



High within-winter and annual survival rates in a declining Afro-Palaeartic migratory bird suggest that wintering conditions do not limit populations

EMMA BLACKBURN^{1,2*} & WILL CRESSWELL^{1,2}

¹*School of Biology, University of St Andrews, St Andrews, Fife KY16 9TS, UK*

²*A.P. Leventis Ornithological Research Institute, Jos, Nigeria*

For migratory birds, it is necessary to estimate annual and overwinter survival rates, identify factors that influence survival, and assess whether survival varies with age and sex if we are to understand population dynamics and thus inform conservation. This study is one of the first to document overwinter and annual survival from the wintering grounds of a declining Afro-Palaeartic migrant bird, the Whinchat *Saxicola rubetra*. We monitored a population of marked individuals for which dispersal was low and detectability was high, allowing accurate estimates of survival. Annual survival was at least 52% and did not differ significantly across demographic groups or with habitat characteristics or residency time in the previous winter. Overwinter survival was very high and monthly survival at least 98% at some sites. Although winter residency varied spatially and with age, lower residency did not correlate with reduced annual survival, suggesting occupancy of multiple wintering sites rather than higher winter mortality of individuals with shorter residency. Our results suggest that mortality occurs primarily outside the wintering period, probably during migration, and that wintering conditions have minimal influence on survival. The similarity between survival rates for all age and sex classes when measured on the wintering grounds implies that any difference in survival with age or sex occurs only during the first migration or during the post-fledging stage, and that selection of wintering habitat, or territory quality, makes little difference to survival in Whinchats. Our findings suggest that the wintering grounds do not limit populations as much as the migratory and breeding stages, with implications for the conservation of declining Afro-Palaeartic migrants more widely.

Keywords: Afro-Palaeartic migrant, overwinter survival, population dynamics, Whinchat, winter ecology.

Migratory birds are affected by conditions in their breeding and non-breeding seasons, both of which can strongly influence life history traits and therefore population dynamics (Moore *et al.* 1995, Newton 2010). Constraints and pressures differ between breeding, wintering and migrating stages, and consequently each stage has different costs and implications for survival. On the breeding grounds, the costs of reproduction and higher abiotic pressures may result in lower survival when breeding than in winter (Newton 2010). Mortality

can occur during migration due to unpredictable weather conditions, degradation or loss of stopover sites and navigational errors (Newton 2006, 2010), and mortality rates may be higher during migration compared with sedentary periods due primarily to the unpredictability and huge energetic costs of migratory flight (Sillett & Holmes 2002, Newton 2006). Survival may differ between migratory journeys because the costs, carry-over effects and migratory strategies differ between breeding and wintering periods (Newton 2010), but whether wintering or breeding conditions are more influential on survival is likely to be both species- and population-specific (Sherry & Holmes 1995).

*Corresponding author.

Email: emma.blackburn05@alumni.imperial.ac.uk

Accurate survival estimates for each stage of the annual cycle are therefore necessary for understanding population trends and consequently for the conservation of Afro-Palaearctic migrants, many of which are experiencing population declines (Sanderson *et al.* 2006, Vickery *et al.* 2014).

Annual strategies and the factors influencing survival often vary with age and sex, and consequently so do the survival rates of different demographic groups throughout the annual migratory cycle. First-winter birds may have lower overwinter survival because the chance of arriving in poorer habitats is greater due to the generally stochastic nature of the first migration (Cresswell 2014). Mortality is likely to be higher during migration for inexperienced individuals, and juveniles often have lower breeding success because their migratory phenology may differ from that of adults (McKinnon *et al.* 2014 and references therein). Consequently, annual survival is often lower for first-winter birds than for adults (Dugger *et al.* 2004). Breeding costs are often also higher for inexperienced first-time breeders, and for females compared with males (Viallefont *et al.* 1995, Hanssen *et al.* 2005), leading to differential survival. Survival may also differ between males and females if migration behaviour differs between the sexes (Ketterson & Nolan 1983). Survival may also vary on the wintering grounds because age and sex differences in dominance may result in sub-dominant birds occupying poorer habitats (Lynch *et al.* 1985, Parrish & Sherry 1994, Figuerola *et al.* 2001, Marra & Holmes 2001, Catry *et al.* 2004), and these individuals often have reduced survival as a result (Rappole *et al.* 1989, Robbins *et al.* 1989, Jones *et al.* 1996, Marra & Holmes 2001, Norris *et al.* 2004). Where this occurs, winter habitat selection often carries over to influence survival and future breeding success (Marra & Holmes 2001, Norris 2005, González-Prieto & Hobson 2013, Rockwell 2013). Alternatively, if migrants can tolerate a wide range of relatively poor wintering habitats (Cresswell 2014), then the non-breeding period is less likely to have strong carry-over effects and there is little need to compete with conspecifics for territories of varying quality. In this case, survival is unlikely to vary with age or sex during winter, which in turn may be an indicator of a lack of dominance-based habitat selection.

We estimate annual survival and overwinter survival, differentiate between long-range dispersal

and mortality during winter, and explore the effects of age, sex, habitat and wintering ecology on survival in a declining Afro-Palaearctic migrant, the Whinchat *Saxicola rubetra*, on its wintering grounds in West Africa. Despite the importance of accurate survival estimates, data are scarce, especially for the wintering period (Grüebler *et al.* 2014) and for the Palaearctic system. Key to estimating survival at any stage is knowing the degree of site fidelity and being able to distinguish between survival and dispersal, and we have established that this wintering population is highly site-faithful and that we can detect local dispersal (Blackburn & Cresswell 2015a). Annual survival estimated from return rates is often lower than true survival because individuals disperse (Gilroy *et al.* 2012, Ergon & Gardner 2013, Schaub & Royle 2013), but if individuals are highly site-faithful and the ability to detect any dispersal is high, it may be possible to estimate true survival as opposed to apparent survival.

In this study we estimate annual survival rates, and assess whether these vary with age and sex, between winters and wintering sites, or with territory size and habitat characteristics in the previous winter. We quantify the winter residency period, and assess whether it influences the probability of returning in the following year. We also estimate overwinter survival rate and assess whether this varies with age and sex.

We predict that annual survival will be similar to or higher than that reported on the breeding grounds because we expect most mortality to occur during migration, and specifically during the first migration from the breeding grounds for first-winter birds because they have no prior knowledge of migration. We expect overwinter survival to be high because ecological constraints and breeding pressures are largely absent during winter, all wintering birds have already migrated successfully, and generalist wintering requirements within the wintering habitat should promote survival under a wide range of conditions (Blackburn & Cresswell 2015b). We expect annual survival to be lower for first-winter birds due to their inexperience during spring migration and as first-time breeders. We predict no demographic differences in overwinter survival and no influence of winter habitat or territory size on annual survival because of the generalist requirements within the chosen wintering habitat and because of the lack of dominance-based wintering ecology that we have shown

previously for this wintering population (Blackburn & Cresswell 2015b).

METHODS

Study site

This study is part of a larger study of the wintering ecology of Whinchats on their wintering grounds in West Africa, on the Jos Plateau, in the Guinea savannah zone of central Nigeria (9°53'N, 8°59'E, approximately 1250 m altitude; Fig. 1). Whinchats were studied over three successive wintering seasons (hereby referred to chronologically as Winters 1, 2 and 3), starting in February 2011 and ending in March 2014. Study sites comprised open, degraded scrubland with sparse human settlements, arable farming and livestock grazing. Graz-

ing intensity increased during the winter (Hulme & Cresswell 2012, Blackburn & Cresswell 2015b). Three study sites were used in all winters (Sites A, B and C; Fig. 1) and we added two sites (D and E) at the end of Winter 2. In Winter 3 we captured birds at two additional sites (marked 'X' in Fig. 1), but only include these individuals in analyses exploring age and sex ratios across sites because their return rates were not assessed in the following winter and these individuals were monitored less closely for overwinter survival. Sites were selected for logistical reasons, being close together and accessible, and not because they differed with respect to habitat or other Whinchat characteristics. Age and sex ratios did not differ across study sites (chi-squared tests on all birds captured across the study in all years: age $\chi^2_5 = 2.7$, $P = 0.75$, $n = 409$; sex $\chi^2_5 = 5.9$, $P = 0.32$, $n = 407$).

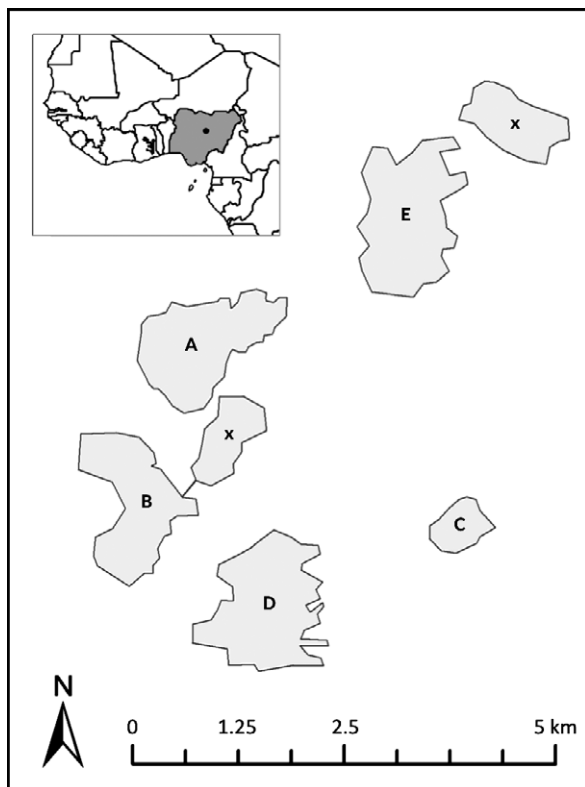


Figure 1. Map of the six study sites and their location within Nigeria in West Africa (●). Sites A, B and C were used in all three winters; Sites D and E in Winters 2 and 3, and sites marked X used in Winter 3 only. The study sites had a combined area of approximately 8 km². Note that sites exist for logistical reasons rather than representing biologically distinct areas, although variation in within-winter residency periods was discovered across sites during the study.

Capturing and resighting individuals

We used spring traps and mist-nets with conspecific playback and live bait to capture Whinchats. Each bird was uniquely colour-ringed, aged as either first-winter or adult (Jenni & Winkler 2004), and sexed and measured (maximum wing cord, tarsus, mass). By resighting colour-ringed birds we determined the location and size of their territories; areas within territories used most often; and the degree of residency and site fidelity within and between winters. In Winters 1 and 2 we focused on obtaining accurate locations of undisturbed birds, and in Winter 3 we focused simply on relocating returning birds. We resighted birds from dawn (c. 06:00 h) until 11:00 h and from 16:00 h until dusk (c. 18:30 h), locating birds with binoculars (Swarovski SV 8 × 32; Absam, Austria), reading colour combinations with a spotting scope (Zeiss Diascope 65 mm with 25× eyepiece; Oberkochen, Germany), and recording locations using a GPS (Garmin GPSMAP 64). Whinchats perch on shrubs and isolated vegetation from which they make frequent sallies to feed, and were easily detected when present. We recorded whether a bird was undisturbed before being sighted and the date and time to the nearest minute. A Whinchat could travel across its territory within seconds, and observations were found to be spatially independent regardless of how close they were in time (general linear model of distance between resightings fitted as a function of observation time (controlling for individual): $F_{1,762} = 0.02$, $P = 0.90$; 765 observa-

tions of 119 individuals). Territories were visited a minimum of once a week, but often more frequently. Resighting locations were viewed and edited where necessary in ARCMAP 10.1 (ERSI 2012) and Garmin BASECAMP software (version 4.2.4; Garmin International, Inc., Olathe, KS, USA). UTM units (Zone 32N) were used for all location analyses to allow for interpretable distance calculations.

Calculating territory size

Territory size was calculated for individuals with at least five undisturbed resightings in either Winter 1 ($n = 33$) or Winter 2 ($n = 39$) (total resightings $n = 72$). We used the mean distance between each resighting and the territory centre (the average of all undisturbed resightings), which was then doubled to give territory diameter and used as an index of territory size. We chose this method over the conventional method of calculating minimum convex polygons (MCPs) to estimate territory or range size because of the large number of resightings MCP requires, to avoid some known biases of the MCP method (see Hansteen *et al.* 1997 and Börger *et al.* 2006, although our method may not necessarily avoid these biases), and because we aimed to determine approximate territory size rather than accurate, defined territory boundaries. We only calculated territory size for birds with a minimum of five resightings to attempt to standardize the influence that increasing resighting sample size has on territory size estimates for birds with only a few resightings (Börger *et al.* 2006) and to maintain adequate sample sizes. When we calculated territory size requiring a minimum of 10 resightings, the average territory diameter across all birds was altered by 4 m (6%) and any results from analyses including territory size were unchanged, suggesting that we could use five resightings to maximize sample sizes (although 10 resightings may also inadequate). We averaged a bird's territory size across both years when it was resighted at least five times in each of 2 years, i.e. birds from Winter 1 returning in Winter 2; the average difference in territory size for the same bird across years was 15.5 m (± 2.9 m, $n = 19$; see below for the average movement of territory centres between years, and Blackburn & Cresswell 2015b). We acknowledge that locations recorded with a GPS have some inaccuracy (approximately 2–3 m at our study site) but assume this error to be equal across all territories and therefore to affect all territories similarly.

Habitat sampling

We sampled territory habitat characteristics in Winter 2 as part of a complementary study exploring the influence of winter habitat on wintering ecology (Blackburn & Cresswell 2015b). Habitat was sampled within a 50-m-diameter plot at the territory centre for 84 birds, for all of which there were at least five resightings. Analyses of these data revealed that shrub density (here a variable resulting from a principal component analysis of original habitat variables) and the presence or absence of maize crops within the territory influenced territory size, whereby increasing shrub density and the presence of maize crops significantly reduced territory size (Blackburn & Cresswell 2015b). We therefore consider these variables, alongside grazing intensity, plant diversity, the degree of vegetation clumping and the percentage of farmland within the area of territory sampled to explore the influence of the previous winter territory's habitat characteristics on annual survival (for methods see Blackburn & Cresswell 2015b).

Residency period

To test whether annual survival (i.e. the probability of return in the following winter) differed between birds that left their wintering sites early in the wintering season, we defined residency period (the amount of time in which a bird was known to be present at the study site) as 'short' or 'long'. Resightings over four winters suggested that Whinchats arrived in mid-September and departed until late April, and so we defined short residency as departure between September and December and long residency as departure after December. We used departure month as a more precise measure of residency (i.e. instead of last resighting date or the time between capture and the last resighting) because we did not know the arrival time of birds. Birds were only included in residency period analyses if they had been resighted at least 30 days after capture to ensure that they were not transient individuals. We tested whether return rates differed between birds that were not resighted at least 30 days after capture and birds that were resighted, and found that these birds were no less likely to return in the following year, albeit with a borderline significant result (generalized linear model (GLM) of returned in following year \sim resight ≥ 30 days after capture: $\beta = 0.71$,

se = 0.40, $z = 1.8$, $P = 0.079$). A bird was considered to have departed if it was not seen for three consecutive visits (but note that vacant territories were often checked frequently during resighting visits after a bird was considered to have departed because territories were close together, and there were no cases in which a bird reappeared later in the same winter after we considered it to have departed). We are therefore confident that month of departure could be determined accurately. We have shown previously that across resident birds (i.e. those seen at least 30 days after capture), departure month varies with age and between sites, with first-winter birds departing before adults, and birds departing early from Sites B and C relative to Site A (Blackburn & Cresswell 2015a; there was also no effect of short or long residency period on the probability of return). Therefore, we tested whether the cumulative number of days a bird was recorded at a site was a function of survival rather than adaptive variation in residency time, because if this were the case we should see higher between-year survival with longer residency time (here defined by departure month).

We have shown previously that apparent survival is likely to reflect true survival in this study population due to high detection probability and extremely high site fidelity at the territory-level both within and between winters (Blackburn & Cresswell 2015a). The probability of resighting a bird if its territory was visited once was 63% and each territory was visited numerous times, e.g. an average of nine times (± 0.51 , range 1–18, $n = 81$) during a period in which we documented resighting effort (1 November 2012 to 24 April 2013), plus further visits were made in which resighting effort was not recorded. Consequently, we had an almost 100% chance of detecting a bird if it was present during the winter (Blackburn & Cresswell 2015a). Furthermore, birds could disperse to up to eight territories (average 544 m \pm 10.9) before the probability of detecting them fell below 50% (Blackburn & Cresswell 2015a). All returning birds reoccupied their previous winter territories, with the average distance between territory centres in different years being only 30 m (± 4.0 m, range 6–58 m, $n = 19$), still within the territory boundary (full details given in Blackburn & Cresswell 2015a). We are therefore confident in our ability to detect resident and returning individuals and we present annual survival estimates as true survival and not apparent survival.

Sample sizes and statistical analyses

We captured 458 birds over three study winters. Birds ringed at Sites D and E at the end of Winter 2 were excluded because their residency was unknown, and all individuals ringed in Winter 3 were excluded because return rates were unknown and overwinter survival was not thoroughly explored in Winter 3. We therefore present data for 154 birds ringed across Winters 1 and 2 and resighted at least once after capture (Winter 1: $n = 38$, Winter 2: $n = 116$). We assumed years to be independent and included all possible birds in Winters 2–3, regardless of whether they had been part of the sample for Winters 1–2 ($n = 21$; Table 1). Birds that could not be confidently aged or sexed were excluded from models including age and sex as predictors. One individual was excluded from analyses including habitat variables because its territory was in an unrepresentative habitat (a dense coffee farm), which grossly inflated the vegetation counts within that territory. Nonetheless, removing this individual did not change any of the main findings.

We used GLMs (logistic regression with binomial error structure) to explore predictors of annual survival (return rates) and the relationship between departure month and annual survival. We ran two models. The first explored the influence of individual characteristics and aspects of wintering ecology on return rates, in which the full model was: returned next year \sim age (adult or first-winter) + sex + bird condition at capture + territory size + winter (study year) + site + residency time (short or long) + age * site + sex * site + age * sex + site * residency time. The second explored the influence of territory habitat characteristics in the previous winter on return rates while controlling for age, sex and site, in which the full model was: returned next year \sim presence of maize + percentage of farm + level of grazing + plant diversity + shrub density + vegetation clumping + vegetation cover + age + sex + bird condition at capture + site (random effect). We used the residuals from an LM of mass \sim wing + tarsus for the variable 'body condition at capture' to control for the relationship between bird size and mass. A GLM was used to assess differences in overwinter survival according to age and sex. We included all birds of known age and sex across all sites because age and sex ratios were the same across sites. When exploring within-winter survival, we focused on birds from a single site (Site A)

Table 1. Numbers of birds in the study and resighted (RS) at least once after capture, separated by age and winter (W).

	First-winter			Adult			Study total		
	Σ RS (%)	Returned (%)	Not returned (%)	Σ RS (%)	Returned (%)	Not returned (%)	Σ RS (+U age)	Returned (%)	Not returned (%)
Winter 1	12 (33)	–	–	24 (67)	–	–	36 (1)	–	–
Winter 2									
W1 birds	–	6 (50)	6 (50)	–	15 (63)	9 (38)	21 (0)	21 (58)	15 (42)
Newly ringed	33 (54)	–	–	28 (46)	–	–	61 (2)	–	–
Winter 3									
W1 birds	–	–	–	–	–	–	–	9 (24)	28 (76)
W1 returned in W2	–	–	–	–	–	–	–	9 (43)	12 (57)
All known from W2	–	19 (58)	14 (42)	–	23 (47)	26 (53)	82 (2)	44 (52)	40 (48)
Birds ringed in W2	–	19 (58)	14 (42)	–	14 (50)	14 (50)	63 (2)	33 (54)	28 (46)
Newly ringed	48 (51)	–	–	46 (49)	–	–	94 (0)	–	–
Total	101 (49.5)	29 (56)	23 (44)	103 (50.5)	38 (50)	38 (50)	196 (3)	65 (54)	56 (46)

Σ RS = total number of birds resighted. Birds ringed at Sites D and E in Winter 2 are not included in the totals because their residency and return status were unknown ($n = 9$; see Methods). Figures are number of individuals, plus percentage of the total individuals in that age category (First-winter and Adult) or of all individuals for that row (Study total) in parentheses. Birds of unknown age ($n = 1$ Winter 1, $n = 2$ Winter 2) are excluded from age-specific totals but not from study total. In four cases, a bird was only resighted the following winter ($n = 2$ Winter 1, $n = 2$ Winter 2). Ages of 'returned' and 'not returned' birds are those of the previous year. First-winter birds from Winter 1 are included in adult totals for following years and are included in Winter 3 return rates if they returned in Winter 2. The total number of individuals that returned or did not return across the study are given in bold (percentages in parentheses).

because winter residency time differed between study sites, but residency time did not predict annual survival (see Results). At this site, a greater number of individuals were ringed and closely followed ($n = 32$) and most birds were resighted for a substantial amount of the wintering period, allowing us to document and explore predictors of survival. We included birds captured or seen at this site before 1 January in Winter 2 for within-winter survival analyses. Because there was no relationship between residency period and between-year survival (see Results), using a site with a high overwinter residency did not necessarily exclude individuals with reduced within-winter survival. Although initially attempted, a mark–recapture analysis was not well suited to our data, mainly because resighting and capture effort varied across the three study winters, and produced substantially lower annual survival rates to those actually observed and with very broad confidence intervals. Although four birds (2%) were only resighted in the winter after their capture, this was because these birds were captured on the boundaries of the study sites, and their territories were only located upon expanding the study boundaries in the following winter, not because they went undetected within the study sites. There were no instances where a bird was not resighted the year

after ringing but then returned in the following winter (i.e. 101 in a capture–mark–recapture analysis). Consequently, we used our simpler, and more robust, approach for establishing within-winter and annual survival.

Analyses were performed in R version 3.0.1 (R Development Core Team 2013) and RSTUDIO. Data were checked for normality and for multicollinearity using variance inflation factors (CARS package; Fox *et al.* 2007) and non-parametric tests were used when necessary. Model selection was based on Akaike's information criterion (AIC) (Bozdogan 1987). For models of the same or similar sample sizes across all variables, the top model was identified using the dredge function in package MuMIn (Bartoń 2012). Cases with missing values were removed from the dataset as required, and resulting top models were produced using complete datasets. When presenting top models derived from the dredge function, we present models within Δ AIC = 3 of the top model to give an adequate sample of top models. We used a likelihood-ratio test (lrtest function in the epicalc package; Chonsuvivatwong 2008) to compare top models with the null model. For all candidate final models, model fit was evaluated from diagnostic model plots and models presented if assumptions were reasonably met (Crawley 2007). Predicted survival probabilities presented in Figures 2 and 3 were

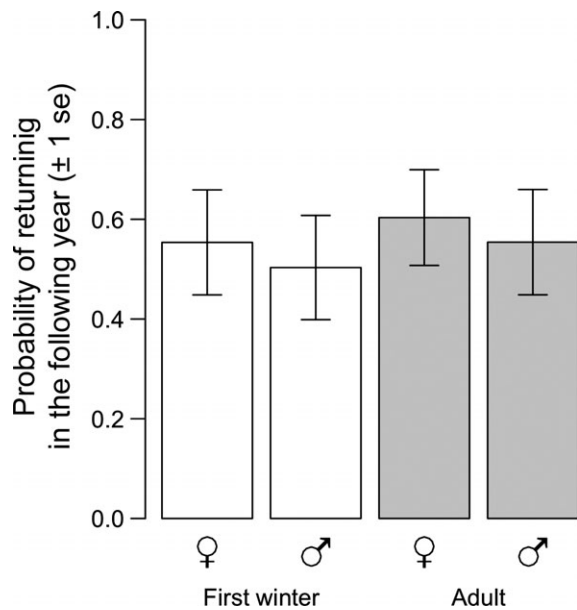


Figure 2. Return rates did not differ with age and sex. Survival probabilities are predicted values (\pm se) for the probability of return in the following winter according to age and sex, calculated from the logistic regression analysis: returned next year \sim age + sex (estimates: age = -0.20 , se 0.44 , $z = -0.5$, $P = 0.65$; sex = -0.20 , se 0.44 , $z = -0.5$, $P = 0.65$; intercept 0.42 , se 0.43 ; $n = 94$). Birds from Winter 1 that returned in both Winters 2 and 3 are included in return rates from Winter 1 to Winter 2 only.

calculated from model parameter estimates and their associated standard errors and were back-transformed. Mean values are shown ± 1 se. A statistical significance level of $P < 0.05$ was chosen to reject null hypotheses.

RESULTS

Annual survival

Annual survival was at least 52% (Fig. 2; Table 1). Across the study period, 54% of individuals seen in Winters 1 and 2 returned to the study area in the following winter (Table 1). Return rates (annual survival) did not differ with age, sex, site or winter (study year), with bird condition at capture, with territory size, or with whether a bird had a long or short residency period in the previous winter (Figs 2 & 3, Table 2, also see below). Although the top model exploring predictors of annual survival included territory size, this model was within Δ AIC = 0.16 of the null model, and a likelihood-ratio test showed no significant effect of territory size on survival (likelihood-ratio test for maximum-likelihood estimation method: $\chi^2_1 = 2.27$, $P = 0.13$). Habitat variables within a bird's territory in the previous winter had no influence on the probability of

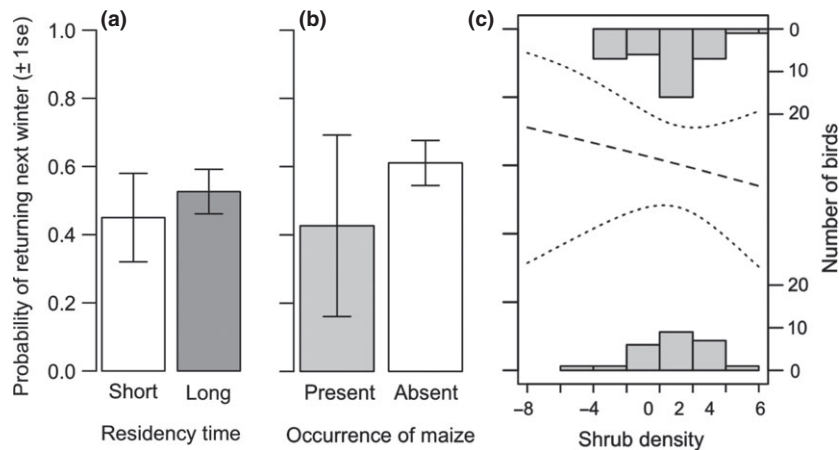


Figure 3. The probability of a bird returning next winter as a result of (a) its residency time in the previous winter (short or long); (b) whether maize was present within the territory in the previous winter; and (c) the density of perching shrubs within the territory held in the previous winter. Values for (a) are predicted from the parameter estimates (\pm se) from a logistic regression of returned \sim residency period (estimate = -0.31 , se = 0.52 , $z = -0.59$, $P = 0.56$; residual deviance for model = 106.4 on 76 df, $n = 77$). Values for (b) are predicted from a logistic regression of returned \sim presence of maize + shrub density (estimate = 0.045 , se = 0.36 , $z = 0.7$, $P = 0.47$; residual deviance for model = 43.9 on 31 df, $n = 32$), using medium values for shrub density. (c) Histograms show shrub density for birds that returned (top bars) or did not return (lower bars), and dashed lines show predicted values \pm se (dotted lines) from logistic regression models of returned \sim shrub density (estimate = -0.070 , se = 0.12 , $z = -0.59$, $P = 0.55$, residual deviance for model = 84.3 on 61 df, $n = 63$). Note that none of the relationships or the differences was significant.

Table 2. The top 12 models (within $\Delta\text{AIC} = 3$ of the top model^a) of all possible models exploring predictors of annual return rates.

Component	Log likelihood	AICc	ΔAICc	Weight
Territory size	-48.77	101.71	0.00	0.17
Null	-49.91	101.87	0.16	0.16
Residency	-49.56	103.29	1.58	0.08
Residency + territory size	-48.50	103.36	1.64	0.08
Winter + territory size	-48.64	103.63	1.91	0.07
Bird condition	-49.73	103.63	1.92	0.07
Winter	-49.77	103.71	2.00	0.06
Age + territory size	-48.69	103.73	2.01	0.06
Bird condition + territory size	-48.69	103.73	2.02	0.06
Age	-49.79	103.76	2.05	0.06
Sex + territory size	-48.75	103.85	2.13	0.06
Sex	-49.88	103.93	2.21	0.06

All terms, including interaction terms were non-significant; $n = 72$. ^a $\Delta\text{AIC} = 3$ was chosen to give a representative number of top models.

it returning in the following year (considering all models within $\Delta\text{AIC} < 3$: vegetation cover had a relative AIC weight of 0.41; sex 0.27; age 0.24; grazing 0.17; plant diversity 0.13; shrub density 0.13; vegetation clumping 0.07; percentage farmland 0.05; presence of maize 0.05; bird condition at capture 0.05), including those habitat variables previously found to influence territory size (presence of maize and territory shrub density, Fig. 3; see Blackburn & Cresswell 2015b). In both cases the null model was therefore one of the best models predicting annual survival.

Winter residency

The cumulative number of days a bird was recorded at a site was not a function of survival rather than adaptive variation in residency time: departure month had no influence on whether a bird returned the following year (logistic regression: $\beta = 0.017$, $se = 0.17$, $z = 0.1$, $P = 0.92$, $n = 73$).

Within-winter survival

At Site A, for birds that were resident (i.e. present for at least 30 days after capture) 100% were still alive after 60 days across all sites ($n = 32$, Fig. 4). At Site A, 84% (27/32) of birds were resighted at least 90 days after capture and 78% (25/32) were resighted at least 120 days after capture. When

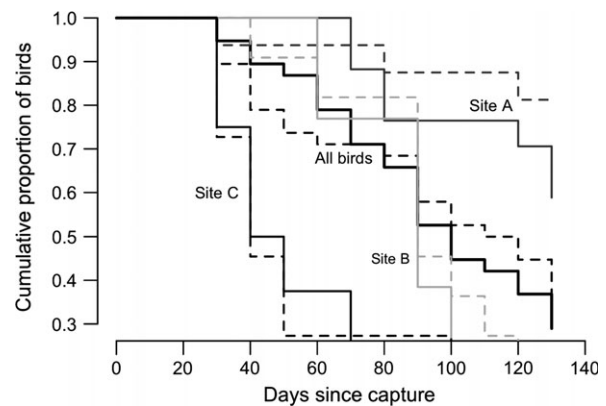


Figure 4. The proportion of resident birds (i.e. sighted at least 30 days after capture) known to be alive at all study sites in days since capture in Winter 2, based on resightings in Winter 2, separated by site. The black line shows data for all birds across all sites. Solid lines are birds that returned to the study site in the following winter (i.e. certain to be alive even if not resighted after day 1); dashed lines are birds that failed to return in the following winter. If cumulative probability of occurrence was related to survival rather than to residency, we would expect a significant difference between the dashed and solid lines matched by site.

accounting for whether birds that were not resighted until these dates returned in the following year (i.e. that must have still been alive even though they were not seen), 97% (31/32) of birds survived at least 90 days after capture and 94% (30/32) survived at least 120 days after capture (Fig. 4). This is equivalent to an average monthly within-winter survival rate of 98%. If it is assumed that all birds were present at the wintering grounds on 1 October when all individuals were likely to have arrived (resightings over four study winters indicate arrival in mid-September), and again accounting for whether missing (i.e. likely early-departed or relocated) individuals returned in the following year, 100% of individuals were present 90 days after arrival and 97% (31/32) were present 120 days after arrival (Fig. 4). This equates to a monthly survival rate of 99% on the wintering grounds. Within-winter survival did not differ with age or sex (age: $F_{1,28} = 0.02$, $P = 0.90$; sex: $F_{1,28} = 0.5$, $P = 0.50$; $n = 31$).

DISCUSSION

Annual survival

Annual survival was at least 52%, and 54% over the two study years. We are confident this reflects

true survival because of our ability to detect dispersing birds coupled with the high winter site fidelity of Whinchats (Blackburn & Cresswell 2015a). Our figures were similar to or higher than those reported for 12 Palaearctic migrant species wintering in the Gambia (King & Hutchinson 2001) and for numerous Neotropical migrants (e.g. Holmes & Sherry 1992, Wunderle & Latta 2000), but lower than those of Willow Flycatchers *Empidonax traillii* (68%, Koronkiewicz *et al.* 2006). Compared with the breeding grounds, our annual return rates were higher than those documented for Whinchats (return rates of 11–47% and annual apparent survival rates of 34–45%; Schmidt & Hantge 1954, Bezzel & Stiel 1977, Bastian 1992), and generally similar to or higher than those reported for other site-faithful Palaearctic migrants (Bensch & Hasselquist 1991, Siriwardena *et al.* 1998, Cowley & Siriwardena 2005, Møller & Szép 2005, Robinson *et al.* 2008, Shitikov *et al.* 2012, 2013). Annual survival rates of Neotropical migrants on the breeding grounds are also similar (Desante *et al.* 1995, Perneluzi & Faaborg 1999), although lower rates of 25–42% are reported for some Neotropical migrants (Conway *et al.* 1995).

For Whinchats, higher return rates on the wintering grounds compared with the breeding grounds suggest: (1) higher survival outside the wintering season; (2) higher mortality during or immediately after breeding or on route to the wintering grounds; (3) higher dispersal (and a failure to detect such dispersal) of adults and juveniles on the breeding grounds than any dispersal during winter, such as the effect of nesting failure on the decision to disperse (Haas 1998); or (4) a combination of these. It is unlikely that survival is higher outside the wintering season, especially considering the documented causes of mortality during the breeding season (Britschgi *et al.* 2006, Gruebler *et al.* 2008). Higher mortality post-fledging and on the first migration coupled with higher dispersal in the breeding region is likely to explain our higher winter annual survival rates. Breeding dispersal has indeed been documented in Whinchats, and dispersal rates are higher for returning juveniles than for adults (Bezzel & Stiel 1977, Bastian 1992, Shitikov *et al.* 2012, 2015). Evidence suggests that our annual survival rates were not confounded by dispersal, as may often be the case when estimating survival on the breeding grounds (Marshall *et al.* 2004). Mortality is also likely to be highest during the first migration to the wintering grounds

(discussed below) due to the naivety of juveniles migrating for the first time and the stochasticity of large-scale wintering site selection for first-winter birds (Cresswell 2014).

Within-winter survival

Within-winter survival was very high, with an average monthly survival rate of 98%, increasing to 99% when accounting for individuals that departed sites early but returned in the following year. Within-winter survival estimates for other migrants are scarce (Holmes *et al.* 1989), especially habitat-specific estimates (Conway *et al.* 1995) and for Palaearctic migrants. In the Neotropics, very high within-winter survival has been documented for Black-throated Blue Warblers *Setophaga caerulescens* (Sillert & Holmes 2002). Holmes *et al.* (1989) reported 80% survival for wintering American Redstarts *Setophaga ruticilla* and 66% for Black-throated Blue Warblers, for example, and high within-winter survival of 80–92% is reported for Willow Flycatchers (Koronkiewicz *et al.* 2006). Likewise, Barn Swallows *Hirundo rustica* also have higher survival during winter than during the post-fledging period (Gruebler *et al.* 2014). For Whinchats, generalist winter habitat requirements within their wintering habitat (Blackburn & Cresswell 2015b), combined with the reduced pressures, abiotic constraints and predation compared with during breeding, are all likely explanations for why within-winter survival is so high, and is indeed higher than survival rates documented on the breeding grounds (e.g. apparent survival of males during the breeding season in Switzerland was *c.* 0.8 for males; Gruebler *et al.* 2008).

There is little doubt that survival estimates are population- and species-specific and that survival may vary between years or between decades, as may the stage in the annual cycle that most influences annual survival. Some migrants have suffered huge population crashes due to extensive droughts on their wintering quarters in some years (e.g. Winstanley *et al.* 1974, Cowley 1979). Within-winter survival has also been shown to vary annually for some Neotropical migrants (Dugger *et al.* 2004). Unfortunately, we lacked data thoroughly to test year effects and the factors responsible, and we may have sampled years in which survival was unrepresentative for wintering Whinchats.

Demographic differences and winter habitat

Neither annual nor within-winter survival differed with age or sex. Within-winter survival is also similar for juvenile and adult Barn Swallows (Grüebler *et al.* 2014), Prothonotary Warblers *Protonotaria citrea* and Northern Waterthrushes *Parkesia noveboracensis* (Calvert *et al.* 2010). In contrast, Holmes *et al.* (1989) present evidence for lower within-winter survival for first-winter Black-throated Blue Warblers and American Redstarts, and first-winter Ovenbirds *Seiurus aurocapilla* and Black-and-White Warblers *Mniotilta varia* have also been found to have lower within-winter survival (Dugger *et al.* 2004). If survival does differ with age, this must occur during the first migratory journey only, when it would be undetected from the wintering ground perspective. Similar survival between the sexes suggests either that the pressures of breeding and migrating are similar for males and females, or that any differential survival for one sex is counteracted by lower survival for the other during another part of the annual cycle. For Whinchats, female mortality is reported to be higher than that of males on the breeding grounds (Grüebler *et al.* 2008). Similar survival rates between sexes are reported for Black-throated Blue Warblers (Sillert & Holmes 2002) but annual survival may be lower for male than female Willow Flycatchers (Koronkiewicz *et al.* 2006).

We also found no evidence that winter habitat or territory size influenced annual survival. For Neotropical migrants where this has been studied, survival is often linked to winter habitat, especially when subordinate individuals are forced into poorer quality habitats (Sherry & Holmes 1996 and references therein). In contrast, our findings support both a lack of dominance-based habitat occupancy on the wintering grounds and generalist wintering requirements within the broad wintering habitat (Cresswell 2014, Blackburn & Cresswell 2015a,b). The ability to use a wide range of ecological conditions and habitat characteristics is likely to allow high survival even in apparently sub-optimal wintering habitats, and reduces any carry-over effects of winter habitat on subsequent survival and possibly also reproduction. We note, however, that our estimate of territory size was crude and based on a small number of resightings. Nevertheless, Whinchats do not change territories between winters even when there are many

adjacent vacancies (Blackburn & Cresswell 2015a). If winter habitat or territory size (and therefore resource availability) does indeed influence annual survival, for example by limiting subsequent pre-migratory fattening that is necessary to survive migration, it may be that individuals compensate by moving to higher quality wintering sites immediately before migrating (Risely *et al.* 2015). If this were the case, we would not expect to find differences in annual survival measured on winter territory habitat characteristics.

Where is mortality occurring?

Our higher estimate of annual survival compared with those reported on the breeding grounds, very high within-winter survival, and no demographic differences in survival strongly suggest that mortality is greatest during the post-fledging period and/or during the first migration to the wintering grounds. In agreement, first-year migrants often have lower annual survival than adults when measured on the breeding grounds (Dugger *et al.* 2004). Post-fledging survival is often low for juvenile Whinchats, especially in managed grasslands (Müller *et al.* 2005, Tome & Denac 2012) where breeding populations have been severely affected by agricultural intensification over recent decades (Orlowski 2004, Müller *et al.* 2005, Broyer 2009, Horch & Birrer 2011, Fischer *et al.* 2012). Juvenile Barn Swallows also have much lower survival during the post-fledging period than during winter or on migration (Grüebler *et al.* 2014).

Very high within-winter survival and the lack of influence of winter habitat or territory size on survival suggests little influence of wintering conditions on Whinchat populations, as suggested by Hulme and Cresswell (2012). Whinchats adjust their territory size according to some habitat features (Blackburn & Cresswell 2015b), suggesting that territory size may indicate resource availability; however, this was not linked to survival. Although wintering conditions do influence some migrant populations (Baillie & Peach 1992, Rappole & McDonald 1994, Sherry & Holmes 1996, Ockendon *et al.* 2012, 2014, Vickery *et al.* 2014), some evidence suggests that this influence is minimal (Sherry & Holmes 1995, Wilson & Cresswell 2006, Hulme & Cresswell 2012). A long-term study for 19 species of Palaearctic migrant concluded that climatic conditions during breeding influence reproductive traits more than wintering

conditions do (Ockendon *et al.* 2013). Mortality during migration is thought to be especially high for migrants (Newton 2006), for example, up to 15 times higher than at any other time for Black-throated Blue Warblers, causing over 85% of the annual mortality for this species (Silleet & Holmes 2002, Holmes 2007). Yet for Barn Swallows, mortality during migration is suggested to be similar to that during winter (Grüebler *et al.* 2014). In general, mortality is likely to be highest outside the wintering season for most migrants, but with some exceptions.

We show that shorter within-winter residency is not due to winter mortality. Individuals with shorter residency are likely to have multiple wintering sites, i.e. when a Whinchat disappeared from its territory, it was because it had moved to another territory rather than having died. This was not due to differences in detectability (Blackburn & Cresswell 2015a); we are confident that we could detect when birds with short residency periods returned in the following winter. There is a possibility that a small number of these individuals went undetected upon return, and this would have decreased our estimates of annual survival. Such movements may be in response to changing conditions, and may be an artefact of extreme conditions in one year being reflected in subsequent migrations, as would be expected under the serial residency hypothesis for a species with such high winter site fidelity (Cresswell 2014). Such 'fixing' of migration phenology may also explain why there was no influence of winter habitat in the previous year on annual survival, even though winter residency differed across sites. That residency period had no influence on the probability of a bird surviving to return in the following year suggests that there are multiple residency strategies that promote survival during the wintering period. Recent studies using geolocators have revealed more than one wintering site for multiple migrants (Heckscher *et al.* 2011, Stach *et al.* 2012, Eraud *et al.* 2013, Lemke *et al.* 2013), although many migrants remain resident at a single site throughout winter (Bächler *et al.* 2010, Tøttrup *et al.* 2012, Jahn *et al.* 2013, Kristensen *et al.* 2013). In some cases, and as our results suggest, both single and multiple wintering site strategies have been found across individuals of the same species (Delmore *et al.* 2012, Cormier *et al.* 2013).

Overall, our results show evidence of very high within-winter survival and suggest that true annual

survival for some populations of Whinchats in Europe are at least 52% annually. Because high site fidelity occurs on the wintering ground and not the breeding ground, Whinchat survival should best be monitored on the wintering grounds. Then, if we confirm connectivity and the serial residency hypothesis (Cresswell 2014) suggests that this will be on a very large scale, we would gain an estimate of average true annual survival rate for Whinchat populations across a large part of their global breeding range.

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