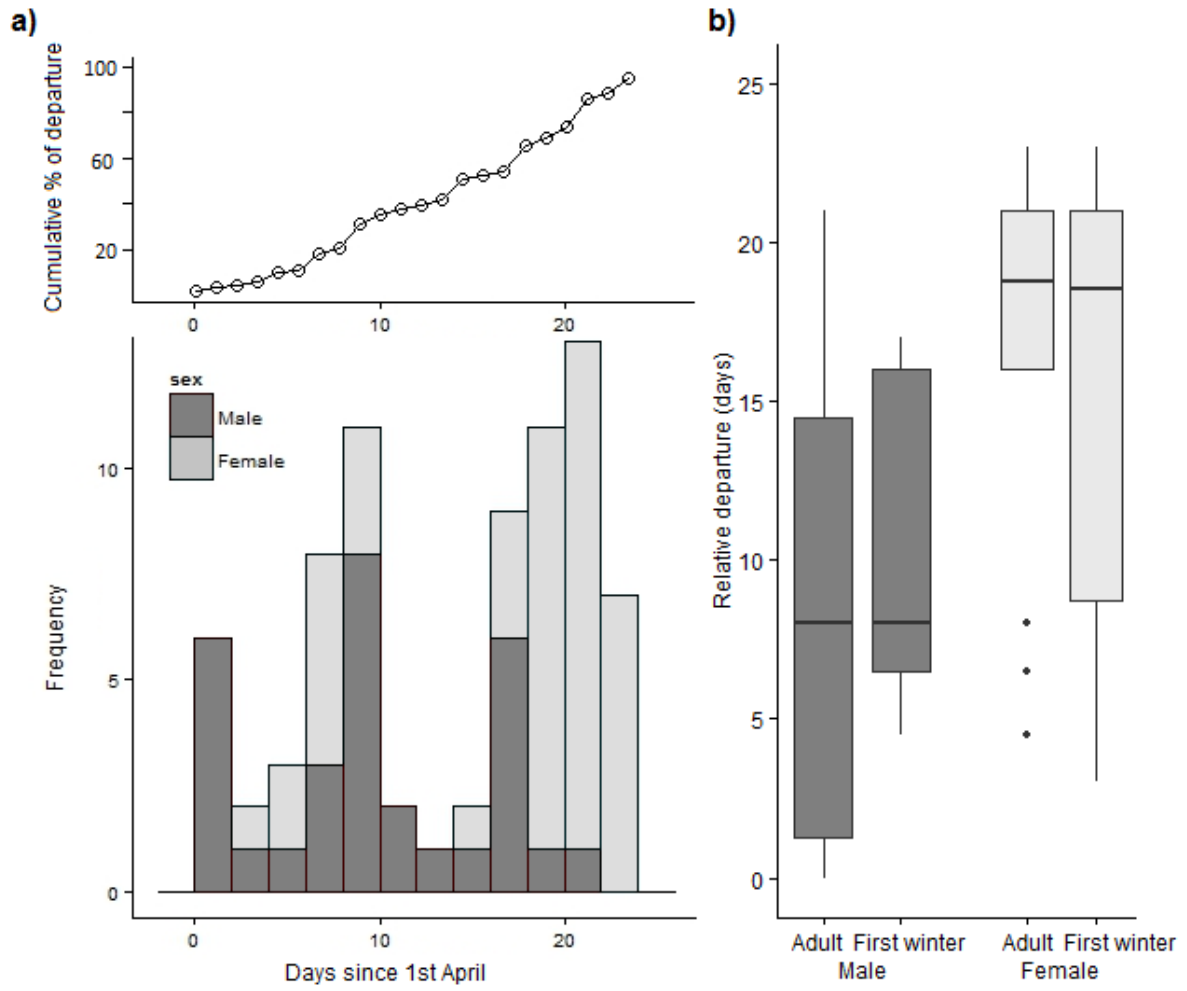
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731 Figure 2.

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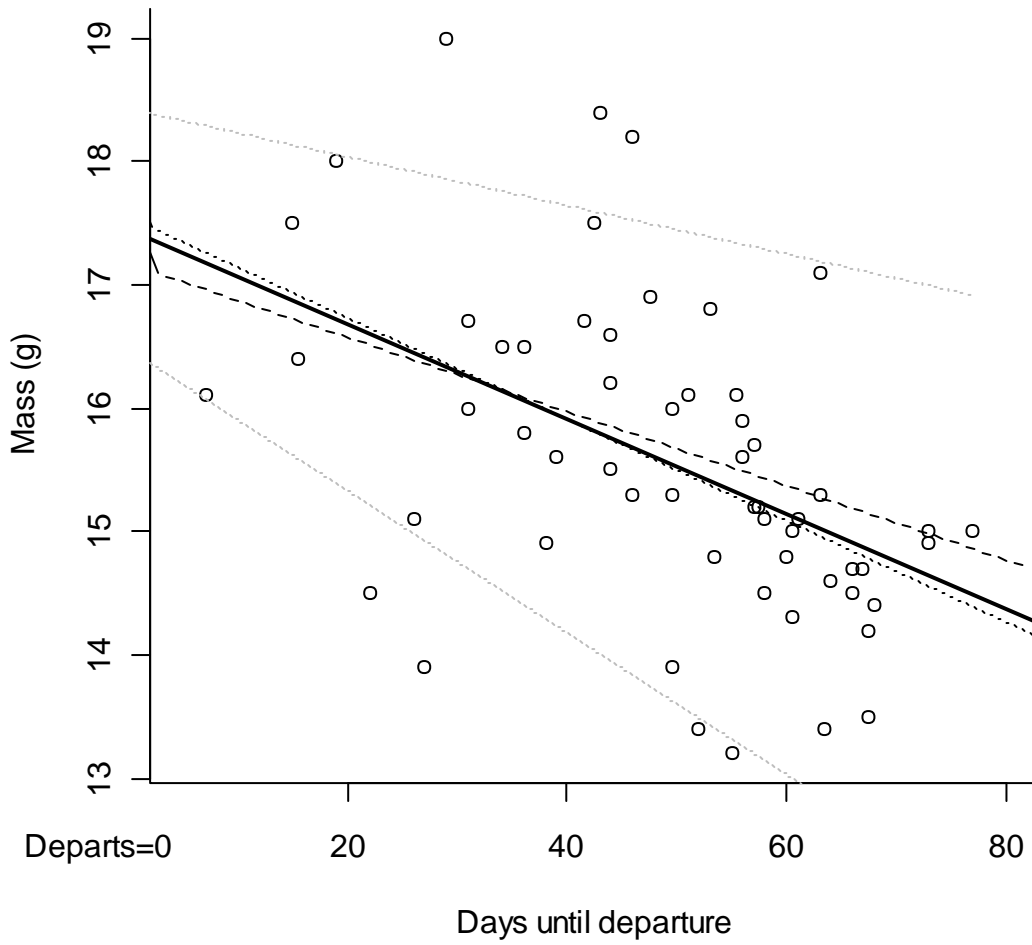
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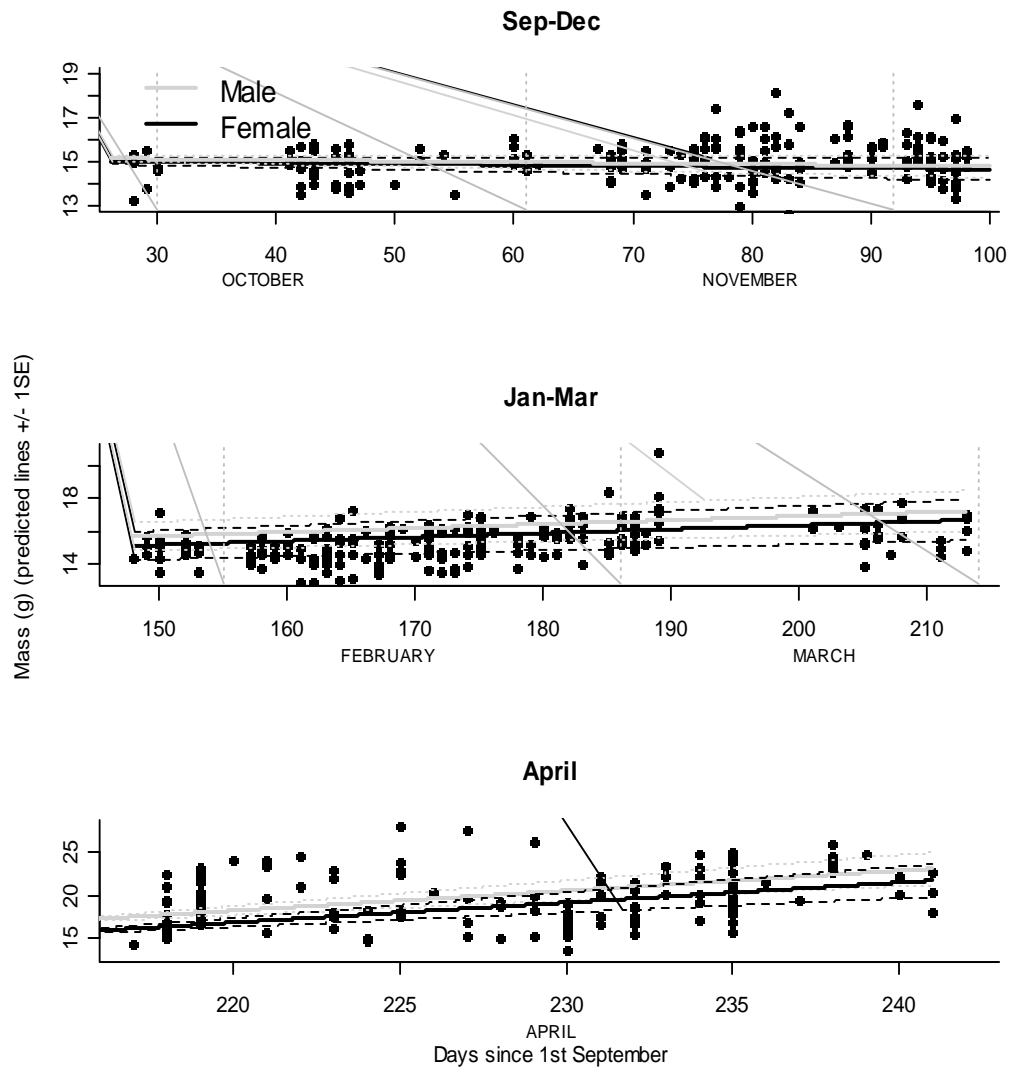
745 Figure 3.



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752 Figure 5.

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