

1 **Whinchat survival estimates across Europe: can excessive adult**  
2 **mortality explain population declines?**

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21

22 **Abstract**

23

24 European farmland birds show massive large-scale population declines due to agricultural  
25 intensification. Long-distance migrants are particularly affected as their populations appear to  
26 undergo larger declines than those of residents and short-distance migrants, raising the question  
27 about the impact of non-breeding environmental conditions and their potential impact on annual  
28 survival. The whinchat *Saxicola rubetra*, an Afro-Palearctic migrant inhabiting open habitats, has  
29 strongly declined over the last decades. Most of the conservation effort for this species has  
30 focused on improving the breeding success in Europe, but it is unclear whether habitat changes in  
31 non-breeding areas may also have contributed to the population declines through a decrease in  
32 adult survival. We studied survival of whinchats from eight breeding populations across Europe  
33 by analyzing capture-recapture data. We found that apparent survival was consistently higher in  
34 males than in females and higher in successful than in failed breeders independently of the sex.  
35 True adult survival may however hardly differ between sexes being about 0.5-0.6 and a simple  
36 population model suggests true juvenile survival to be between 0.2-0.35. Adult survival was  
37 unrelated to population trends suggesting that the main demographic problem of the whinchats is  
38 likely insufficient reproduction, a feature that is shared with other declining grassland specialists.  
39 Finally, in line with results on other migratory farmland species, our study suggests that  
40 conservation activities for whinchats should in first place focus on Europe.

41

42 **Keywords:** Adult survival; Afro-Palearctic migrant; capture-recapture; juvenile survival;  
43 mortality; *Saxicola rubetra*; sex-specific survival

## 44 **Introduction**

45 Populations of farmland birds have strongly declined in Western Europe over the last  
46 decades (Newton, 2004; Sanderson et al., 2006) due to the intensification of agricultural practices  
47 (Donald et al., 2001). Formerly common and widespread species are now extirpated from large  
48 areas and some of them got listed on the Red List of Threatened Species (IUCN 2019).

49 Knowledge about demographic rates of farmland birds is fundamental to diagnose the underlying  
50 demographic mechanisms of the decline and to suggest effective management measures. At large  
51 spatial scales, dispersal (i.e. emigration and immigration at the local population level) can be  
52 ignored because it acts as a redistribution process and thus does not contribute to changes in the  
53 overall number of individuals over time (Newton, 2004). The potential demographic mechanisms  
54 driving the large-scale decline of European farmland birds may consequently be characterized by  
55 two fundamental processes: survival and reproduction.

56 Among farmland birds, long-distance migrants received recently particular attention  
57 (Blackburn and Cresswell, 2016a; Johnston et al., 2016), as their populations have declined more  
58 severely compared to those of resident species or short-distance migrants (Both et al., 2010;  
59 Vickery et al., 2014). These species-specific differences related to migratory strategies suggested  
60 environmental conditions away from breeding sites as a potential reason for differential  
61 population trends. Past studies have occasionally related population declines in European  
62 breeding species to a decrease in survival owing to deterioration of non-breeding conditions in  
63 Africa. For example, breeding population collapses of Afro-Palaearctic migrants such as common  
64 whitethroats *Sylvia communis* (Winstanley, 1974), sand martins *Riparia riparia* (Bryant and  
65 Jones, 1995) or white storks *Ciconia ciconia* (Kanyamibwa et al., 1990) in the 1970s and 1980s,  
66 have been related to severe droughts in the Sahel revealing a strong decrease in survival.

67 However, it is unclear whether the current large-scale population declines of long-distance  
68 migratory farmland birds can also be explained by similar deterioration in the non-breeding areas  
69 in Africa (Sanderson et al., 2006; Vickery et al., 2014). Thus, improved knowledge of survival in  
70 these species is critical to obtain a better understanding of the demographic processes that  
71 resulted in population declines.

72 An understanding of demographic processes across large spatial scales requires several  
73 years of intense data collection involving different monitoring programs run in parallel. Such  
74 monitoring programs are highly time-consuming and costly. Difficulties are particularly acute for  
75 the investigation of survival which furthermore poses methodological challenges. To estimate  
76 representative survival of a given bird population, a large number of individuals (i.e. typically in  
77 the order of hundreds of individuals) have to be captured, marked individually and tracked over  
78 years. Additionally, permanent emigration from the study area is confounded with mortality and  
79 thus estimates of survival often reflect apparent rather than true survival (Lebreton et al., 1992).  
80 Finally, sex, age and breeding success can affect both dispersal and survival in different ways  
81 resulting in a challenging estimation of age and sex-specific survival. These difficulties may  
82 explain why our understanding of survival as a demographic driver of population dynamics is  
83 still limited, especially in passerine birds (Anders and Marshall, 2005). Finally, our  
84 understanding of survival processes over large spatial scales is typically impeded by the very  
85 small number of populations studied.

86 The whinchat *Saxicola rubetra* is an Afro-Palaearctic migrant that inhabits a range of open  
87 habitats in both the breeding and non-breeding areas. As most farmland birds, whinchats have  
88 undergone a massive decline over the last decades. At the European scale, they suffered a  
89 population decline of 88% between 1980 and 2017 and are currently still decreasing (EBCC

90 2019). Although most of the conservation effort is allocated to improve the breeding success, it  
91 remains unclear whether habitat changes in non-breeding areas may also add to the negative  
92 population trend (Bastian 2015). While the breeding ecology has been intensively studied  
93 (Britschgi et al., 2006; Calladine and Bray, 2012, appendix S3), our knowledge about survival is  
94 limited. Here, we analysed capture-recapture and population count data of whinchats originating  
95 from eight breeding populations across Europe. We estimated apparent survival and performed a  
96 multi-population comparison for testing the consistency of effects of age, sex and breeding  
97 success (successful vs. failed) on survival estimates. Based on these results and with the use of a  
98 simple population model we estimated true adult and juvenile survival. Finally, we investigated  
99 the potential relationship between adult survival and the large-scale population decline of  
100 whinchats in Europe. Using two complementary approaches focusing on two different aspects of  
101 the survival (i.e. mean and year-to-year variation), we assessed the relationships between the  
102 adult apparent survival and the growth rates of these eight breeding populations.

103

## 104 **Material and Methods**

### 105 Study species and populations

106 The whinchat is a small (15g), insectivorous Afro-Palearctic migrant that inhabits a range of open  
107 habitats including agricultural landscapes in breeding and non-breeding areas (Cramp 1988).

108 Whinchats show high annual mortality and the maximal lifespan ever recorded is seven years  
109 (Fransson et al. 2017). They are monogamous, nest on the ground and usually raise one brood per  
110 year (Cramp 1988). Individuals are sexually mature at the age of one year. Females incubate the

111 clutch (containing typically 5-6 eggs) and brood the hatchlings, but both parents contribute to  
112 feed the nestlings (Cramp 1988).

113 Our study is based on capture-recapture and population count data of whinchats sampled  
114 in eight populations from five European countries (United Kingdom (1, UK), Slovenia (1, SL),  
115 Russia (1, RU), Ukraine (1, UKR), Germany (3, Ba, We, Ob), Switzerland (1, SW)). Most  
116 populations were located either in cultivated grassland managed with low intensity (1-2 cuts per  
117 year) or in uncultivated grassland. The study site from Switzerland, however, was cultivated at a  
118 higher level of intensity (2-3 cuts per year, Müller et al., 2005). A previous study has shown that  
119 the breeding success and female survival during incubation are both negatively affected by this  
120 intense grassland management (Grüebler et al., 2008).

#### 121 Data collection

122 The study durations varied between 5 to 17 years (Table S1). In each population, both adults and  
123 nestlings were ringed with aluminium rings and colour plastic rings. The sex was systematically  
124 recorded for adults (i.e. at least one year old) based on plumage dimorphism (Jenni and Winkler,  
125 1994), while marked nestlings remained unsexed unless if reencountered as adults. Re-encounters  
126 were either recaptures or resightings during the breeding season. Whinchat nests were searched  
127 and the presence of fledglings was recorded in all but the Swiss population. A marked individual  
128 was considered successful if it had produced at least one fledgling. However, the breeding  
129 success of 10 to 25% of the individuals (depending on the population) could not be assessed.  
130 These individuals were classified as breeders with unknown breeding output. In addition to the  
131 collection of capture-recapture data, the number of breeding pairs was counted each year. As the  
132 area from where the population counts originated changed over time in some populations, we  
133 reported densities rather than absolute counts.

134 Data analysis

135 Age and sex-specific apparent survival estimates

136 The capture-recapture data from the different populations were modelled jointly with three  
137 different Cormack-Jolly-Seber (CJS) models. Estimates from these models were then used for  
138 further analyses. Parameters directly estimated by the CJS models were  $\phi$ , the annual apparent  
139 survival probability, and  $p$ , the recapture probability (Lebreton et al., 1992). Apparent survival  
140 probability was dependent on year, population, age (juvenile: survival from ringing as nestling  
141 until one year old; adult: survival from the age of one year onwards) and sex for adults. As the  
142 sex of juveniles was unknown at the ringing age, we did not include a sex-specific survival  
143 probability for this age-class. These parameters were modelled with different linear models,  
144 which then build our three CJS models.

145 CJS<sub>1</sub> aimed to obtain average (with respect to year) age- and sex-specific apparent survival  
146 estimates for each population and therefore used the following linear model:

147  $logit(\phi_{i,t}^{juv}) = \mu_i^{\phi^{juv}}$  and  $logit(\phi_{i,s,t}^{ad}) = \mu_{i,s}^{\phi^{ad}}$  where  $i$ ,  $s$  and  $t$  are indices for  
148 population, sex and year, respectively.  $\mu_i^X$  is the population specific mean of parameter  $X$  and is  
149 treated as a fixed effect.

150 CJS<sub>2</sub> aimed to obtain typical age- and sex-specific apparent survival probabilities of whinchats  
151 and the variability of survival among populations. We therefore modelled age- and sex-specific  
152 apparent survival with a population random effect:

153 
$$logit(\phi_{i,t}^{juv}) = \mu^{\phi^{juv}} + \varepsilon_i^{\phi^{juv}} \quad \text{with} \quad \varepsilon_i^{\phi^{juv}} \sim Normal(0, \sigma_{\varepsilon^{\phi^{juv}}}^2)$$

154 
$$logit(\phi_{i,s,t}^{ad}) = \mu_s^{\phi^{ad}} + \varepsilon_{i,s}^{\phi^{ad}} \quad \text{with} \quad \varepsilon_{i,s}^{\phi^{ad}} \sim Normal(0, \sigma_{\varepsilon^{\phi^{ad},s}}^2)$$

155 where  $\mu^{\phi^{juv}}$  and  $\mu_s^{\phi^{ad}}$  are the mean juvenile and sex-specific adult survival which are fixed  
 156 effects, and  $\varepsilon_i^{\phi^{juv}}$  and  $\varepsilon_{i,s}^{\phi^{ad}}$  are the age- and sex-specific population random effects with  
 157 corresponding variances of  $\sigma_{\varepsilon^{\phi^{juv}}}^2$  and  $\sigma_{\varepsilon^{\phi^{ad},s}}^2$ . For comparing among-population variances  
 158 between sex and age classes, we provide absolute and relative variances. The absolute variances  
 159 are the variances among the populations-specific estimates on the [0,1]. The relative variances are  
 160 absolute variance scaled by the maximally possible variance value which is given by  $\mu^*(1-\mu)$   
 161 where  $\mu$  is the corresponding mean survival (Gaillard and Yoccoz, 2003).

162 With CJS<sub>3</sub> we estimated year-specific adult apparent survival with annual random effects,

$$163 \quad \text{logit}(\phi_{i,s,t}^{ad}) = \mu_i^{\phi^{ad}} + \varepsilon_{i,t}^{\phi^{ad}} \quad \text{with} \quad \varepsilon_{i,t}^{\phi^{ad}} \sim N(0, \sigma_{\varepsilon^{\phi}}^2)$$

164 and juvenile survival was modeled as in CJS<sub>1</sub>.

165 In all three CJS models we used the same structure for the recapture probabilities. We considered  
 166 sex-specific recapture probabilities because males are typically more conspicuous than females  
 167 during the breeding season. Due to the small sample size of some datasets we modelled the sex  
 168 effect on recapture probability with a population random effect to obtain more reliable estimates.

169 We also used an additive random year effect nested within the population effect:

$$170 \quad \text{logit}(p_{i,s,t}) = \mu_i^p + v_i^p + \varepsilon_{i,t}^p \quad \text{with} \quad v_i^p \sim \text{Normal}(\bar{v}, \sigma_v^2) \quad \text{and} \quad \varepsilon_{i,t}^p \sim \text{Normal}(0, \sigma_{\varepsilon,i}^2)$$

171  $v_i^p$  is the population-specific sex effect on the recapture probability, which is assumed to be  
 172 normally distributed with mean  $\bar{v}$ , i.e. the average difference between female and male recapture  
 173 probability, and variance  $\sigma_v^2$ .  $\mu_i^p$  is the population-specific mean recapture probability of males.

174



175 Effect of breeding success on apparent survival

176 To investigate the effect of the breeding success on apparent survival we formulated a multi-  
177 event capture-recapture model (Pradel, 2005). Multi-event models allow estimating state specific  
178 survival accounting for state uncertainty, which originated by the observation of marked  
179 individuals whose reproductive success was unknown. We provide more details about the  
180 specification of this model in appendix S1.

181 Assessing the importance of emigration

182 To investigate the importance of emigration in our estimates of apparent survival we performed  
183 two complementary analyses based on the results of CJS<sub>1</sub>. First, we investigated the relationship  
184 between the average survival of both juveniles and adults with the size of the monitored study  
185 areas using the following linear regression:

186 
$$\text{logit}(\phi_i) = \beta_0 + \beta_1 * \text{study.area}_i + \varepsilon_i^\phi$$

187 where  $\phi_i$  is the average survival of population  $i$ ,  $\beta_0$  is the intercept,  $\beta_1$  is the slope describing the  
188 relationship between average survival and the size of the study area, and  $\varepsilon_i^\phi$  is the residual term  
189 that we assumed to be normally distributed with mean 0 and variance  $\sigma_\varepsilon^2$ . As emigration is  
190 expected to decrease with increasing size of the study area, apparent survival should be positively  
191 related to the study area.

192 Second, we assessed the relationship between juvenile and adult apparent survival at the  
193 population level. Emigration is likely to differ among populations due to differences among the  
194 study sites (e.g. size, shape, connectivity with other populations). However, all other things being  
195 equal, juvenile and adult emigration rate should vary consistently with features of the study areas.

196 For instance, if juvenile emigration is high in a study population due to its small size or isolation,  
197 adult emigration should also be relatively high. To assess the relationship between juvenile and  
198 adult apparent survival, we used a linear regression based on the estimated survival probabilities  
199 of CJS<sub>1</sub>. The average juvenile survival rate was predicted by the average adult survival rate:

$$200 \text{logit}(\phi_i^{juv}) = \beta_0 + \beta_1 * \phi_i^{ad} + \varepsilon_i^{\phi^{juv}}$$

201 where  $\phi_i^{juv}$  is the average juvenile survival in population  $i$ ,  $\beta_0$  is the intercept,  $\beta_1$  is the slope  
202 describing the relationship between average juvenile survival and average adult survival ( $\phi_i^{ad}$ ),  
203 and  $\varepsilon_i^{\phi^{juv}}$  is the residual term that we assumed to be normally distributed with mean 0 and  
204 variance  $\sigma_\varepsilon^2$ . The females of the Swiss population have been excluded for both analyses because  
205 their apparent survival is negatively impacted by hay cutting (Grüebler et al., 2008). Thus we  
206 have *a priori* knowledge that female apparent survival probability may not reflect emigration in  
207 the same way as for other populations.

#### 208 Estimation of true juvenile survival

209 Juvenile survival is a key demographic rate, yet poorly known (Anders and Marshall, 2005; Cox  
210 et al., 2014; Naef-Daenzer and Grüebler, 2016). Juvenile apparent survival estimates are likely to  
211 be strongly affected by permanent emigration (Weatherhead and Forbes, 1994), and true juvenile  
212 survival cannot be estimated from capture-recapture data alone. In order to get a possible estimate  
213 of true juvenile survival, we used a simple population model (Anders and Marshall, 2005). Based  
214 on average values of true adult survival ( $s_{ad}$ ) and fecundity ( $fec$ ), we calculated the needed level  
215 of juvenile survival ( $s_{juv}$ ) to ensure the long term persistence of a population. Thus we estimated  
216 the long-term average juvenile survival of a viable population which may not apply to our studied  
217 populations. The underlying population model assumed no age effect on reproduction, full

218 recruitment at the age of 1 year and an even sex ratio at birth. The population growth rate is then  
219  $\lambda = 1 = S_{juv} * fec/2 + S_{ad}$ , and thus juvenile survival becomes:

$$220 \quad S_{juv} = (1 - S_{ad}) / (fec * 0.5)$$

221 The likely range of adult survival was based on the results of this study (see discussion). We  
222 conducted a literature review to find estimates of fecundity. Fecundity was decomposed into two  
223 processes, the breeding success ( $\gamma$ , the probability that an initiated brood produces at least one  
224 fledging) and the productivity given success ( $\delta$ , the mean number of fledglings per successful  
225 brood). Whinchats usually produce one brood per year, but replacement broods may occur in case  
226 of failure. Thus, we also included a reneating probability ( $\alpha$ ). Including these parameters, the  
227 previous equation to estimate the true juvenile survival becomes:

$$228 \quad S_{juv} = (1 - S_{ad}) / ((\gamma + \alpha * (1 - \gamma)) * \delta * 0.5)$$

### 229 Population growth rate and its relationship with adult apparent survival

230 We used a state-space model to estimate the population growth rates from the population count  
231 data (de Valpine and Hastings, 2002). State-space models decompose an observed time series of  
232 counts into a state process describing the dynamics of the population and an observation process  
233 describing the relationship between the true population size and the counts. We modelled the  
234 state process with an exponential growth model,  $\hat{y}_{i,t+1} = \hat{y}_{i,t} * \lambda_{i,t}$  with  $\log(\lambda_{i,t}) \sim N(\bar{\lambda}_i, \sigma^2_\lambda)$ ,  
235 where  $\hat{y}_{i,t}$  is the estimated density of population  $i$  in year  $t$ ,  $\bar{\lambda}$  is the average population growth  
236 rate of population  $i$ , and  $\sigma^2_\lambda$  is the residual variance of the population growth rates on the log-  
237 scale. We considered a normally distributed error for the observation process that links the  
238 observed population density with the true population density, i.e.  $y_{i,t} \sim N(\hat{y}_{i,t}, \sigma^2_{obs})$ , where

239  $\sigma^2_{obs}$  is the variance of the observation error. Population counts were expressed as density and  
240 were further standardized within each population by the observed density in the first year. This  
241 allowed to jointly estimate the population growth rates using the shared parameters  $\sigma^2_{\lambda}$  and  
242  $\sigma^2_{obs}$ . This choice was motivated by the short duration of some time series.

243 We assessed the relationship between annual population growth rates and the estimated annual  
244 adult apparent survival probabilities using two complementary approaches. First, we assessed the  
245 relationship between the average growth rate and the apparent survival from CJS<sub>1</sub> in a joint linear  
246 model:

$$247 \quad \log(\bar{\lambda}_i) = \beta_0 + \beta_1 * \phi_i + \varepsilon_i^\lambda$$

248 where  $\bar{\lambda}_i$  is the average growth rate of population  $i$ ,  $\beta_0$  is the intercept,  $\beta_1$  is the slope describing  
249 the relationship between average population growth rate and average adult apparent survival ( $\phi$ )  
250 and  $\varepsilon_i^\lambda$  is the residual term that we assumed to be normally distributed with mean 0 and variance  
251  $\sigma_\varepsilon^2$ . If population declines are driven by a decrease in adult survival, we should observe a positive  
252 relationship between adult apparent survival and population growth rate.

253 However, because permanent emigration may affect the estimate of adult apparent survival  
254 differently in each population, the power of the first analysis might be limited. Therefore, we also  
255 investigated the relationship between population growth rate and adult apparent survival on an  
256 annual basis. We assessed the relationship of the residual term of survival  $\varepsilon_{i,t}^\phi$  as obtained from  
257 CJS<sub>3</sub> with the annual population growth rate using a joint linear model:

$$258 \quad \lambda_{i,t} = \beta_{0,i} + \beta_1 * \varepsilon_{i,t}^\phi + \varepsilon_{i,t}^\lambda$$

259 If the year-to-year variations of adult apparent survival rate drive the annual variations of the  
260 population growth rate, we should find a positive relationship ( $\beta_1 > 0$ ).

### 261 Model implementation

262 We used the Bayesian approach and Markov chain Monte Carlo (MCMC) simulation for  
263 parameter estimation. The analyses were conducted in JAGS (Plummer, 2003) via the R package  
264 jagsUI (Kellner, 2016) using code from Kéry and Schaub (2012) that was adapted where  
265 necessary. Details about model implementation are provided in appendix S2. We report posterior  
266 means and 95% credible intervals. Inference for specific tests was based on the probability that  
267 an estimate was positive.

268

## 269 **Results**

### 270 Annual survival

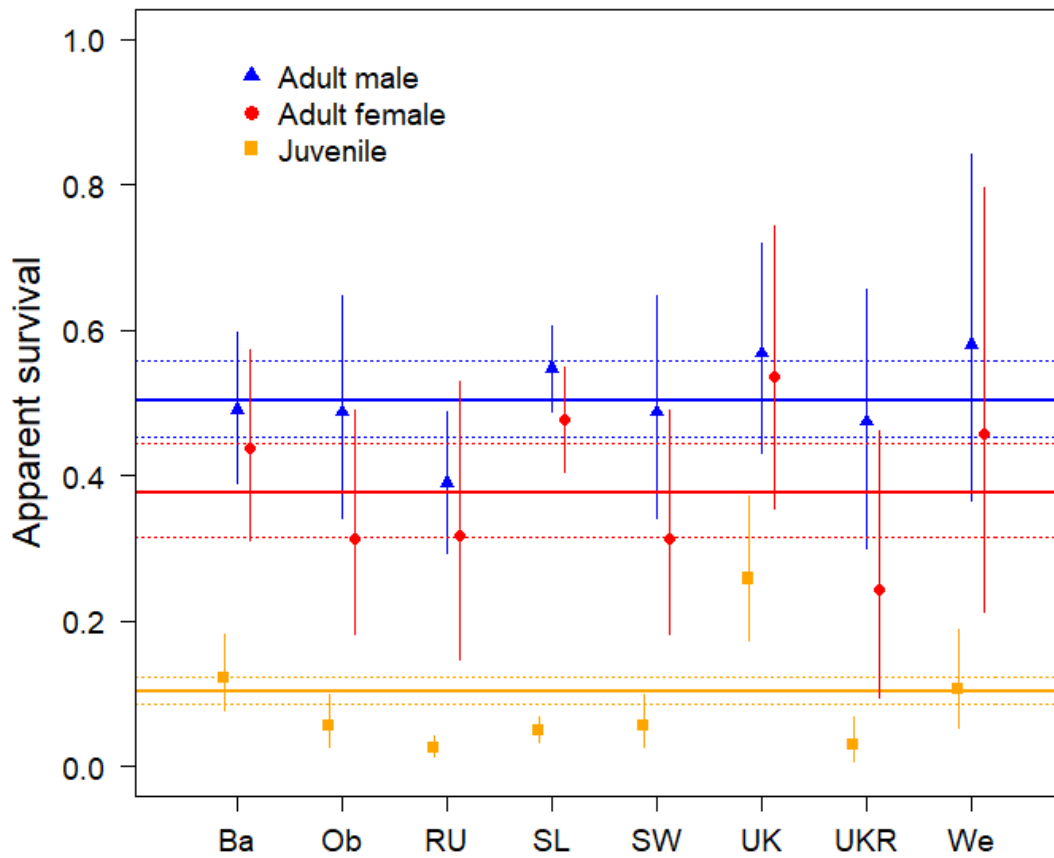
271 Estimates from CJS<sub>1</sub> suggested consistent age and sex effects on apparent survival in all eight  
272 populations (Fig. 1). Juvenile apparent survival was around 0.10 but varied from 0.03 to 0.26  
273 among populations. Adult males had higher apparent survival than adult females with averages of  
274 0.50 and 0.36, respectively. The sex effect varied among populations and the difference between  
275 the sexes decreased with female apparent survival ( $\beta_1 = -3.27 [-5.87, -0.65]$ ,  $p(\beta_1 < 0) = 0.99$ , Fig.  
276 2).

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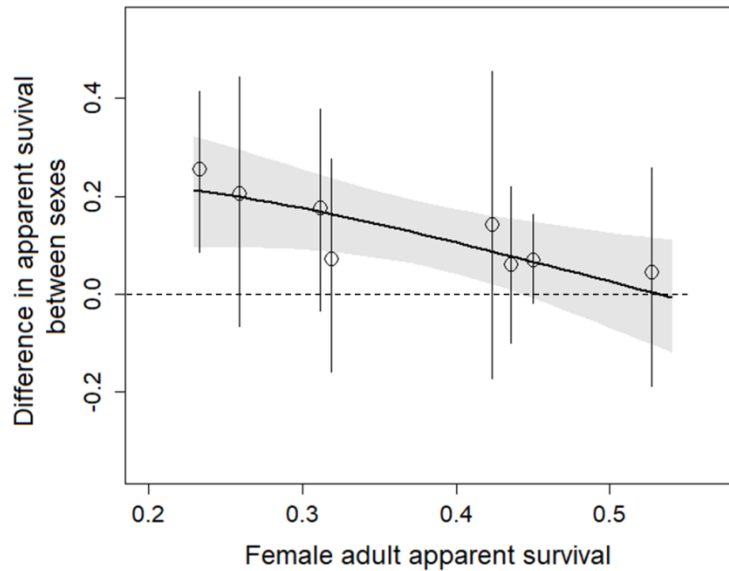
279

280 Figure 1: Age- and sex-specific apparent annual survival probabilities of whinchats from eight  
281 European populations estimated with CJS<sub>1</sub> (see text for the abbreviations of the populations). The  
282 dots are the population specific posterior means. The vertical lines show the 95% credible  
283 intervals. The solid and dashed horizontal lines show the average apparent survival for each age  
284 and sex class with the corresponding 95% credible intervals.  
285



286  
287  
288  
289

290 Figure 2: Relationship between female apparent adult survival and the difference in apparent  
 291 survival between sexes (male - female apparent survival) in eight European whinchat  
 292 populations. The dots show the relationship ( $\pm$  95% credible interval) obtained from CJS<sub>1</sub>, the  
 293 bold line shows the relationship as a linear function of adult female survival and the shaded area  
 294 shows the 95% credible interval of the slope.



295

296

297 Table 1: Mean annual age- and sex-specific apparent survival probabilities and their spatial  
 298 absolute and relative variances across eight European whinchat populations based on CJS<sub>2</sub>. See  
 299 methods section for the definition of absolute and relative variances. Given are posterior means  
 300 with the 95% credible intervals in square brackets.

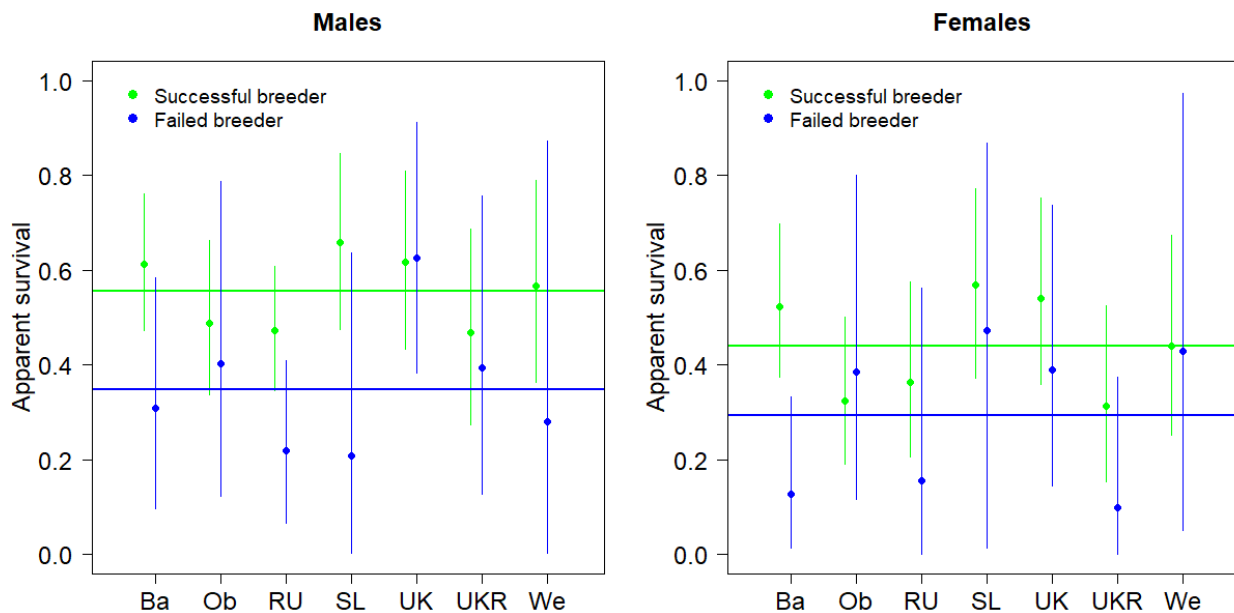
Stage	Mean	Absolute variance	Relative variance
Juveniles	0.09 [0.04,0.20]	0.0051 [0.0027,0.0103]	0.0623 [0.0290,0.1942]
Adult females	0.36 [0.26,0.46]	0.0032 [0.0001,0.0214]	0.0137 [0.0004,0.0960]
Adult males	0.49 [0.43,0.55]	0.0002 [0.0000,0.0065]	0.0010 [0.0000,0.0262]

301

302 Modelling apparent survival with population random effects (CJS<sub>2</sub>) suggested similar  
303 average age and sex specific estimates (Table 1). The variation among populations in apparent  
304 survival was highest for juveniles and lowest for adult males while adult females showed  
305 intermediate values. The variation among populations was roughly 10 times higher for adult  
306 females than for adult males.

307 The multi-event model suggested a consistent effect of the breeding success on apparent  
308 survival among populations (Fig. 3). The apparent survival of failed breeders was on average  
309 35% lower than that of successful breeders. There was no interaction effect between breeding  
310 success and sex on apparent survival (interaction = 0.06 [-2.72, 2.69]).

311  
312 Figure 3: Sex- and state-specific apparent survival of whinchats estimated with a multi-event  
313 model from eight European populations. The dots are the population specific posterior means; the  
314 vertical lines show the 95% credible intervals. The solid horizontal lines show the average  
315 apparent survival for each state.





317           The review on productivity of whinchats revealed that breeding success was highly  
318 variable among populations ranging roughly from 30 to 70%. The number of fledglings per  
319 successful brood was less variable being 5.2 on average and the renesting probability after failure  
320 has rarely been estimated accurately. To parameterize the population model for estimating true  
321 juvenile survival we used different values (0.3, 0.4, 0.5, 0.6, 0.7) for breeding success to account  
322 for its variability, 5.2 for the number of fledglings and two different values (0.4 and 0.8) for the  
323 renesting probability that should reflect the assumed range. Detailed results and additional  
324 comments about the review are provided in appendix S3. Finally, based on our previous results,  
325 we assumed that the true adult female survival is likely to be in the range of 0.5 to 0.6 (see  
326 discussion). Using the simple population model we found that the true average juvenile survival  
327 of a viable population is unlikely to be lower than 0.2. To ensure population persistence when the  
328 breeding success is between 0.4 and 0.7 the true average juvenile survival needed to be between  
329 0.2 and 0.35 (Fig. 4). However, if the long-term breeding success is only around 0.3, the average  
330 juvenile survival required for a stable population was 0.35-0.45.

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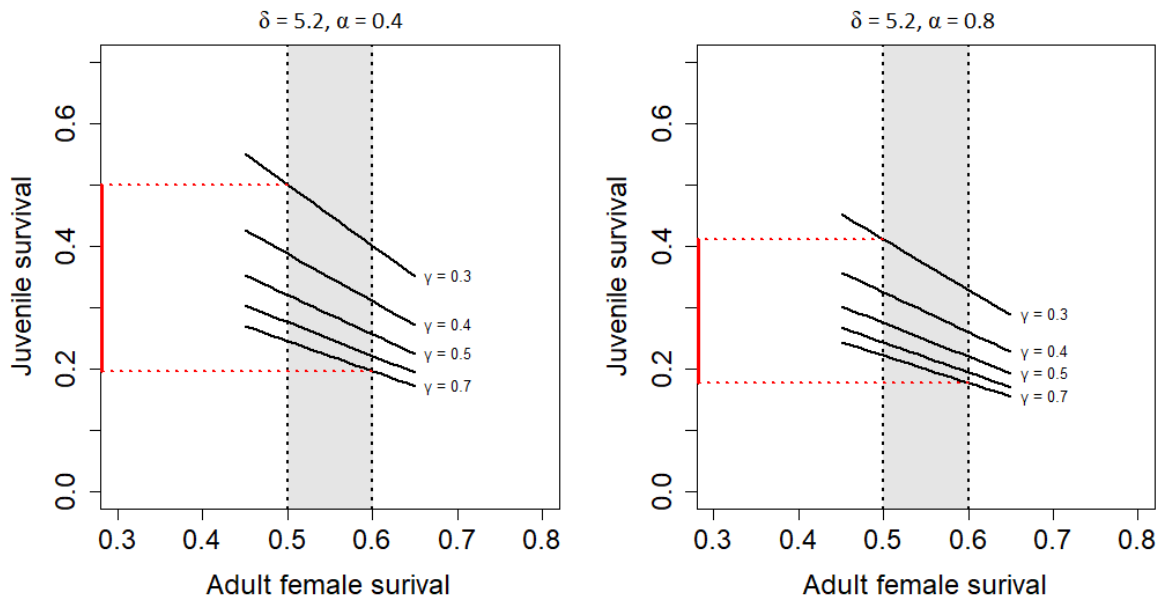
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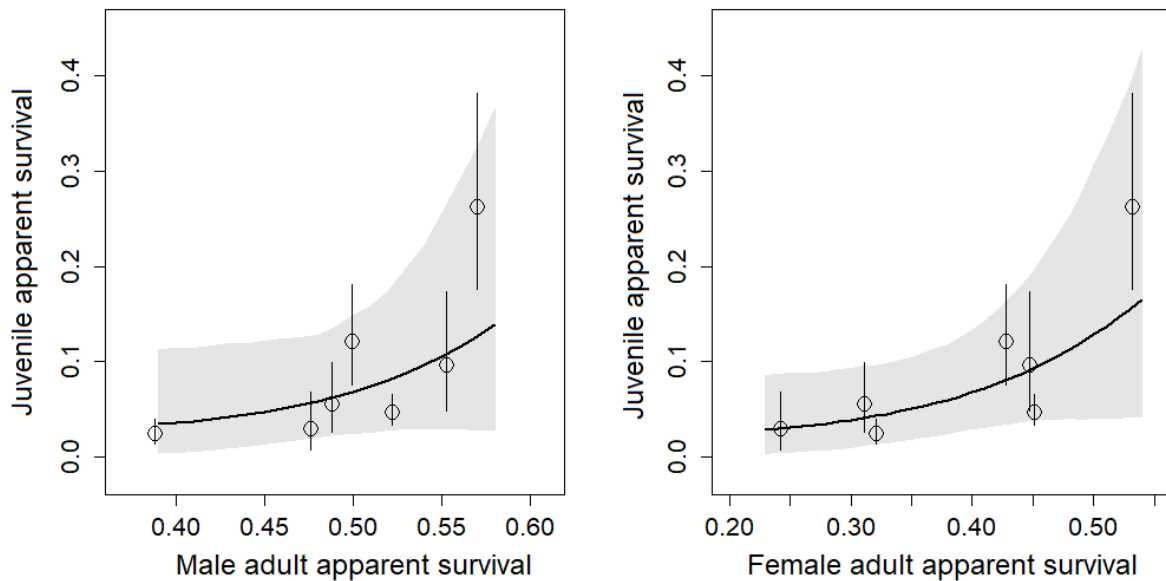
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338 Figure 4: Average juvenile survival that is needed in a stable population with balanced dispersal.  
 339 Estimates are provided for different values of breeding success ( $\gamma = 0.3, 0.4, 0.5, 0.6, 0.7$ ) and  
 340 under the assumption that adult female survival is between 0.5 and 0.6. The reneating probability  
 341  $\delta$  ( $\alpha$ ) after failure was fixed at 0.4 on the left panel and 0.8 on the right panel. The productivity  
 342 per successful brood ( $\delta$ ) was assumed to be 5.2. The red lines show the ranges of the predicted  
 343 juvenile survival according to the different scenarios.



344  
 345  
 346 We found a positive relationship between the size of the study area and juvenile apparent  
 347 survival ( $\beta_1 = 0.56 [-0.35, 1.49]$ ,  $p(\beta_1 > 0) = 0.92$ ), but no clear evidence for similar relationships  
 348 in adult female survival ( $\beta_1 = 0.14 [-0.39, 0.76]$ ,  $p(\beta_1 > 0) = 0.73$ ) and adult male survival ( $\beta_1 =$   
 349  $0.04 [-0.25, 0.37]$ ,  $p(\beta_1 > 0) = 0.59$ ). At the population level, juvenile survival was positively  
 350 correlated with both adult female survival ( $\beta_1 = 6.69 [-0.95, 15.09]$ ,  $p(\beta_1 > 0) = 0.96$ ) and adult  
 351 male survival ( $\beta_1 = 8.85 [-6.01, 22.24]$ ,  $p(\beta_1 > 0) = 0.93$ ) as expected if breeding dispersal beyond  
 352 the study area occurs (Fig. 5).

353 Figure 5: Relationship between juvenile and sex-specific adult apparent survival probabilities of  
354 whinchats from eight European populations. The open dots show the relationship using estimates  
355 of juvenile survival ( $\pm$  95% CRI) from CJS<sub>1</sub>, the bold lines show the relationship with estimates  
356 of juvenile survival obtained from a linear function of adult survival and the shaded areas show  
357 the 95% CRI of these estimates.

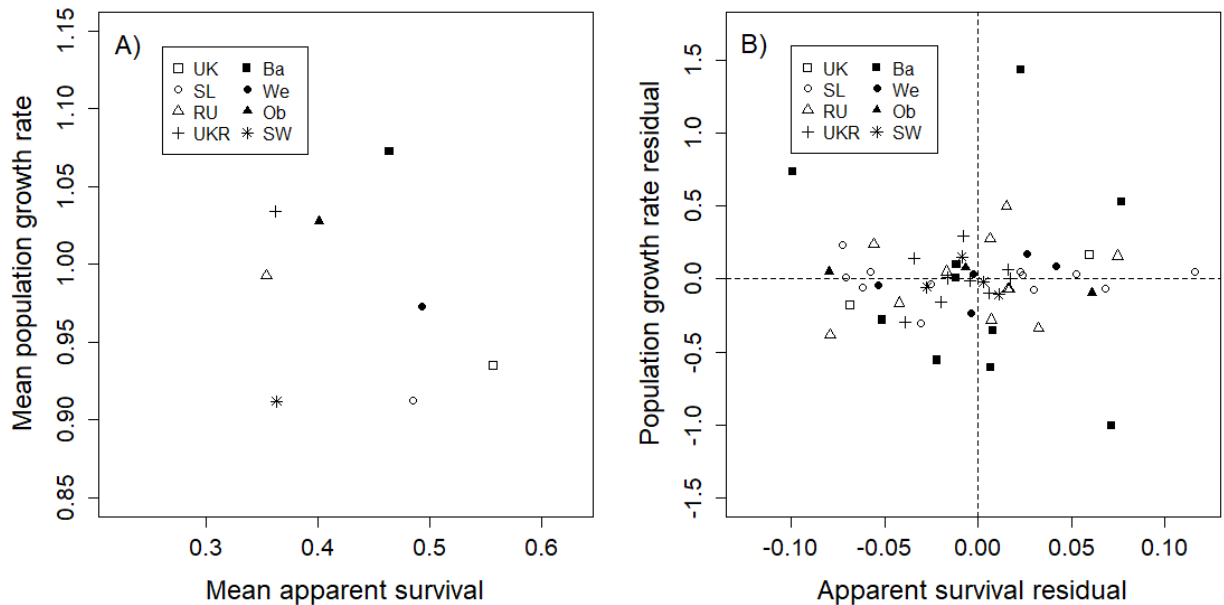


358

359 We found no relationship between population growth rate and adult apparent survival.  
360 Although population trends varied among populations (Fig S1), there was no evidence of a  
361 positive relationship between population growth and the average adult apparent survival ( $\beta_1 = -$   
362  $0.18 [-1.18, 0.77]$ ,  $p(\beta_1 > 0) = 0.33$ ). Accounting for sex-specific survival did not change this  
363 result. The absence of the relationship between the population growth rate and the apparent  
364 survival can be illustrated by comparing populations from Slovenia (SL) and Germany (Balingen,  
365 Ba). Although the Slovenian population was decreasing, adults had a higher apparent survival  
366 than adults from the increasing Balingen population (Fig. S2). Consistently, there was also no

367 evidence of a positive relationship between population growth and adult apparent survival on an  
368 annual basis ( $\beta_1 = 0.10 [-1.4, 1.5]$ ,  $p(\beta_1 > 0) = 0.50$ ). Within populations, years with high  
369 population growth rate were not associated with years of high adult survival (Fig. 6).

370  
371 Figure 6: Relationship between adult apparent survival averaged over sexes as obtained from  
372 CJS<sub>3</sub> and population growth rate in eight European whinchat populations based on mean  
373 estimates (A) and temporal residuals (B).



374  
375 **Discussion**

376 We studied survival of whinchats from eight populations across Europe. Annual apparent  
377 survival showed consistent effects of age, sex and breeding success, which allowed gauging  
378 likely values of both true juvenile and adult survival. We also investigated the relationship  
379 between adult survival and population dynamics. The lack of evidence for a positive relationship

380 between adult survival and population growth suggests that recruitment is the main driver of  
381 whinchat population dynamics and that conditions outside the breeding areas are unlikely to have  
382 contributed to the large-scale declines of European whinchat populations.

### 383 Sex-specific differences in adult survival

384         Adult apparent survival was consistently higher in males than in females in all eight study  
385 populations. The sex-specific difference in apparent survival might be caused by a difference in  
386 true survival in favor of males or by stronger dispersal in females resulting in permanent  
387 emigration from the study areas. Higher mortality in females seems frequent in birds (Donald,  
388 2007). This phenomenon can be explained by their longer exposure to nest predators since  
389 females often have a more dominant role in incubation and brooding compared to males (Lack,  
390 1954; Owens and Bennett, 1994). Incubation and chick brooding is performed only by females in  
391 whinchats, which may therefore suffer from a higher mortality. However, the available  
392 information about predation in our study populations does not support this interpretation. Indeed,  
393 although females from the UK population suffering from strong nest predation (Border et al.,  
394 2017), they have only slightly lower apparent survival probabilities than males.

395         The other possibility for the occurrence of sex-specific differences in adult apparent  
396 survival is sex-specific breeding dispersal. Generally in birds, males tend to be more faithful to  
397 their breeding site than females (Clarke et al., 1997; Greenwood, 1980) and consequently we  
398 expect lower apparent survival in females compared to males. Because breeding dispersal is  
399 known to be stronger in whinchat females than males (Bastian, 1992; Greenwood, 1980), the  
400 lower female apparent survival is at least partially the result of differential breeding dispersal.  
401 However, this is only valid for populations in which breeding dispersal results in permanent

402 emigration, namely in populations with small spatial extension with respect to dispersal  
403 distances. Adult apparent survival from the largest and most isolated population (UK) was high  
404 and very similar for both sexes. This suggests that true adult survival is similar in both sexes.  
405 Annual survival estimated from capture-recapture data collected in the non-breeding area, which  
406 is assumed to reflect true survival due to high site fidelity (Blackburn and Cresswell, 2016b),  
407 shows similar adult survival for both sexes of about 0.53 (Blackburn and Cresswell, 2016a). In  
408 our study we found that the sex effect was almost negligible when adult female apparent survival  
409 was above 0.5. Thus, although adult apparent survival was typically higher in male than in female  
410 whinchats, true adult survival might actually hardly differ between sexes, at least when no  
411 intensive grassland management occurs that results in additional mortality in brooding females  
412 (Grüebler et al. 2008).

#### 413 Effect of breeding success and true adult survival

414 We found that breeding success had a strong positive effect on apparent survival, which  
415 was similar for males and females. Apparent survival of successful individuals was on average  
416 0.55 and 0.45 in males and females, respectively (Fig. 3). The effect of breeding success on  
417 apparent survival can be explained by the reduced breeding dispersal of successful breeders.  
418 Previous studies have demonstrated that successful individuals are more faithful to their breeding  
419 site and that, while males are generally more philopatric than females, males and females  
420 responded similarly to the variation of breeding success (Haas, 1998; Hoover, 2003). Under the  
421 assumption that successful breeders do not disperse, their apparent survival should be identical to  
422 true survival, hence around 0.55 in adult whinchat males (Fig. 3). Female survival was more  
423 variable rendering the conclusions more uncertain. Because whinchats have a male-territorial  
424 social system, a sex-specific difference in breeding dispersal might still be expected among

425 successful breeders. The assumption that successful breeders do not disperse may be weaker for  
426 females. Nevertheless, for three populations (UK, SL, Ba), survival of successful females was  
427 higher than 0.5. These estimates are in line with female survival estimated on the non-breeding  
428 ground in Africa (0.53, Blackburn and Cresswell, 2016a). Thus, we suggest that true female  
429 survival is likely to be between 0.5-0.6 at least for UK, SL and Re populations. Estimates of  
430 apparent survival in small passerines are often in the range between 0.3 and 0.4 (e.g. Johnston et  
431 al., 2016), and may strongly underestimate true survival (Marshall et al., 2004). In migratory  
432 species which are often more faithful to their non-breeding than to their breeding site (Blackburn  
433 and Cresswell, 2016b), annual apparent survival estimated in the non-breeding area is often  
434 higher than in the breeding grounds, e.g. garden warbler *Sylvia borin* 0.40 vs. 0.54 (Johnston et  
435 al., 2016; Peach et al., 2001) or *Saxicola rubetra* 0.44 vs. 0.53 (this study, Blackburn and  
436 Cresswell, 2016a). Consistently, survival of small passerines from populations where permanent  
437 emigration is negligible reach values of 0.6-0.7 (siberian tit *Poecile cinctus* Orell et al., 1999,  
438 willow tit *Poecile montanus* Lampila et al., 2006, house sparrow *Passer domesticus* Ringsby et  
439 al., 1999, song sparrow *Melospiza melodia* Dybala et al., 2013, ortolan bunting *Emberiza*  
440 *hortulana* Steifetten and Dale, 2006).

#### 441 Juvenile survival

442 Juvenile apparent survival was low (0.1 on average) and highly variable among  
443 populations. Due to high natal dispersal rates, apparent survival is certainly lower than true  
444 juvenile survival and the variability among populations reflects primarily variation in permanent  
445 emigration (Clarke et al., 1997; Greenwood, 1980; Weatherhead and Forbes, 1994). Based on the  
446 assumption that true adult female survival is between 0.5-0.6, our population model shows that  
447 average juvenile survival is unlikely to be lower than 0.2 and is probably between 0.2 and 0.35.

448 This is consistent with previous conclusions about juvenile survival in this species (Müller et al.,  
449 2005) and with estimates of other passerines with similar methodology (0.2-0.3, Donovan et al.,  
450 1995; Lack, 1954). Our rough estimate is also in line with the few empirical estimates of true  
451 juvenile survival for other passerines where natal dispersal was negligible (0.24, house sparrow  
452 Ringsby et al., 1999; 0.30, song sparrow Dybala et al., 2013; 0.32, ortolan bunting Steifetten and  
453 Dale, 2006; 0.34, seaside sparrow *Ammodramus maritimus* Gilroy et al., 2012). Given that the  
454 average juvenile apparent survival is about 0.1 and true survival 0.2-0.35, about 50% to 75% of  
455 all juveniles are expected to disperse from the study areas.

456 Survival during the first month after fledging (post-fledging survival) is low in passerines  
457 (Cox et al., 2014; Naef-Daenzer and Gruebler, 2016) and has been estimated to be 0.52 in  
458 whinchats (Tome and Denac, 2012). The combination of low post-fledging survival with the  
459 likely range of the annual juvenile survival (0.2-0.35), suggests that the survival of juvenile  
460 whinchats older than one month is close to adult survival ( $(0.25 \text{ to } 0.3) / 0.52 = 0.48 \text{ to } 0.58$ ).  
461 Consistently, survival of juvenile whinchats is not distinguishable from adults after autumn  
462 migration (Blackburn and Cresswell, 2016a). This is in agreement with previous studies  
463 suggesting that the post-fledging period is the main bottleneck for juveniles, whereas during the  
464 rest of the year survival of juveniles is close to that of adults (Gruebler et al., 2014; Magrath,  
465 1991).

#### 466 Are whinchat populations driven by adult survival?

467 We did not find evidence of a positive relationship between adult survival and population  
468 growth rate. This suggests that adult survival was not the driver of population dynamics and that  
469 a degradation of conditions outside the breeding areas with potentially negative effects on



470 survival is an unlikely cause for the large-scale decline of European whinchat populations. The  
471 strongest support for this suggestion originates from the fact that the two populations with the  
472 highest male survival showed the strongest declines (SL and SW). Pioneering studies on the  
473 ecology of whinchats in their non-breeding area came to a similar conclusion. They suggested  
474 that the availability of suitable non-breeding habitat is unlikely to be a limiting factor and that  
475 survival is high during the presence of the individuals at the non-breeding sites (Blackburn and  
476 Cresswell, 2016a; Hulme and Cresswell, 2012). The population dynamics of whinchats is  
477 therefore likely driven by recruitment (productivity, juvenile survival, natal dispersal), which is in  
478 line with several studies in other species (Arcese et al., 1992; Grant and Grant, 1989; Schaub et  
479 al., 2013).

480 Land-use changes have strongly affected species occupying agricultural habitats (Donald et al.,  
481 2001; Newton, 2004; Sanderson et al., 2006; Stanton et al., 2018) and the whinchat is no  
482 exception to this general pattern. The increasing use of fertilizers in grassland and the resulting  
483 change in timing and frequency of mowing has caused serious damage to this species (Müller et  
484 al., 2005). Modern agricultural practices strongly reduced breeding success directly through nest  
485 destruction and indirectly through a decrease of food abundance (Britschgi et al., 2006; Tome and  
486 Denac, 2012). Both processes are likely to affect recruitment. Habitat degradation and  
487 fragmentation may also indirectly weaken remaining populations by a decrease of immigration  
488 and the disappearance of a potential rescue effect. There is further strong evidence that the main  
489 factor for the large-scale population decline of whinchats is the degradation of the breeding  
490 habitat. In Switzerland and France, where whinchat populations crashed like in Europe in  
491 general, mountain areas have acted as refuges. The species disappeared in the lowland where  
492 habitat modifications have been more pronounced and advanced compared to mountain areas

493 (Archaux, 2007; Müller et al., 2005). Whinchats persist today at higher elevations in a habitat that  
494 was previously found to be sub-optimal (Calladine and Bray, 2012; Müller et al., 2005). In  
495 Southern England and Wallonia, where whinchats have undergone a massive decline following  
496 the intensification of the agricultural practice, the two last significant populations persist in  
497 military training areas with large, extensively managed and largely protected grasslands  
498 (Salisbury Plain, Taylor, 2015; Elsenborn military camp, Jacob et al., 2010). Finally, while the  
499 large-scale population trend was strongly negative, some whinchat populations have been able to  
500 increase locally where the breeding habitat remained suitable (e.g. Lithuania in the 1990s,  
501 Kurlavičius 2015).

502         Yet, we acknowledge that other factors may still act synergistically (Vickery et al., 2014).  
503 For example, as a long-distance migrant, global warming may have a negative effect on whinchat  
504 reproduction affecting the phenological matching with prey abundance (Henderson et al., 2014).  
505 Populations of long-distance migrants decrease at a faster rate than residents or short-distance  
506 migrants likely because they are not able to adjust their migration timing to track the shift in  
507 spring resource pulse (Both et al., 2010). However, from a conservation perspective, current  
508 evidence suggests that breeding habitat deterioration in Europe is by far the most important factor  
509 for the large-scale decline of whinchats (Bastian 2015; Hulme and Cresswell, 2012). This  
510 conclusion is in line with results on other farmland bird species showing that their declines are  
511 independent on their migration strategies (Bowler et al., 2019; Reif and Vermouzek, 2019). These  
512 consistent results reinforce the urgent need to integrate conservation biodiversity more efficiently  
513 into agricultural policies of European countries.

514

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