



Characterising demographic contributions to observed population change in a declining migrant bird

Jennifer A. Border, Ian G. Henderson, Dominic Ash and Ian R. Hartley

J. A. Border (<http://orcid.org/0000-0001-9481-6809>) (jennifer.border@bto.org) and I. R. Hartley, Lancaster Environment Centre, Univ. of Lancaster, Lancaster, UK. – J.A.B and I. G. Henderson, British Trust for Ornithology, The Nunnery, Thetford, UK. – D. Ash, Defence Infrastructure Organisation, Catterick Garrison, North Yorkshire, UK.

Populations of Afro-Palaearctic migrant birds have shown severe declines in recent decades. To identify the causes of these declines, accurate measures of both demographic rates (seasonal productivity, apparent survival, immigration) and environmental parameters will allow conservation and research actions to be targeted effectively. We used detailed observations of marked breeding birds from a 'stronghold' population of whinchats *Saxicola rubetra* in England (stable against the declining European trend) to reveal both on-site and external mechanisms that contribute to population change. From field data, a population model was developed based on demographic rates from 2011 to 2014. Observed population trends were compared to the predicted population trends to assess model-accuracy and the influence of outside factors, such as immigration. The sensitivity of the projected population growth rate to relative change in each demographic rate was also explored. Against expectations of high productivity, we identified low seasonal breeding success due to nocturnal predation and low apparent first-year survival, which led to a projected population growth rate (λ) of 0.818, indicating a declining trend. However, this trend was not reflected in the census counts, suggesting that high immigration was probably responsible for buffering against this decline. Elasticity analysis indicated λ was most sensitive to changes in adult survival but with covariance between demographic rates accounted for, most temporal variation in λ was due to variation in productivity. Our study demonstrates that high quality breeding habitat can buffer against population decline but high immigration and low productivity will expose even such stronghold populations to potential decline or abandonment if either factor is unsustainable. First-year survival also appeared low, however this result is potentially confounded by high natal dispersal. First-year survival and/or dispersal remains a significant knowledge gap that potentially undermines local solutions aimed at counteracting low productivity.

Over the last 30 years, long-distance Afro-Palaearctic migrants have shown severe population declines in Europe (Sanderson et al. 2006, Vickery et al. 2014). Several reviews attempt to explain these declines, but largely highlight the need for further knowledge (Sanderson et al. 2006, Newton 2008, Vickery et al. 2014). Common life-history traits shared by these species include migration itself and wintering in sub-Saharan Africa, with the probability that either or both have contributed to lowering survival rates. However, the condition of European breeding habitats may also contribute to population decline due to poor productivity, or by exacerbating parental fitness consequences (Newton 2004a, Calvert et al. 2009). Evidence that existing habitats or interactions could alleviate decline is critical knowledge for targeting conservation and research effort.

Population change is determined by differences in demographic vital rates (reproduction, mortality) and immigration and emigration, as influenced by both localised and large scale factors affecting habitat condition, predation, weather or competition (Newton 1998). Careful studies will identify current, vulnerable life history phases (Caswell

2001, Sim et al. 2011, Hastings and Gross 2012, Gruebler et al. 2014) that limit the annual cycle (Green 1995, Newton 1998, Calvert et al. 2009). The analytical process demands accurate measures of both demographic and environmental parameters in order to locate candidate sources of change. One such approach is to study sub-populations that appear to buck the common trend, under the rationale that the source of the difference in trends represents a missing fundamental condition. This approach generates testable hypotheses for local (habitat, food, weather and predation) or external processes (survival and emigration). The test requires close observations of known individuals and habitat with accurately quantified demographic rates in seasonal productivity, survival and immigration (Sim et al. 2011).

The whinchat *Saxicola rubetra*, is a grassland, ground nesting, insectivorous, Afro-Palaearctic migrant which has undergone widespread long-term population declines across Europe (European Bird Census Council 2012). Agricultural intensification on the breeding grounds is probably responsible for the whinchat's historical, long-term decline (Gruebler et al. 2008, Fischer et al. 2013, Henderson et al. 2014). However,

large-scale declines across even stronghold populations of the UK suggest that in more recent times (last 20 yr), survival outside the breeding season (i.e. post-fledging, migration or over-winter survival) may not compensate for mean levels of breeding productivity (Henderson et al. 2014). Studies in Nigeria indicate that over winter survival may not be limiting (Hulme and Cresswell 2012, Blackburn and Cresswell 2016). In the present study we look for evidence of a demographic imbalance within a breeding population.

Against the declining trend a large and persistent lowland population of whinchats remains present on Salisbury Plain, in south-west England (Stanbury et al. 2005). Salisbury Plain covers 40 000 ha and has been retained for military training since 1897 (Ash et al. 2011). Consequently, the open grassland habitat on Salisbury Plain has effectively escaped intensive agricultural change common to most of lowland Britain. Breeding bird surveys carried out on the plain in 2000 and 2005 revealed a population of approximately 400–500 pairs of whinchats (Stanbury et al. 2005), representing approximately 1% of the population in Great Britain (47 000 pairs; Musgrove et al. 2013). The persistence of this population implies the species benefits there from favourable habitat or demographic qualities, which are likely to be important for conservation planning.

In this paper, we develop a population model to predict future population trends in the Salisbury Plain whinchats based on the demographic rates of breeding success, adult survival and first-year survival from 2011 to 2014. Observed population trends from 2011 to 2014 are compared to the predicted population trends for each year to assess the accuracy of the model and the influence of outside factors, such as immigration. The sensitivity of the projected population growth rate to relative change in each demographic rate is explored in a 'prospective analysis'. A 'retrospective analysis' was also conducted to determine how much past temporal variation in each demographic rate has contributed to temporal variation in the population growth rate (Caswell 2000). The study coincided closely with a national assessment of the range and population status in this species (among others), to provide large scale, up-to-date context to the study (Balmer et al. 2013). The study data are based on an intensive annual programme of individual marking, population survey and bird re-sighting work, providing data too on the non-breeding recruitment pool. Our principal rationale was that: 1) persistence in the face of a strong historical national decline implies a high quality breeding habitat with strong productivity, and 2) nevertheless, levels of connectedness, exposure or reliance of this nominally discrete population to the external pool would provide evidence of vulnerability or resistance to external change, in spite of breeding habitat quality (Schaub et al. 2006).

Material and methods

Study site

The main study area consisted of an area of 92.76 km² in the western part of Salisbury Plain (Latitude 51°11'52"N–51°16'4"N; Longitude 1°57'32"W–2°9'32"W, Supplementary material Appendix 1 Fig. A1). The majority

of the study area was classified as agriculturally unimproved grassland (Walker and Pywell 2000), mainly *Bromopsis erectus* grassland with *Festuca rubra* – *Festuca arundinacea* sub-community and *Arrhenatherum elatius* grassland with *Festuca rubra* sub-community (Rodwell 1992). There were also areas of scattered scrub and small blocks of plantation, but these covered less than 4% of the total study area. Low level grazing occurs on parts of the plain but, prior to 1995, the area was un-grazed for over 50 yr (Ash et al. 2011). All land management on the site is strictly controlled to limit any potential negative impacts on the ecosystem (Ash et al. 2011).

Colour-ringing

Marking was conducted at core sub-sites within the study area holding high whinchat breeding densities (Supplementary material Appendix 1 Fig. A2). In 2010 and 2011 preliminary fieldwork established a population of colour-ringed individuals, with more intensive studies conducted in 2012, 2013 and 2014. In total, 74 adult males, 66 adult females and 292 nestlings were ringed. All birds were aged upon capture following Jenni and Winkler (1994) and Svensson (1992).

Whinchat surveys

Surveys were conducted to be both comprehensive (core sites) and representative (random square selection). First, mapping surveys were conducted using standard common bird census techniques (Bibby 2000), ensuring the core study sites were covered in a comprehensive manner. In 2010 and 2011, the core sites were surveyed at least once a week, from late April to the end of July, in 2012, 2013 and 2014 the core sites were surveyed a minimum of every two days. The order of site visits was rotated to ensure an equal coverage at peak times. Secondly, during the peak breeding season, hilltops and valleys surrounding the core sites were also surveyed at least once yearly, along with 32 randomly selected 1 km by 1 km grid squares (in 2012 and 2013) and 267 random points (in 2014) using stratified, representative sampling (Border et al. 2017). These additional surveys located marked birds that had moved from the core sites. Surveys were completed between 06:00–11:00 and 16:30–20:30, when the birds were most active. For all observations, ring combination, time, sex, activity and location coordinates were recorded.

We are confident that surveys within the core study sites found all returning whinchats that had established territories there due to the intensive survey effort applied to these areas. However, we cannot be as confident that our surveys of the surrounding areas also found all returned whinchats. The grid square and random point surveys also covered some of the intensively surveyed core sites. From this we calculated a detection probability, grid surveys found 86% of whinchats known to be present and the random point surveys, 66%.

Breeding and natal dispersal distances

To help better understand the impact of dispersal on the probability of resighting a colour ringed bird, breeding

and natal dispersal distances were calculated for re-sighted individuals to give a measure of site-fidelity. However, it should be noted that the site fidelity recorded here is apparent site fidelity. We were not able to calculate dispersal distances for whinchats that either returned to an area far from the study region, or were not seen during our searches. Dispersal distances used nest locations (or in the case of birds re-sighted outside the main study sites, the location at which they were first observed) to calculate between-year changes in inter-nest distances. The effect of age, sex and previous breeding success on dispersal distance was modelled using a linear model (LM). Dispersal distance was positively skewed and therefore was log-transformed prior to modelling, to an approximately normal distribution.

Breeding success

Annually, first and subsequent nests were found for every observed pair within the six core study sites between 2012 and 2014, and for a high proportion of pairs during the 2010 and 2011 pilot seasons. Some additional nests were also found and monitored for pairs outside the core study areas (17 nests out of a total of 240). While it is possible that some nests were not found before they failed, the intensive daily survey effort and the high percentage of nests found during the laying or egg stages (87%) suggests that the majority of nests within the core study areas were found. Nests were checked every two days (mean: 2.85 ± 0.02 d), or not less than once a week in 2010 and 2011, until either the nest failed or at least one nestling fledged. A nest was considered to have failed due to predation if the contents had disappeared or the eggs were damaged, and was considered abandoned if the parents were not present in the territory on three consecutive visits and the eggs were cold but undamaged or the nestlings were dead. A nest was considered successful if nestlings were still alive at 12 d old. Daily survival rates (DSR) for nesting attempts were calculated using logistic exposure models (Shaffer 2004). Three model variations were trialled: first with a fixed effect of chick or egg phase, second with a fixed effect of year and third a null model. More complex models including a wider range of variables were considered inappropriate here because the aim was to calculate DSR for the whole population rather than to assess which variables influenced DSR. DSR was also calculated for only final attempts for each pair to quantify pair productivity as opposed to the probability of success of a single nesting attempt. Fledglings per pair (FPP) was calculated from the total number of fledglings recorded from the study nests each year divided by the total number of pairs. This method was considered suitable because nests were found for all pairs known to be in the core areas. A pair moving outside the study area to re-nest may have gone undetected but, in practice, large-scale intra-seasonal movements are rare (Grüebler et al. 2015).

Apparent survival

Apparent survival rates were estimated using Cormack-Jolly-Seber models (Lebreton et al. 1992) derived using MARK ver. 6.1 (McClintock and White 2012). Data from whinchats ringed either as adults or nestlings were analysed

to examine differences in adult and first-year survival, with data from ringed adults only used to assess the influence of sex on survival. Colour rings enabled nestlings to be identified by year and site of hatching but not as individuals. This affected only eight observations, so models were run both assuming returning birds of the same sex and colour combinations were the same individuals, and assuming they were not.

Global models were assessed for goodness of fit using the three methods available in MARK: median $c\text{-hat}$, bootstrapped re-samples and the program RELEASE. These tests allow estimation of the amount of over-dispersion present in the global model, via the variance inflation factor, $c\text{-hat}$, and thereby measure the lack of fit (Cooch and White 2014). The global model for the adult (>2 nd calendar year and older than first breeding year) and first-year data (2nd calendar year and first breeding season) assumed survival varied between years and in the first-year of life, but was constant within a year for adults. The recapture probability was assumed to be constant within a year for adults and first-years, as it was considered unlikely that first-years that returned to the study site would be harder to re-sight than adults, but was allowed to vary between years. The most conservative estimate of $c\text{-hat} = 1.34$ and the global model was adjusted to this value of $c\text{-hat}$ (Lebreton et al. 1992, Cooch and White 2014). The global model for just adult data assumed the survival and recapture probabilities both varied with sex and year. In this case, the recapture probability was allowed to differ for the separate sexes as females are less conspicuous than males. For this model, the most conservative estimate of $c\text{-hat} = 1.52$ and the global model was adjusted to this value. As $c\text{-hat}$ was adjusted for both global models, the candidate models were compared using the quasi-likelihood version of Akaike's Information Criterion adjusted for small sample sizes (QAICc), the model with the lowest QAICc was chosen as the final model. The analysis was also run with $c\text{-hat} = 1$ to ensure that changing $c\text{-hat}$ did not change the overall outcome; the apparent survival estimates, recapture estimate and top models ($\Delta\text{AICc} < 2$) were qualitatively similar; the only difference was that the standard errors when $c\text{-hat} = 1$ were slightly smaller.

MARK calculated survival rates were the same for all years. Forcing MARK to give different yearly survival estimates by including year in the model gave estimates with large overlapping confidence intervals for each year and the pattern of change over years from these estimates did not match the observed pattern of change from the percentage of returning colour-ringed whinchats. Therefore, the proportions of returning colour-ringed adults and first-years, out of the number known to be alive the previous year (return rate) were used for calculating the integrated elasticities. The return rates were adjusted by the recapture probability of 0.537 calculated from the MARK model, to account for detectability. The recapture probability did not vary significantly between years in this study and survey effort was high and constant in all years. Therefore, variation in return rates should still reflect temporal variation in adult survival. Despite this, the results of the integrated elasticity calculation which uses the adjusted return rates need to be interpreted cautiously as the four years of data from this study were not sufficient to accurately predict temporal

variation in survival. However, elasticities are robust to large changes in the matrix demographic parameters (Caswell 2000), and will give good predictions of future responses despite environmental stochasticity, unless the environment is extremely variable or catastrophic events are common (Benton and Grant 1999).

Additionally, the ratio of returning adults to first-year whinchats occupying territories in the study area was assessed each year to get a better understanding of dominance and territory availability. A high proportion of adults occupying territories would suggest that first-year birds face strong competition and may be forced to move elsewhere.

Observed and expected population growth rate

The realised population growth rate λ_r was calculated as in Eq. 1, where N_t = the population size at the beginning of the breeding season in year t (Cooch and White 2014).

$$\lambda_r = \frac{N_{t+1}}{N_t} \quad (1)$$

The observed population size was compared to the population size predicted from the survival and breeding success rates the previous year (Eq. 2).

$$N_{t+1} = N_t \times ((P_{juv} \times F) + P_{ad}) \quad (2)$$

where N_t = the population size in year t , P_{juv} = first-year survival from year t to year $t+1$, P_{ad} = adult survival from year t to year $t+1$ and F = breeding success measured as the number of fledglings per individual breeding whinchat per breeding season, calculated as $0.5 \times$ the number of fledglings per pair per season (adapted from a population model in Sim et al. 2011). This model does not include immigration into the population but permanent emigration from the population is accounted for in the MARK survival estimate (Lebreton et al. 1992). Any discrepancies between predicted and actual values for population growth rate will be due to stochastic variation in the demographic parameters and immigration into the population.

Projected population growth rate

Two stage classes were used due to the limited data available and the relatively short life span of whinchats (Supplementary material Appendix 1 Fig. A3). This life cycle translates to give the following matrix of demographic parameters (Hastings and Gross 2012).

$$A = \begin{bmatrix} 0 & F \\ P_{juv} & P_{ad} \end{bmatrix} \quad (3)$$

The projected population growth rate was calculated as the dominant eigenvalue of the projection matrix (Caswell 2001). The 95% confidence intervals for λ were calculated from 1000 bootstrap resamples of the projection matrix, assuming a normal distribution for each demographic parameter based on the means and variances from the observed data, and calculating λ for each of these matrices. The 95% confidence intervals were the 2.5 and 97.5% quantiles from the distribution of λ .

Basic and integrated elasticities

The elasticity calculates the proportional change in the population growth rate when one demographic rate is altered but the others are held constant (de Kroon et al. 1986, Caswell 2001). The integrated elasticities (IE) are an extension of basic elasticities; they quantify the total effect of a specific demographic rate on λ including direct and indirect effects, by accounting for covariance between demographic parameters (van Tienderen 1995). Integrated elasticities (IE) ensure the population consequences of variation in a demographic rate are predicted accurately (van Tienderen 1995, Saether and Bakke 2000, Sim et al. 2011), as co-variation between demographic parameters is very common (Caswell 2000).

Elasticities for the population matrix were calculated using the 'popbio tool' (Stubben and Milligan 2007) in R ver. 2.3.1 (R Core Team). The elasticity for an element of the matrix, a_{ij} , is given by:

$$\frac{\partial \log \lambda}{\partial \log a_{ij}} = \frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \quad (4)$$

where ∂ is the partial differential (de Kroon et al. 1986, Caswell 2001).

The integrated elasticities are calculated by the following equation:

$$IE_i = \sum_j r_{ij} \times e_j \times \frac{CV_j}{CV_i} \quad (5)$$

(van Tienderen 1995, Saether and Bakke 2000), where e = elasticity, CV = coefficient of variation for a demographic rate and r_{ij} is the correlation coefficient between the time series of two demographic parameters, matrix elements i and j .

The integrated elasticity calculations were calculated to identify correlations between demographic parameters and to determine how robust the conclusions based on the basic elasticities were likely to be (Sim et al. 2011). Pairwise correlations were calculated for F from 2010–2013 and adult and first-year return rates from 2011–2014, as it is possible that the number of fledglings produced could affect adult survival the following year (Sim et al. 2011). For correlations in survival rates, the correlation between adult return rates from 2011–2014 and first year return rates from 2011–2014 was used.

Just accounting for direct effects, the variation in the realised population growth rate is:

$$\text{Var}(\lambda) = \sum_x e_x^2 CV_x^2 \quad (6a)$$

Or, when accounting for direct and indirect effects:

$$\text{Var}(\lambda) = \sum_x IE_x^2 CV_x^2 \quad (6b)$$

So the proportional contribution of each matrix element to the total variation in the realised population growth rate is (Caswell 2001, Sim et al. 2011):

$$X_x = e_x^2 \frac{CV_x^2}{\text{Var}(\lambda)} \quad (7a)$$

or

$$X_x = IE_x^2 \frac{CV_x^2}{\text{Var}(\lambda)} \quad (7b)$$

Data deposition

Data available from the Dryad Digital Repository: <<http://dx.doi.org/10.5061/dryad.c41jc>> (Border et al. 2017).

Results

Breeding success

Out of the 240 monitored nests (including first and second attempts), 64.6% failed to fledge any young (Table 1). The majority of nest failures were attributable to predation (89.7%), desertion at the egg (6.45%), or nestling stages (2.58%), and 1.29% were run over by military vehicles. No partial brood predation was recorded and partial brood mortality was very rare, occurring in only 3% of nests. DSR per nesting attempt was 0.941 ± 0.005 ($n = 912$ observations from 231 nests, $AIC_c = 893$). However, if repeat nesting attempts are accounted for, with the final attempt taken for each pair (i.e. if a pair failed and had another attempt, data from the second attempt was used), the DSR per pair was 0.955 ± 0.005 ($n = 722$ observation intervals from 169 nests, $AIC = 612$). DSR was found not to differ significantly between years (Supplementary material Appendix 1 Table A1, $AIC = 898$) or between the chick and egg phases (egg phase survival relative to chick phase: $Est = -0.180 \pm 0.170$, $p = 0.29$, $AIC = 894$).

Apparent survival

The best survival model (Supplementary material Appendix 1 Table A2) showed that apparent survival was lower for returning first-year birds than for returning adults (Table 1). The qualitative model output remained unchanged whether first-years that could not be individually identified were assumed to be the same bird or different birds. Therefore, only the models that assumed the returning birds with the same sex and ring combinations were the same individuals are included here. The best model had a $\Delta QAIC_c > 4$ compared to the next best model, therefore model averaging was not used (Supplementary material Appendix 1 Table A2). The best model only contained an effect of age on the apparent survival parameter and a constant recapture probability (0.537 95% CI: 0.365–0.700). There was no significant difference in apparent survival estimates between the sexes; the beta parameter for sex included zero in its 95% confidence intervals, ($\beta = 0.629$, 95% CI: -0.357 – 1.62 , Supplementary material Appendix 1 Table A2). However, the mean apparent survival estimate was lower for females (0.359) than for males (0.512) and the 95% confidence interval for the beta parameter is biased towards positive values.

Observed occupancy and proportion of returning ringed birds

In 2012 and 2014, more adults than first-years occupied the territories in the core study sites: in 2012 76.9% of territories were occupied by adults and only 23.1% by first-years and in 2014 the ratio of adults to first-years occupying territories was 69.7%:30.3%. However, in 2013 this

Table 1. Breeding statistics, apparent survival rates and return rates for the Salisbury Plain whinchats from 2010–2014. Hatching success refers to the percentage of laid eggs that hatch excluding predation and abandonment. The total sample size for the year is included in brackets next to the relevant result. Mean clutch size and mean brood size include first and second attempts from all pairs that were monitored during the egg or nestling phases. Fledglings per pair is based on final nesting attempts for each pair. DSR is based on all nesting attempts. Apparent survival estimates ± 1 SE are calculated for adult (older than first breeding year) and first-year (in first breeding year) whinchats ($n = 396$). The percentages of returning colour-ringed birds for each year adjusted by the MARK calculated recapture rate of 0.537.

	2010	2011	2012	2013	2014
Mean clutch size	5.80 ± 0.20 (5)	5.75 ± 0.25 (4)	5.53 ± 0.13 (59)	5.56 ± 0.13 (68)	5.51 ± 0.14 (57)
Mean brood size	5.00 ± 0.52 (6)	5.33 ± 0.33 (9)	5.38 ± 0.18 (24)	4.94 ± 0.26 (18)	5.32 ± 0.75 (19)
Hatching success			95.3% (172)	89.4% (151)	92.8% (166)
Fledglings per pair (excluding predation)	5.00 ± 0.52 (6)	5.33 ± 0.33 (9)	5.38 ± 0.18 (24)	4.94 ± 0.26 (18)	5.32 ± 0.17 (19)
Fledglings per pair (including predation)	2.73 ± 0.83 (11)	3.20 ± 0.73 (15)	2.63 (49)	1.89 (47)	2.02 (50)
Daily survival rate (DSR) per nesting attempt	0.956 ± 0.022 (11)	0.954 ± 0.014 (20)	0.945 ± 0.009 (64)	0.939 ± 0.009 (63)	0.933 ± 0.009 (73)
Adult apparent survival	NA	0.52 ± 0.06	0.52 ± 0.06	0.52 ± 0.06	0.52 ± 0.06
First-year apparent survival	NA	0.20 ± 0.04	0.20 ± 0.04	0.20 ± 0.04	0.20 ± 0.04
Proportion returning colour-ringed adults	NA	0.57 (23)	0.65 (34)	0.48 (58)	0.46 (90)
Proportion returning colour-ringed first-years	NA	0.17 (35)	0.15 (39)	0.20 (129)	0.13 (89)

pattern was reversed with 70.2% of territories being occupied by first-year breeders and 29.8% of territories being occupied by adults. This is reflected in the higher first-year return rate and lower adult return rate in 2013 compared to other years (Table 1), suggesting a degree of adult-driven exclusion contributing to observed first-year return rates. However, in 2014 both adult and first-year return rates were low (Table 1).

Dispersal

Breeding dispersal was significantly lower than natal dispersal (LM: Est = -2.05 ± 0.47 , $p < 0.001$, $n = 57$) with median natal dispersal distances of 1.21 km (IQR: 2.03 km) compared to median breeding dispersal distances of 0.21 km (IQR: 0.46 km). There was no significant difference in dispersal distances of adult males versus adult females (LM: Est = -0.583 ± 0.558 , $p = 0.304$, $n = 37$) but there was a significant difference in relation to breeding success the previous year, with successful birds showing lower dispersal distances (LM: Est = -1.24 ± 0.558 , $p = 0.033$, $n = 37$). This difference was not dependent on sex (LM: Est = 1.07 ± 0.950 , $p = 0.267$, $n = 37$).

Observed and predicted population trends

From 2011 to 2014, the observed trend in population size remained relatively stable while the predicted trend, based on survival and productivity values, suggested a decline of approximately 35% (Fig. 1a). Data from whinchat surveys in 2005 (Stanbury et al. 2005) covering the same sites suggests that the Salisbury Plain population has increased since 2005 to a high in 2010 before levelling off more recently (Fig. 1b). During the same time period, the UK whinchat population declined by 43.6% between 2005 and 2011 but increased non-significantly since then, by 12.2% (Fig. 1b).

Prospective and retrospective analysis

The projection matrix based on mean demographic parameters for 2011–2014 gave a dominant eigenvalue of $\lambda = 0.818$ (95% CI: 0.663 – 0.971), meaning that under time invariance the population is projected to decline by 18.2% per year on average. The projected population growth rate (λ) was almost twice as sensitive to change in adult survival than to changes in first-year survival and breeding success (Table 2). To deliver a self-sustaining population ($\lambda = 1$), breeding success or first-year apparent survival would have to double, to 2.40 or 0.44 respectively, or adult survival would need to be approximately 1.5 times higher, at 0.79. Breeding success was positively correlated to adult and first-year return rates the following year, and adult return rates were negatively correlated to first year return rates from the same year (Table 2). Using return rates for adults and first-years, as opposed to apparent survival estimates, did not change the qualitative pattern of the elasticities which gives us confidence that the adjusted return rates are a good proxy for yearly apparent survival estimates. When accounting for indirect effects (via IE), the projected population growth rate was still most sensitive to changes in adult return rates.

However, it was more sensitive to changes in breeding success than changes in first-year return rates.

When examining only direct effects through elasticities, most of the temporal variation in the projected population growth rate was explained by temporal variation in the adult return rates, closely followed by breeding success (Table 2). These variables together explained 84% of temporal variation, with the remainder explained by variation in first-year return rates. However, when incorporating indirect effects due to correlations between the demographic parameters, the majority of variance in the projected population growth rate was explained by variance in breeding success, with less than 7% explained by variance in first-year return rates.

Discussion

Low breeding success and low apparent first-year survival appear to be the main factors limiting whinchat population expansion on Salisbury Plain. At current levels of breeding success, adult apparent survival and first-year apparent survival, and assuming no change in these values in future years, the Salisbury Plain whinchat population is predicted to decline. However, the observed population remains stable due to new recruitment and natal dispersal was high compared to adult dispersal possibly confounding first-year survival estimates. Here, we identify important interactions between major demographic parameters (Sim et al. 2011) and breeding habitat quality in a migrant bird. We reveal how the local breeding population may also be vulnerable to processes operating beyond the immediate influence of the breeding conditions (Schaub et al. 2006).

One of our predictions was that the breeding habitat quality or extent of Salisbury Plain would buffer the overall change relative to the national population, but the mechanism by which this has operated was not expected. We expected high productivity to dominate, due to the anticipated quality of the breeding habitat, but unexpectedly high nestling predation rates, relatively low apparent first-year survival rates and consequent suggestion of high immigration were the outstanding demographic characteristics of the site.

Prospective analyses predicted that at current levels of low breeding success and reasonable adult apparent survival, but relatively low first-year apparent survival, the Salisbury Plain whinchat population should have declined by approximately 18.2% per annum. In fact, the study population on Salisbury Plain has remained relatively stable since 2005. The difference between the modelled and the observed data suggests high immigration either from elsewhere on Salisbury Plain (an estimated 400–500 pairs) or, more likely, from the wider UK population (and estimated 47 000 pairs: Musgrove et al. 2013). However, it is also possible that the discrepancy arises partly because of high natal dispersal leading to an underestimate of first-year survival, which we discuss below. Significant immigration from elsewhere on the plain is only likely if mean productivity levels there are higher than for our study sub-population. We have no data on this but assume the study sites are representative and that the same processes apply

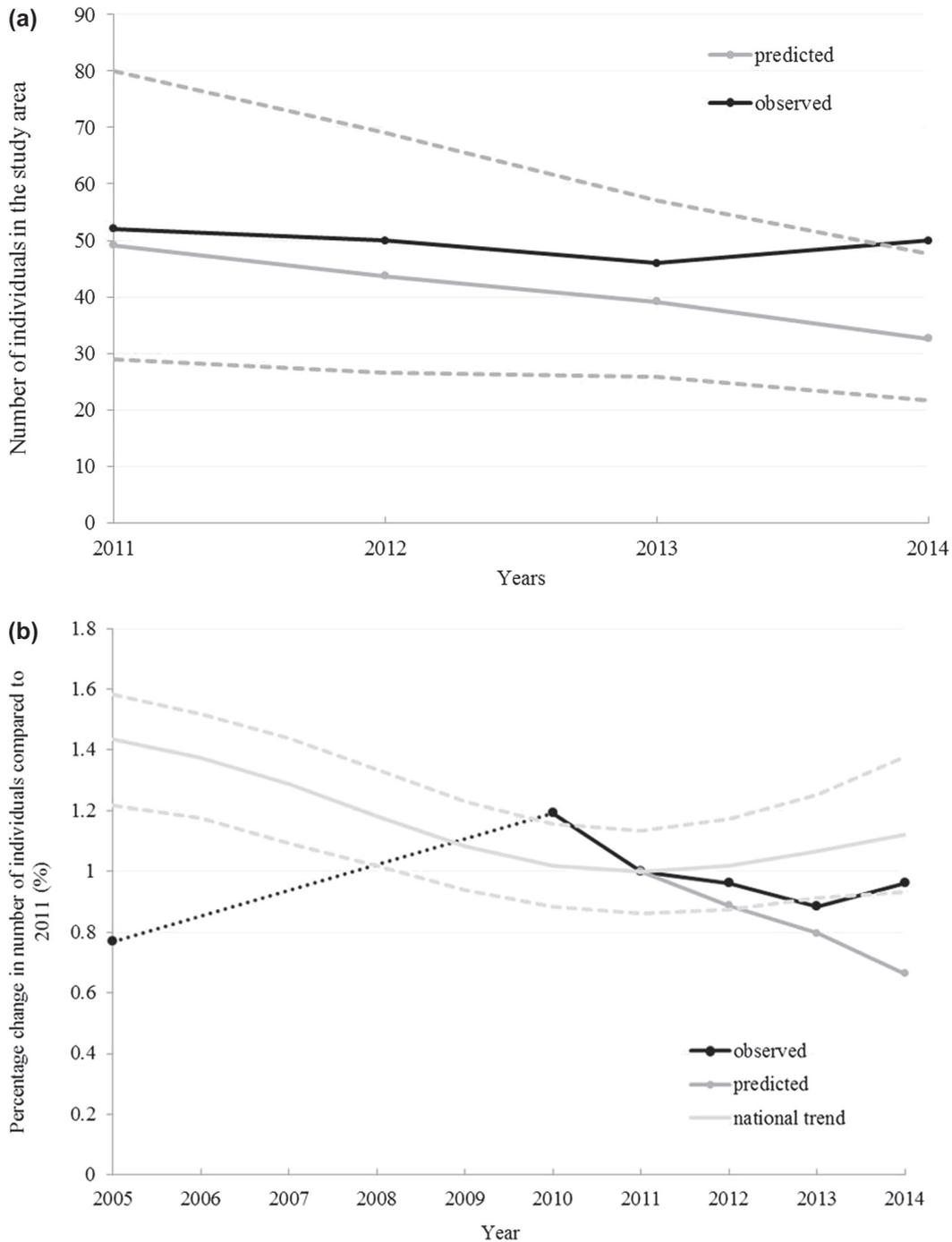


Figure 1. The observed population trend from 2011–2014 and the predicted trend (based on the previous years' population size and observed demographic rates). (a) The actual number of whinchats observed or predicted (dotted lines are the confidence intervals for the prediction, using the lower 95% confidence interval for each demographic rate for the lower line and the upper 95% confidence interval for each demographic rate for the upper line). (b) The percentage change in trends since 2005 compared to the national trend (dotted lines are the 95% confidence intervals) (Baillie et al. 2014). No surveys were undertaken after 2005 until 2012 and therefore the population in these intervening years is not known (hence the dotted representation). The observed population size uses only the core sites which were surveyed in all 5 years to allow for a more accurate comparison between years.

throughout. Therefore, it seems more likely that most immigration will emanate, ultimately, from the wider UK population.

Salisbury Plain is likely to be an attractive location to whinchats purely due to its size and location; it is the largest area of agriculturally unimproved grassland in northwest Europe (Ash et al. 2011) and is situated relatively close to

the English south coast, en route to the larger breeding populations in the north and west. Additionally, our other work has suggested a non-limiting supply of suitable breeding habitat and high quality feeding habitat where in the absence of predation, brood reduction was low and reproductive output was high (Table 1; Taylor 2015). Higher first-year territory occupancy occurred in years when adult

Table 2. The mean values (± 1 SE) and elasticity (e) using apparent survival rates. Additionally (using return rates adjusted by the MARK recapture rate) the correlation matrix, mean values, standard deviation (SD), coefficient of variance (CV) and integrated elasticities (IE) for each demographic parameter and the temporal variation in the population growth rate (λ) explained by each parameter including direct effects only (e^2CV^2) as a proportion of the total temporal variation in growth rate (X_e) and direct and indirect effects (IE^2CV^2 and as a proportion = X_{IE}). F = breeding success (number of fledglings per individual), P_{ad} = adult apparent survival, P_{juv} = first-year apparent survival, A_r = proportion of returning colour ringed adults adjusted by the recapture rate, J_r = proportion of returning colour ringed first-years adjusted by the recapture rate.

	Mean	E	Correlation matrix			Mean	SD	CV	e	e^2CV^2	X_e	IE	IE^2CV^2	X_{IE}	
			F	A_r	J_r										
F	1.22 ± 0.15	0.257	F	1	0.88	0.33	1.22	0.30	0.25	0.241	0.0035	0.29	0.594	0.022	0.53
P_{ad}	0.52 ± 0.04	0.487	A_r	0.88	1	-0.14	0.54	0.09	0.16	0.519	0.0068	0.55	0.809	0.016	0.40
P_{juv}	0.20 ± 0.04	0.257	J_r	0.33	-0.14	1	0.16	0.03	0.19	0.241	0.0021	0.17	0.282	0.003	0.07

return rates were low, supporting the existence of a large pool of potential first-year recruits (from elsewhere on the plain or beyond) ready to occupy vacant territories, but also demonstrating significant reliance on high recruitment in this breeding population, given that productivity values were low.

Overall, fledglings per pair on Salisbury Plain (Table 1) was low compared to studies in late-cut meadows (3.3 ± 0.3 , SE) in Germany (Fischer et al. 2013) and abandoned fields in Poland (4.17 ± 0.24 ; Frankiewicz 2008) or Russia (3.77 ± 3.07 ; Shitikov et al. 2015). Nest survival per pair on Salisbury Plain was 26.3% (CI: 18.5–34.1%, via the delta method: Powell 2007) compared to a mean nest survival of 35% in Russia (mean calculated from 9 yearly estimates; CI: 23.1–46.5; Shitikov et al. 2015), or nest survival rates of 41 and 55.7% in late mown meadows in Slovenia (CI: 27.4–55.7%) and Switzerland respectively (D. Tome and D. Denac pers. comm., M. Gruebler pers. comm.). From our analysis with covariates, seasonal breeding success was the second most influential parameter on population growth rates for whinchats on Salisbury Plain and therefore a possible target for conservation action. The largest cause of nest-loss was nocturnal predation (Taylor 2015). Foxes *Vulpes vulpes* and badgers *Meles meles* are common on Salisbury Plain though populations are not monitored. In Europe generally, numbers of foxes and badgers have increased (Newton 2004b, Langgemach and Bellebaum 2005), but the predation problem is difficult to address (Roodbergen et al. 2012, Malpas et al. 2013) without better knowledge of their ecology and inter-relationships with weather, alternative prey availability and habitat quality.

Survival estimates: adults

Prospective analysis suggested that improving adult survival would have the most benefit on the population growth rate, although considering the currently high adult survival compared to similar species, this may not be possible. Mean annual apparent survival of adult whinchats on Salisbury Plain (0.52) was similar to historical estimates for Europe (Sæther 1989; 0.48), but higher than for Russia (0.27) where breeding sites were dispersed and site-fidelity low (Shitikov et al. 2015). In alpine meadows in Switzerland, male survival (0.48) was similar to Salisbury Plain, but female survival (0.21) was low due to mowing-related mortality during incubation (Müller et al. 2005). With comparable estimates from the non-breeding grounds (0.52–0.54:

Blackburn and Cresswell 2015), adult whinchats on Salisbury Plain occupy the upper end of survival estimates for open-nesting, Palearctic migrants (0.25–0.53; Boddy 1994, Siriwardena et al. 1998, Low et al. 2010, Sim et al. 2011), especially for adult male survival. Female apparent survival tends to be lower than in males in most studies above (Müller et al. 2005, Low et al. 2010, Sim et al. 2011) due to incubation mortality, higher physiological demands for parental care (Gustafsson and Pärt 1990), or lower site fidelity (Shitikov et al. 2015). We could not detect a difference in male and female site fidelity in our analysis here but we were restricted to a small sample size (37), and would not have included birds that returned outside our study area. Certainly, the effect of female-biased mortality on population change deserves closer inspection in whinchats as well as in other migrant species.

Survival estimates: first-years

Apparent survival of fledglings (Salisbury Plain = 0.20) into their first breeding year was low relative to mean estimates for other open-nesting migrant species (0.24–0.48; Boddy 1994 and Siriwardena et al. 1998), except for ring ouzels *Turdus torquatus*, where the apparent survival rate was exceptionally low (0.05; Sim et al. 2011). Our analyses suggest that the projected population growth rate is least sensitive to variations in this demographic rate (Caswell 2000, 2001), though recruitment is important and may rely on variations in survival.

In birds, low apparent survival may in part be due to permanent juvenile dispersal from the study area (Sedgwick 2004). On Salisbury Plain, considerable effort was devoted to measuring and calculating dispersal in returning birds, far beyond the maximum recorded dispersal distance of our first-year whinchats from their natal site (5.8 km, mean = 1.5 km). However, median natal dispersal distances were six times higher than median breeding dispersal distances and despite an extensive area being searched some individuals outside the core sites could have been missed. Only two first-years out of the total of 30 that returned were found outside the core areas, which could suggest that first-years are not dispersing into the immediate area surrounding the core study sites but it could also reflect the lower survey effort in these outside areas. The apparent survival rates adjust for recapture probability but cannot account for permanent emigration from the study site. Therefore, it is likely that at least part of the low first-year survival is probably due to a high

proportion of first-years permanently emigrating from the study site. Additionally, the published estimates on first-year survival (Boddy 1994, Siriwardena et al. 1998) are calculated using birds ringed as mist-netted flying fledglings whereas we used nestlings just before they left the nest. Therefore, our estimates may be lower due to the inclusion of both post fledging losses and losses on migration and overwinter.

'First-year apparent survival' covers several different life-history phases (Newton 2008): post-fledging (Tome and Denac 2012, Gruebler et al. 2014), migration, wintering (Tarof et al. 2011). Separating their individual effects is difficult and will depend on the level of site fidelity and connectivity between wintering and breeding populations (Newton 2008, Calvert et al. 2009, Sim et al. 2011, Cresswell 2015). In Africa, at one location, whinchats have adapted well to anthropogenic habitats, with adult and first-year survival not differing significantly (Blackburn and Cresswell 2015). This study suggests first-year mortality must occur mainly during the post-fledging stage or on migration north, yet for any metric the key issue yet to be addressed is change accounting for regional differences in land-use patterns on a representative (for the species in question) geographic scale in Africa or Europe (Adams et al. 2014).

Conclusions

Understanding the mechanisms behind population change, or stability, helps explain potential limiting factors within the lifecycles of organisms (Green 1995, Saether and Bakke 2000). For migrant bird species these details have conservation implications for promoting management (Rushing et al. 2016). On Salisbury Plain, a self-sustaining population of whinchats without high recruitment would require a 50% increase in seasonal productivity per pair and first year survival, or a doubling of one of these parameters. Even allowing for an underestimate of true first-year survival due to natal dispersal, the high brood productivity in the absence of predation and availability of suitable habitat and food (Taylor 2015) suggests that Salisbury Plain is an area of high quality habitat in most respects but with a stable population that is currently maintained by immigration/recruitment. The area can be considered high quality in terms of habitat availability and food supply, but of relatively low quality in terms of predation pressure. There is increasing awareness of similar incidences where apparently high quality habitats are associated with low productivity in modern landscapes (Purcell and Verner 1998, Misenhelter and Rotenberry 2000, Hollander et al. 2015, Lameris et al. 2016). This study demonstrates the potential of high quality breeding habitat to dampen the rate of population decline and seemingly provide a remedy to that decline. However, this remedy is likely to be unsustainable if the decline in the wider UK or source population continues to reduce the pool of potential recruits, with abandonment of many previously well populated areas (Henderson et al. 2014). No single study can provide absolute generality and we would welcome similar demographic analyses from other breeding populations in other landscape contexts, but our results suggest that focussing conservation action on improving productivity is an important immediate strategy for Europe. Meanwhile, greater

research emphasis is needed, in migrant birds generally, on the physical (such as land-use) as well as demographic barriers to immigration and recruitment; separating the confounding effects of natal dispersal from first-year survival and importantly, understanding the relationship between spatial or temporal change in demographic rates versus population trajectory in breeding and non-breeding populations.

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Supplementary material (Appendix JAV-01305 at <www.avianbiology.org/appendix/jav-01305>). Appendix 1.