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Survival of Afro-Palaearctic passerine migrants in western Europe and the impacts of seasonal weather variables

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Populations of migratory songbirds in western Europe show considerable variation in population trends between species and regions. The demographic and environmental causes of these large-scale patterns are poorly understood. Using data from Constant Effort mist-netting studies, we investigated relationships between changes in abundance, adult survival and seasonal weather conditions among 35 western European populations of eight species of migratory warblers (Sylviidae). We used cross-species and within-species comparisons to assess whether annual variation in survival was correlated with weather conditions during passage or winter. We estimated survival using CJS mark-recapture models accounting for variation in the proportion of transient individuals and recapture rates. Species wintering in the humid bioclimatic zone of western Africa had significantly higher annual survival probabilities than species wintering in the arid bioclimatic zone of Africa (the Sahel). Rainfall in the Sahel was positively correlated with survival in at least some populations of five species. We found substantially fewer significant relationships with indices of weather during the autumn and spring passage periods, which may be due to the use of broad-scale indices. Annual population changes were correlated with adult survival in all of our study species, although species undergoing widespread declines showed the weakest relationships.

Keywords: capture mark-recapture, climate change, Constant Effort Sites, demography, Sahel rainfall, Sylviidae.

In recent years, there have been dramatic declines in many populations of Afro-Palaearctic migrant birds (Sanderson *et al.* 2006, Heldbjerg & Fox 2008, Hewson & Noble 2009), but many of these species exhibit regional heterogeneity in population trends (Saether *et al.* 1999, Morrison *et al.* 2010, Møller *et al.* 2010, Ockendon *et al.* 2012). Historically, population fluctuations of Afro-Palaearctic migrant species have often been linked to factors operating in the non-breeding areas (Peach *et al.* 1991, Baillie & Peach 1992, Ockendon *et al.* 2014), but there is also growing evidence to suggest that some declines may be linked to factors that are specific to breeding areas (Green & Taylor 1995, Holt *et al.* 2011) or to interactions between breeding and non-breeding areas, such as carry-over effects (Both *et al.* 2005, 2010, Ockendon *et al.* 2012, Ockendon *et al.* 2013, Morrison *et al.* 2013). The complex life cycle of migrants can make it particularly difficult to determine the causes of population declines (Robbins *et al.* 1989, Sillett & Holmes 2002, Holmes 2007, Vickery *et al.* 2014). Quantifying demographic rates for different breeding populations of a particular species may reveal some of

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the causes of population change (Bjørdstad *et al.* 1999, DeSante *et al.* 2001) and hence provide indications of any environmental causes of variation in population trends, both within and between species.

Survival is one of the demographic determinants of population dynamics and understanding environmental causes of variation in survival may suggest processes that are leading to population declines. There is good evidence from single-species studies that weather affects the survival of many migrant species (Sillett *et al.* 2000, Mazerolle *et al.* 2005, Schaub *et al.* 2005, Altwegg & Anderson 2009, Zwarts *et al.* 2009a, Mihoub *et al.* 2010, LaManna *et al.* 2012). Weather may affect survival directly, for instance through increased metabolic requirements in cold weather (e.g. Clark 2004, Pendlebury *et al.* 2004) or strong winds during migration (e.g. Newton 2006, Drake *et al.* 2014); or it may impact survival indirectly, for example by determining food availability (e.g. Peach *et al.* 1991, Szep 1995). In many environments, rainfall has been positively correlated with winter survival or annual survival (Peach *et al.* 1991, LaManna *et al.* 2012, Norman & Peach 2013, García-Pérez *et al.* 2014). Rainfall is thought to affect survival through impacts on food availability (Brown & Sherry 2006) and may be particularly important in arid environments (Blendinger & Ojeda 2001, Herrmann *et al.* 2005, Studds & Marra 2007, Mullié 2009, Smith *et al.* 2010, Tøttrup *et al.* 2012). A reduction in food availability or food quality may affect survival by reducing the body condition of migrants (Sherry *et al.* 2005, Brown & Sherry 2006), which can reduce the numbers surviving winter (Johnson & Sherry 2001, Latta & Faaborg 2001). Reduced food availability in wintering or stopover sites may also impact the fattening rate of migrants (Gordo 2007) and hence may impact migration phenology (Strong & Sherry 2000, Bayly 2006, Gordo & Sanz 2008, Alerstam 2011, Ockendon *et al.* 2012). Mortality during migration appears to be very high for some species (Sillett & Holmes 2002, Klaassen *et al.* 2014, Blackburn & Cresswell 2016), potentially limiting populations. Therefore, correlations between winter weather and annual survival may describe the effects of weather on overwintering survival or migration survival.

There is considerable evidence that rainfall in the Sahel, a semi-arid region to the south of the Sahara, is positively correlated with the annual survival probabilities of Afro-Palaearctic migrants. The Sahel region is a critical area for migrants that spend the winter there (Peach *et al.* 1991, Szep 1995, Newton 2004, Cowley & Siriwardena 2005) but it is also a very important staging and fattening area for migrants wintering further south, as it is the first place to refuel after the Sahara on the southward migration and the last place to refuel before crossing the Sahara on the northward migration (Jones 1995, Zwarts *et al.* 2009b, Åkesson *et al.* 2012). Low rainfall and consequent depressed food availability may reduce survival of migrants wintering or passing through this zone (Stoate & Moreby 1995, Newton 2006, Schaub *et al.* 2011, Ockendon *et al.* 2014). This may be particularly relevant during the northward spring migration, when conditions have deteriorated and migrants need to fuel before crossing the Sahara (Saino *et al.* 2007, Zwarts *et al.* 2009a, Robson & Barriocanal 2011). We predict that survival is more strongly related to Sahel precipitation for species that spend the entire winter in that region, compared with species that use it as a stopover site on migration. We also predict that species populations with similar wintering locations will show similar survival patterns, due to shared wintering environmental conditions and migration routes.

Variation in survival may drive long-term population declines or increases (Peach *et al.* 1995) but does not necessarily lead to long-term population change. Annual fluctuations in survival may be compensated for in the subsequent breeding season by density-dependent reproduction or juvenile survival, such that the population size in the following year is not adversely affected by survival. Compensatory mechanisms such as these, which buffer against long-term population change, may mean that annual survival is correlated with short-term population fluctuations, but not longer-term population change.

Here, we estimate the annual adult survival of eight species of migrant warblers in five breeding locations. The spatial range of breeding locations and suite of eight species enable us to test a variety of mechanisms for the impact of weather on survival. We construct models of annual survival probabilities for birds from five breeding regions, which cover much of Western Europe, encompassing substantial variation in a wide range of climate and land management practices. We assess patterns in annual survival across species, wintering regions and breeding regions, and also test for correlations between annual survival rates and weather in particular seasons of the migrants' annual life cycle. In addition, we examine the extent to which variation in survival is associated with annual population changes in Afro-Palaearctic migrant birds by assessing correlations between survival and annual population change.

METHODS

Field methods

Data were collated from four European Constant Effort Site (CES) schemes, which gather data on the relative abundance, productivity and survival of passerine birds using standardized mist-netting conducted during the breeding season (Peach *et al.* 1990, 1996, DeSante *et al.* 1995). Observers aim to visit each site a set number of times within the local breeding season: in the UK, 12 visits are made approximately every 10 days from early May to late August, in the Netherlands 12 visits are made between mid-April and mid-August, in Catalonia (northeast Spain) 10 visits are made approximately every 10 days from mid-May to mid-August, and in France 3–5 visits are made from early May to July. In practice, 4–5% of visits are missed due to poor weather or other factors (Miles *et al.* 2007). Within each site, the same configuration of mist-nets is erected on any given visit and these are surveyed for approximately the same length of time; and the effort expended is therefore approximately constant within sites across time. Birds caught in the nets are ringed with a uniquely numbered metal ring, which enables identification of the individual if it is recaptured during subsequent visits or in subsequent years. The small differences in sampling methodology between schemes are likely to lead to different average recapture probabilities. Each scheme also had different metadata, for example some schemes did not report habitat types and the interpretation of habitat type may also vary with region. For these reasons, we created separate models for each species within each region.

We used data from the UK (1983–2008; 429 sites), France (1989–2008; 199 sites), Catalonia (1991–2008; 58 sites) and the Netherlands (1994–2008; 65 sites). Very few juveniles were recaptured at the same site, which is likely to be due to low juvenile survival and high natal dispersal of those which survive (Paradis *et al.* 1998). These two processes are confounded when using mark-recapture data and accurate estimation of juvenile survival is therefore affected by high emigration rates. The proportion of juveniles recaptured is low, which leads to unreliable estimates of survival. In the UK, Across the eight species, only 0.9–4.5% of juveniles were recaptured in subsequent years and these percentages are only 12–31% of the proportion of adults recaptured in subsequent years, across the eight species. For this reason, we only estimate adult survival probabilities (hereafter termed 'survival') and we therefore only used data from birds first captured when they were adults, or birds ringed as juveniles and re-captured as adults.

Data sources

Mark-recapture data were collated for each individually ringed bird of the eight focal species, which were chosen as they are closely related and well-monitored by the CES schemes. The species were: Blackcap *Sylvia atricapilla*, Garden Warbler *Sylvia borin*, Whitethroat *Sylvia communis*, Lesser Whitethroat *Sylvia curruca*, Sedge Warbler *Acrocephalus schoenobaenus*, Reed Warbler *Acrocephalus scirpaceus*, Chiffchaff *Phylloscopus collybita* and Willow Warbler *Phylloscopus trochilus* (see Supporting Information Table S1 for sample sizes). Given the slight methodological differences between the data collection in different countries, separate analyses were conducted for each of five regions: Netherlands, France, Catalonia, UK North and UK South (split due to large sample size, and a known north–south gradient in population trends; Morrison *et al.* 2013). These breeding populations were chosen to represent a single western European flyway, so are from a relatively restricted range of longitudes. We conducted mark-recapture analyses on 35 datasets; of the 40 possible region-by-species combinations, five had insufficient data for analysis.

We aimed to assess the extent to which weather drives variability in survival during different seasons in the annual cycle, so we used weather variables relevant to the following seasons: winter, autumn migration and spring migration. Previous studies have found that rainfall in the Sahel region during the rainy season (May–September) is correlated with the annual survival of migratory birds. This area covers a wide region of West Africa, comprising a large portion of the arid and semi-arid region south of the Sahara, and rainfall in the summer season determines the overwinter food resources available (Zwarts *et al.* 2009b, Tøttrup *et al.* 2012). Monthly rainfall in the Sahel region (10–20°N, 20°W–10°E; Janowiak 1988) was used to calculate annual rainy season (May–September) rainfall anomalies from the 1950–79 average. The rainfall data were standardized for use in the survival models.

Given limited information about the timing and migratory routes of these species, we used broad-scale climatic indices to describe weather conditions during the migration period. Data on the strength of the North Atlantic Oscillation (NAO; Jones *et al.* 1997, Osborn 2006) were used to capture continental-scale weather patterns during the two migration periods. NAO represents the broad weather pattern over Europe and Africa north of the Sahara and influences many biological processes at this scale (Coulson *et al.* 2001, Post & Forchhammer 2002, Stenseth *et al.* 2002). Lower values of NAO are associated with an easterly airflow, leading to cooler, drier conditions in the early spring (which may affect vegetation growth) and some evidence of reduced storm activity in the autumn. Spring and autumn migration periods were defined separately for each species (Table S1) using Wernham *et al.* (2002) and expert opinion. Mean NAO values were calculated for each migration period and year. The NAO variables all had means close to zero and standard deviations close to one, so the scales were comparable to the standardized rainfall variables. All European breeding populations of a given species had the same weather variables, as we have little evidence that different breeding populations occupy different areas in the non-breeding season (Wernham *et al.* 2002).

Species were classified as wintering in the 'arid bioclimatic zone', the 'humid bioclimatic zone' or 'north of the Sahara' following Ockendon *et al.* (2012). The arid zone includes the Sahel and Sudan savannahs of the northern tropics, which are those areas with less than 1000 mm annual precipitation. The humid zone includes the relatively moist Guinea savannah and forest regions of the northern and equatorial tropics of western Africa, and these areas largely have greater than 1000 mm annual precipitation (Ockendon *et al.* 2012).

Mark-recapture models

The recapture data from CES sites were combined into capture histories, with a '1' if the bird was captured on any of the visits within a year and a '0' otherwise. If an individual was captured at more than one site (which occurred with fewer than 1% of the individuals), a capture history was created for each site on which it was captured, as some of the parameters were site-dependent. Goodness-of-fit (GOF) tests run in RELEASE through program MARK (White & Burnham 1999) were used to assess the capture histories for violations of standard Cormack–Jolly–Seber (CJS) capture-recapture assumptions (Lebreton *et al.* 1992). Of the 35 models, 26 had sufficient data to run the GOF tests (which were more general than the models used for survival estimation, as they used a fully time-dependent recapture structure). GOF tests identified transience as the only significant and consistent violation of the standard CJS mark-recapture assumptions. Pradel *et al.*'s (1997) method was used to estimate and account for the presence of transients in the populations. If an individual was captured more than once during the first capture season, it was assumed to be a resident in the main catchment area. If a bird was seen only once, it may have been a resident (which happened to be caught only once) or a transient individual (available to be caught only once). A '1' (known resident) or '0' (transient/resident) was inserted into the capture histories after the first capture occasion, and the estimated 'survival' to this time period was the estimated probability of a bird being a resident. The estimated 'recapture' at this time period was the probability that a resident bird was identified as such (by being caught more than once in the first year of capture). Covariates of the residency/transience parameter can be fitted as covariates of 'survival' in the first time period, in the normal mark-recapture framework. This method of accounting for transient individuals assumes that individuals caught in subsequent years at the same site are residents at that site.

As some sites are expected to attract re-fuelling migrants, and some be more suitable for breeding birds, transience was *a priori* considered to be site-specific. Some of this variation may be due to habitat, although other factors such as geographical location may also affect transience probabilities. Initial modelling suggested the estimation of site-specific transience parameters could be supported by the data from the UK and Netherlands, but not by the data from France and Catalonia. Transience in Catalonia was therefore modelled as habitat-specific, and in France as constant (as habitat data were not available). However, all models were also checked for parameter identifiability, and if there were 10 or more non-identifiable site parameters or one non-identifiable habitat parameter, the transience model was reduced in complexity. Non-identifiable site parameters were due in all cases to very low numbers of ringed birds at a site and therefore a small number of sites with non-identifiable parameters would not exert much influence on the estimates of survival and recapture. Most transience models were habitat-specific in the final models (Supporting Information Table S2). The associated transience 'recapture rate', which was the probability of capturing an individual more than once within the first season, was modelled as constant, reflecting the common capture methodology across sites, within regions.

As the model structure accounted for transience, but did this using more complex model specification than that in the GOF tests, it was not possible to re-run the RELEASE GOF tests on these models. However, as transience was considered to be the main violation of the assumptions we assessed the degree of extra-binomial variation without the presence of transients by reducing the data sets to include only individuals which were confirmed 'residents', i.e. those caught more than once at a site in their first year of capture. These reduced datasets were run with a basic CJS model with survival as a function of year (as a factor) and recapture as a function of year (as a trend), which were the most generic models used in the main modelling procedure. Bootstrap GOF tests were run to calculate $\hat{c}$, or the degree of extra-binomial variation in the data, when transients were not present. The mean $\hat{c}$ value was 1.33 and all values were less than 2, except for Lesser Whitethroats in the Netherlands ($\hat{c} = 2.13$). They were all therefore deemed to have reasonable amounts of extra-binomial variation to accommodate with an overdispersion parameter (Lebreton *et al.* 1992). These values of $\hat{c}$ were subsequently included in the main modelling procedure by calculating the Quasi Akaike Information Criterion (QAICc) which accounts for overdispersion in the calculation of AIC (Burnham and Anderson 2002). Some of the datasets did not have sufficient identifiable variables in the time-specific CJS models and $\hat{c}$ was therefore not calculated for these datasets. The main models were simpler than these standard CJS models (as recapture was not fully time-dependent), and where datasets were identifiable in the simpler model, but did not have $\hat{c}$ values, they were given $\hat{c} = 1.3$, which was the mean across all other datasets, given the similar data structure across the datasets.

Recapture rates were modelled with the following potential explanatory variables: site (as a factor), habitat where available (as a factor with up to six levels in each country: reedbed, wet scrub, dry scrub, woodland, farmland and gardens) and site age (number of years since the site was first used as a CES site). Site age was included to allow for possible effects of succession or other habitat changes; for example, increased vegetation heights are expected to reduce capture probabilities as birds are more likely to fly over the nets. Non-redundant linear combinations of the three variables were also modelled (i.e. site age + habitat; site age + site; with no interactions). Due to the constant effort between years at each site, recapture probabilities were not modelled with any year-dependent structure.

Model selection

It was not possible to fit all combinations of covariates, due to computational limitations. Models were initially run with general models: survival as a function of year (as a factor) and recapture as a function of year (as a continuous variable). First, the transience model that was fully identifiable was selected, as described above. Secondly, the selected transience model was run with the survival as a function of year (as a factor) and various recapture models. The best recapture model was chosen using QAICc. Finally, the selected recapture model and the identifiable transience model were used with the survival models described above: (1) time-specific survival and (2) survival as a function of weather covariates.

The weather covariates were: Sahel rainfall, autumn NAO and spring NAO. All combinations of year (as a factor), year (as a continuous variable) and the weather covariates were evaluated, and the most parsimonious model was chosen using QAICc. These models tested the hypotheses that weather during different seasons affected the annual survival of the eight passerine migrants. All survival estimates presented here represent minimum survival rates because there is the potential for permanent emigration from the capture sites, which cannot be distinguished from mortality. The sequential model selection procedure is described as an example for one species and region (Appendix 1). All models were run within R (R Core Team 2015) using the package 'RMARK' (Laake 2011) to construct models for program MARK (White & Burnham 1999).

Annual survival within wintering zones and breeding regions

Using results from the fully time-dependent survival model and the selected recapture and transience models, we tested predictions of whether species wintering in the same bioclimatic zones have similar survival, and whether breeding locations affect the survival of different species similarly. We created a mixed model with the logit-transform of the estimated survival as a response variable in a Gaussian linear mixed model. To account for different precision of estimates, the reciprocal of the standard errors of the survival estimates were included as weights. Breeding region and wintering bioclimatic zone were included as fixed covariates. Species was included as a random effect, and because each species winters in a single bioclimatic zone, species was nested within the fixed effect of bioclimatic zone. We tested the significance of fixed effects by using chi-squared tests on nested models fitted with maximum likelihood. The final model was fitted with restricted maximum likelihood (REML). Models were run in R (R Core Team 2015) with package 'LME4' (Bates *et al.* 2015).

Correlations between annual population changes and annual survival estimates

We predicted that survival is positively correlated with annual population changes. Annual population changes for each species were estimated by fitting the number of individual adult birds captured on a CES site in a given year as the response variable in an over-dispersed Poisson GLM with a log-link function, with site and year (as a factor) as covariates (Peach *et al.* 1998). Although this is not an independent dataset for estimates of national population change, this lack of independence will be small, due to the relatively low recapture rates of individuals and, additionally, the survival model that accounts for variable recapture rates. This approach ensures that the estimates of population change are derived from the part of the population in the same locations and habitats as the survival estimates. Previous work has shown that medium-term changes measured using this approach are well correlated with national change measures based on mapping censuses, indicating that these methods do produce robust measures of population change (Peach *et al.* 1998, Saracco *et al.* 2008).

To assess the correlation between survival probability and population change, we modelled the estimated annual population change (calculated as the ratio of successive terms of the year parameter from the GLM above) in a GLM with estimated survival probability, species and region as covariates. Interactions of survival × species and survival × region were included to test for variation in the relationship between survival and population change in different species and/or regions. The reciprocal of the standard error of the estimated population change was included in the GLM as a weighting term, to account for variation in precision of the population change estimate. Data points for which the estimated annual survival had boundary confidence limits (0–1) were excluded from the analysis. Likelihood ratio tests were used to test the significance of the covariates.

RESULTS

Estimates of survival, transience and recapture probabilities

Mean species-specific estimates of annual adult survival probability from the time-specific model ranged from 0.30 to 0.42 (Table 1). Chiffchaff, Sedge Warbler and Lesser Whitethroat all had low estimates of mean survival in all regions (approximately 0.30). The site-specific estimates of transience were related to habitat in most cases (Table S2). Average transience rates were generally higher in Catalonia and the Netherlands, and generally lower in France. Reed Warbler had consistently high estimates of site-specific transience, with other species showing inconsistent patterns across regions. Site age was related to recapture probability in 20 of the 35 models and generally suggested lower recapture rates in older sites. Habitat was less important overall and was related to recapture rate in 12 of the models (Supporting Information Table S5). Recapture probabilities were the lowest for Lesser Whitethroat and the highest for the *Phylloscopus* species.

Weather correlates of survival

The winter variable was present in more of the most parsimonious models than the other weather variables and, generally, higher rainfall was associated with higher survival (except in France). The magnitude of the winter coefficients suggested that they also had larger effects on survival than the other seasonal variables (Table 2, Fig. 1). Spring and autumn variables were present in fewer models and had smaller impacts, but were at a broad geographical scale, so were not so closely linked to weather in particular locations. Where these terms were significant, high NAO generally led to higher spring survival and lower autumn survival.

Annual survival within wintering zones and breeding regions

Both wintering bioclimatic zone ($\chi^2_2 = 10.05$, $P = 0.007$) and the breeding region ($\chi^2_4 = 10.17$, $P = 0.04$) were significantly correlated with adult survival across species. Survival of migrants wintering in the humid bioclimatic zone was significantly higher than survival of those wintering elsewhere (Table 3). Estimates of survival were 45% higher for an average species wintering in the humid zone compared to the arid zone (Fig. 2).

Correlations between annual population changes and annual survival estimates

Mean annual population change was negative for the three humid zone migrants and positive for the other five species (Supporting Information Table S7). The annual population change was significantly positively correlated with estimated survival probability, but the strength of the relationship differed between species (Fig. 3, Supporting Information Table S8). The steepest slopes, which suggest the strongest correlation between estimated survival and annual population fluctuations, were for Whitethroat and Sedge Warbler. The shallowest slopes were for Garden Warbler and Willow Warbler (Fig. 3), which were the only two species to record declining trends in all five breeding regions (Table S7). Likelihood ratio tests identified a significant effect of interactions between the species and survival ($F1,7 = 5.7$, $P < 0.0001$) and between the breeding region and survival ($F1,4 = 3.8$, $P = 0.0049$).

DISCUSSION

We estimated annual adult survival probabilities for eight Afro-Palaearctic passerine migrants and found that average estimates of annual adult survival were significantly higher for species wintering in the humid zone compared with those wintering in the less climatically stable arid zone. Sahel rainfall had a larger and more consistent impact on annual survival compared with NAO during the autumn or spring migration. There was a significant link between survival and annual population change, which varied in strength between species.

Correlation of annual survival and weather patterns during winter and migration

The Sahel rainfall variable had a significant relationship with survival in at least one region for seven of

Table 1. Mean estimates of survival (and standard error) for each species and region, averaged over all years. Species and region combinations without estimates of survival had insufficient data.

WBZ	Species	Catalonia	France	Netherlands	UK South	UK North	Mean
North	Blackcap	0.48 (0.05)	0.48 (0.03)	0.37 (0.03)	0.29 (0.01)	0.33 (0.02)	0.39
Arid	Chiffchaff		0.40 (0.04)	0.28 (0.03)	0.27 (0.02)	0.27 (0.02)	0.30
	Whitethroat	0.27 (0.10)	0.46 (0.05)	0.33 (0.03)	0.33 (0.02)	0.36 (0.02)	0.35
	Lesser Whitethroat			0.32 (0.04)	0.32 (0.04)	0.28 (0.03)	0.31
	Sedge Warbler		0.34 (0.05)	0.31 (0.03)	0.28 (0.01)	0.30 (0.02)	0.31
Humid	Garden Warbler	0.20 (0.06)	0.49 (0.06)	0.45 (0.02)	0.46 (0.02)	0.42 (0.02)	0.40
	Reed Warbler	0.30 (0.05)	0.43 (0.05)	0.45 (0.02)	0.47 (0.01)	0.45 (0.02)	0.42
	Willow Warbler		0.46 (0.05)	0.36 (0.01)	0.32 (0.01)	0.34 (0.01)	0.37
	Mean	0.31	0.44	0.36	0.34	0.34	0.36

WBZ, Wintering Bioclimatic Zone.

Table 2. Coefficients of weather variables (and standard error) in the survival models for all species and regions. Covariates in bold differed significantly from zero (confidence intervals not overlapping zero).

Bioclimatic zone	Species	Region	Autumn	Winter	Spring
North	Blackcap	Catalonia	0.108 (0.102)	−0.096 (0.127)	0.115 (0.174)
		France	0.069 (0.117)	**−0.735 (0.194)**	−0.054 (0.170)
		Netherlands	−0.252 (0.135)	0.052 (0.145)	−0.117 (0.172)
		UK South	−0.002 (0.047)	0.070 (0.052)	−0.010 (0.050)
		UK North	−0.041 (0.056)	**0.359 (0.066)**	0.059 (0.059)
Arid	Chiffchaff	France	**0.455 (0.106)**	**−0.472 (0.134)**	0.203 (0.121)
		Netherlands	**−0.259 (0.086)**	−0.004 (0.077)	0.062 (0.047)
		UK South	−0.112 (0.057)	0.064 (0.059)	**0.114 (0.036)**
		UK North	**−0.253 (0.095)**	−0.126 (0.098)	0.039 (0.062)
	Whitethroat	Catalonia	0.577 (0.745)	−0.944 (1.016)	−0.989 (1.166)
		France	−0.024 (0.120)	−0.145 (0.213)	−0.137 (0.160)
		Netherlands	0.093 (0.118)	0.175 (0.169)	0.128 (0.197)
		UK South	−0.035 (0.045)	**0.165 (0.067)**	0.020 (0.056)
		UK North	0.046 (0.046)	**0.202 (0.060)**	0.045 (0.055)
	Lesser Whitethroat	Netherlands	0.078 (0.199)	−0.014 (0.280)	0.248 (0.326)
		UK South	−0.087 (0.106)	0.270 (0.155)	0.097 (0.128)
		UK North	0.147 (0.078)	0.060 (0.112)	−0.040 (0.090)
	Sedge Warbler	France	0.078 (0.218)	−0.663 (0.444)	−0.101 (0.467)
		Netherlands	−0.098 (0.069)	**0.196 (0.092)**	−0.011 (0.115)
		UK South	**−0.096 (0.029)**	**0.133 (0.040)**	−0.051 (0.035)
		UK North	**−0.089 (0.028)**	0.049 (0.038)	−0.047 (0.036)
Humid	Garden Warbler	Catalonia	−0.287 (0.264)	0.034 (0.397)	0.744 (0.517)
		France	0.115 (0.102)	**−0.376 (0.178)**	−0.043 (0.167)
		Netherlands	0.055 (0.060)	−0.085 (0.087)	0.025 (0.101)
		UK South	**−0.119 (0.052)**	0.049 (0.068)	0.019 (0.065)
		UK North	−0.053 (0.052)	0.058 (0.072)	0.039 (0.069)
	Reed Warbler	Catalonia	0.059 (0.100)	**0.299 (0.137)**	−0.016 (0.181)
		France	**0.234 (0.075)**	−0.185 (0.119)	−0.184 (0.112)
		Netherlands	−0.013 (0.032)	**0.102 (0.043)**	−0.081 (0.053)
		UK South	−0.013 (0.019)	**0.067 (0.026)**	**0.061 (0.024)**
		UK North	0.045 (0.026)	**0.183 (0.035)**	−0.027 (0.033)
	Willow Warbler	France	**−0.472 (0.210)**	**−1.361 (0.356)**	**−0.770 (0.243)**
		Netherlands	−0.042 (0.039)	**0.171 (0.056)**	0.030 (0.062)
		UK South	−0.007 (0.028)	**0.135 (0.035)**	−0.045 (0.031)
		UK North	−0.026 (0.020)	0.033 (0.026)	0.038 (0.024)
Weighted mean coefficient			−0.022	0.085	0.013
No. of significant coefficients			8	15	3
Weighted mean of significant (bold) coefficients			**−0.078**	**0.123**	**0.072**

the eight species. It was significant in more models than the weather variable from either spring or autumn, and the average effect size for the standardized variables was larger. This suggests that, across all species, the precipitation conditions in the Sahel are a more important determinant of survival than the broad weather conditions during the autumn or spring migration periods. For those species wintering further south, conditions in the Sahel may also be correlated with conditions in the humid bioclimatic zone and other wintering areas, or conditions in the Sahel stopover may be more critical for overwinter survival than conditions in wintering areas (e.g. Willow Warbler in Ockendon *et al.* 2014).

Some species had both positive and negative significant effects of rainfall in different regions, but the majority of the significant coefficients for Sahel

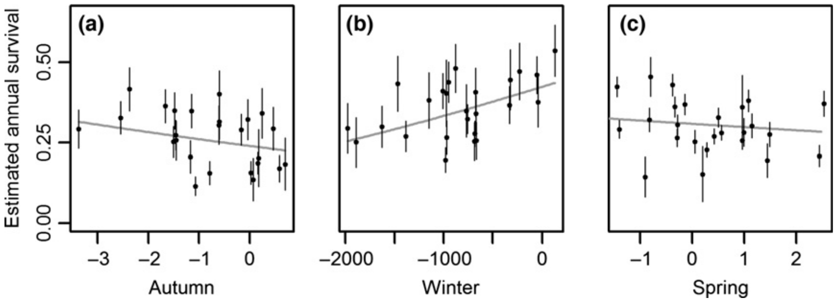

Figure 1. Estimates of annual survival and associated standard errors from a time-specific model, plotted against species-specific weather covariates for a sample of species for which weather variables were important. Plots show estimated survival and 95% confidence limits of (a) Sedge Warbler in the north of the UK, (b) Whitethroat in the north of the UK and (c) Chiffchaff in the south of the UK. Note that the rainfall variable was standardized in the model-fitting process, but is shown here on the original scale.

Table 3. Fixed effect coefficients for the effects of wintering bioclimatic zone and breeding region on species-specific logit estimates of survival. The intercept coefficient represents the survival for an average species breeding in UK-South and wintering in the Humid bioclimatic zone.

Factor type	Factor level	Estimate	se	*t*-value
Intercept		−0.454	0.120	−3.784
WBZ	North	−0.288	0.235	−1.229
	Arid	−0.551	0.156	−3.526
Breeding region	UK-North	0.043	0.047	0.918
	Netherlands	0.071	0.058	1.223
	France	0.208	0.068	3.054
	Catalonia	0.144	0.128	1.124

rainfall were positive (11/15). Several studies have also found a positive relationship between Sahel rainfall and higher overwinter survival for individual Afro-Palaearctic migrant species (Peach *et al.* 1991, Szep 1995, Newton 2004, Cowley & Siriwardena 2005). Food resources in arid regions are limited by rainfall (Mullié 2009, Zwarts *et al.* 2009a, Tøttrup *et al.* 2012) and therefore conditions in the Sahel are likely to be strongly affected by rainfall. As the Sahel is the first stop-off location after the autumn Sahara crossing, and the last re-fuelling location before the spring Sahara crossing (Schmaljohann *et al.* 2012), the food availability in this region may impact survival for species passing through the region as well as those species wintering there (Ockendon *et al.* 2014). Survival of species that use the Sahel as a stopover location may be affected by weather due to direct effects of competition or lack of sufficient food resources, or indirectly by causing a longer period of fattening and sub-optimal timing of departure on migration (Newton 2006, Saino *et al.* 2007, Studds & Marra 2011). Rainfall and climatic indices have been demonstrated to impact body condition of migrants during winter (Brown & Sherry 2006) and at stopover locations (Wolfe & Ralph 2009). Future climate in western Sahel is predicted to be drier than current climate (Buontempo 2010), so the negative impacts of drought in the Sahel may further reduce annual adult survival.

There were strong *a priori* reasons to use Sahel rainfall as a variable for survival in the winter (Peach *et al.* 1991, Payevsky 2006, Walther *et al.* 2011, Ockendon *et al.* 2012, 2014). However, much less is known of the most relevant weather variables and locations of birds during the migration period. For this reason, we used the large-scale climatic index NAO, which alongside the El Niño Southern Oscillation (ENSO) has been found to be correlated with survival (Sillett *et al.* 2000, Mazerolle *et al.* 2005, Kéry *et al.* 2006, LaManna *et al.* 2012, Salewski *et al.* 2013) and migration phenology (Zalakevicius *et al.* 2006) across a range of species. The positive spring coefficient for NAO indicated higher annual survival in years with a more westerly (mild, oceanic) airflow over Europe, which may result in earlier and greater vegetation growth (Scheifinger *et al.* 2002). In autumn, survival was apparently higher when the airflow was more easterly (lower NAO value) and storm activity generally lower (Allan *et al.* 2009). However, the smaller number of significant effects with NAO may be a result of the lower precision of the variable, both geographically and climatically, rather than a reduced importance of weather during the migration periods compared to winter. We found greater evidence for effects of autumn NAO than spring NAO on annual survival across all species. There are few studies looking at effects of weather during the migration period, but

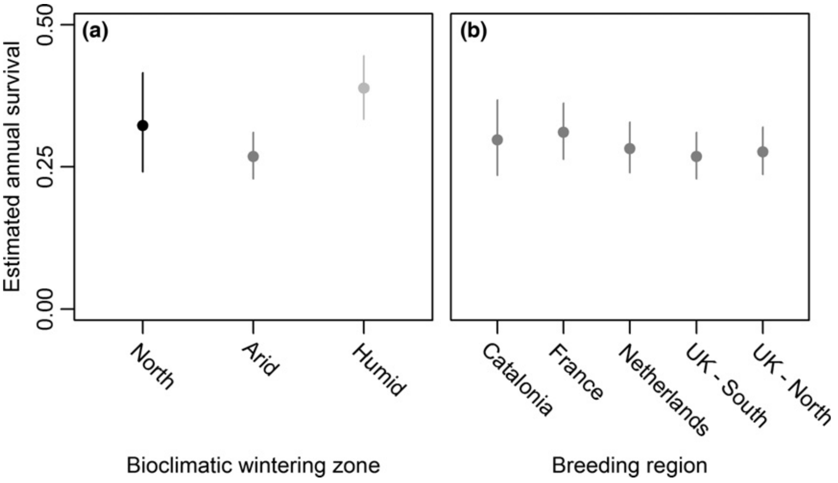

Figure 2. Estimated survival for an average species from the model relating survival to (a) bioclimatic wintering zone and (b) breeding region. The 95% confidence intervals represent the confidence intervals for the fixed effects only and do not incorporate the variance described by the random effect of species. Colours represent North bioclimatic zone (light grey), Arid bioclimatic zone (dark grey) and Humid bioclimatic zone (black). These match the colours in Figure 3 for ease of comparison. For predictions in (a) the breeding region is set as UK-South and for the predictions in (b) the bioclimatic wintering zone is set as Arid.

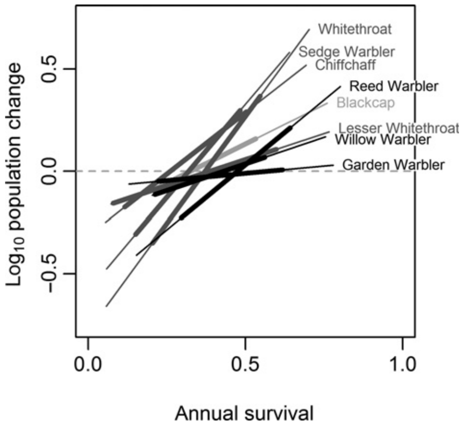

Figure 3. Model-averaged relationship between estimated annual survival and estimated annual population change for different species. The thin lines represent the extent of survival estimates for each species and the thick part of the lines the central 90% of survival estimates for each species. Species that winter further south are shown in darker colours: the Mediterranean (light grey), the arid bioclimatic zone (dark grey) and the humid bioclimatic zone (black).

House Martin *Delichon urbicum* adult survival was severely affected by conditions during autumn migration (Stokke *et al.* 2005). Overall, we found only a low correlation between survival and migration weather coefficients, in agreement with other studies (Nevoux *et al.* 2008, Schaub *et al.* 2011, Salewski *et al.* 2013).

Annual survival within wintering zones and breeding regions

Differences in estimated survival were greater between bioclimatic wintering locations than between breeding locations. This suggests that bioclimatic wintering location has a larger effect on annual survival than breeding location. Although other studies have found that survival can vary over small spatial scales (Saracco *et al.* 2010), so the aggregation to a large breeding region may be masking some variation in survival. There was a significantly higher mean survival for species that winter in the humid bioclimatic zone compared with those that winter in the arid bioclimatic zone. One theory suggests that longer distance migrations evolve because abiotic and biotic factors at greater distances confer higher survival in the non-breeding season (Gauthreaux 1982), a pattern which would be supported by the survival probabilities estimated here. The humid bioclimatic zone is a less adverse environment than the arid zone (due to higher rainfall), which may explain the higher survival. This pattern of higher survival of longer-distance migrants has previously been found within species (Adriaensen & Dhondt 1990, Hestbeck *et al.* 1992, Sanz-Aquilar *et al.* 2012), but not between species (Sandercock & Jaramillo 2002). The higher survival of longer distance migrants may alternatively be due to other factors such as different timing of migration, migration strategies or carry-over effects from the winter to the breeding season. Further knowledge of the wintering areas and migration routes of different populations will be required to fully disentangle the impacts of wintering habitat and migration on survival. The increasing availability of electronic tracking devices will lead to more detailed information on migration routes, stopover sites and wintering locations for a wider range of species (e.g. Bächler *et al.* 2010, Schmaljohann *et al.* 2012).

Correlations between annual population changes and annual survival estimates

Strong correlations between annual population change and survival suggest that low survival can be a contributing factor to breeding population size. However, it is important not to assume that a correlation defines a causal relationship; density dependence in survival and other demographic rates may compensate for or exacerbate effects of survival in subsequent breeding seasons (Green 1999). Among migratory species, survival rates have previously been implicated in declines of Willow Warbler (Peach *et al.* 1995), Common Sandpiper *Actitis hypoleucos* (Pearce-Higgins *et al.* 2009) and Red Knot *Calidris canutus* (Baker *et al.* 2004). Here we demonstrate that the link between survival rates and population change in the last 20 years is variable among species. Whitethroat, Chiffchaff, Sedge Warbler and Reed Warbler had strong relationships between survival and population change, the first three of which had the most positive average population trends of the eight species. Three of these species also showed significant and positive coefficients of Sahel rainfall in at least two regions, suggesting that higher Sahel rainfall in recent years (Herrmann *et al.* 2005) may have led to increasing breeding populations of these species. However, it should be noted that while Whitethroat populations increased over our study period, their abundance is still far below that before the 70% population crash that occurred during the winter of 1968–69 (Winstanley *et al.* 1974).

Conversely, Garden Warbler and Willow Warbler have the two steepest average population declines, and exhibit the weakest relationships between survival and population change. These latter two species both spend the winter in the humid zone, and migrants there tend to have more negative population trends than migrants in the arid zone (Ockendon *et al.* 2012). This study suggests these negative population trends are not due to variation in survival driven by these climate and weather variables. Population change in these species is therefore potentially driven by reduced productivity or juvenile survival. Compensatory density-dependence in productivity would not mask population change in this dataset, because population size in the breeding season is estimated before juveniles have entered the population. Few studies of migrants have estimated juvenile survival, due to the challenges of the large-scale movements of juveniles through migration and dispersal. However, juvenile survival is implicated in population declines of some species (Thomson *et al.* 1997, Robinson *et al.* 2004) and juveniles may be more sensitive to detrimental weather conditions (Rockwell *et al.* 2012).

The causes of the declines in many populations of Afro-Palaearctic migrants are still unclear; we demonstrate that links to survival suggest influences of weather on adult survival of these eight passerine migrants. However, there was not strong evidence that these impacts on adult survival have led to population declines, and therefore quantifying factors affecting productivity, recruitment of individuals into breeding populations and juvenile survival should be a research priority.

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APPENDIX 1
EXAMPLE OF MODEL SELECTION ROUTINE

SEDGE WARBLER IN THE NETHERLANDS

1. Transience selection

Survival	Transience	Recapture	No. of parameters	No. of unidentifiable parameters
Year as a factor	**Site**	**Site**	**98**	**2**
Year as a factor	Habitat	Site	62	0
Year as a factor	Constant	Site	57	3

Site-specific transience is selected as the most general model with a low number of unidentifiable parameters.

2. Recapture selection

Survival	Transience	Recapture	npar	QAICc	DeltaQAICc	Weight	QDeviance
Year as a factor	**Site**	**Habitat**	**62**	**22276.6**	**0**	**0.71**	**20880.8**
Year as a factor	Site	Habitat + site age	63	22278.4	1.83	0.29	20880.6
Year as a factor	Site	Constant	58	22287.9	11.37	< 0.01	20900.4
Year as a factor	Site	Site age	59	22289.4	12.81	< 0.01	20899.8
Year as a factor	Site	Site	98	22296.9	20.38	< 0.01	20826.8
Year as a factor	Site	Site + site age	99	22298.4	21.87	< 0.01	20826.2

Habitat-specific recapture is selected as the more parsimonious model.

3a. Final year-specific model

Survival	Transience	Recapture	npar	QAICc	QDeviance
Year as a factor	Site	Habitat	62	22276.6	20880.8

3b. Weather variable selection

Survival	Transience	Recapture	npar	QAICc	DeltaQAICc	Weight	QDeviance
Winter	Site	Habitat	49	22264.7	0	0.25	20895.6
Autumn + winter	Site	Habitat	50	22265.0	0.24	0.22	20893.8
Constant	Site	Habitat	48	22265.9	1.12	0.14	20898.7
Winter + spring	Site	Habitat	50	22266.6	1.83	0.10	20895.4
Autumn	Site	Habitat	49	22266.8	2.07	0.09	20897.7
Autumn + winter + spring	Site	Habitat	51	22267.0	2.28	0.08	20893.8
Spring	Site	Habitat	49	22267.3	2.55	0.07	20898.1
Autumn + spring	Site	Habitat	50	22268.6	3.82	0.04	20897.4

Models selected in each stage are shown in bold.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. Number of individuals of each species caught in each region and used in the mark-recapture analysis. Numbers in grey were insufficient to estimate survival.

Table S2. Final transience models. Blank cells represent models which were not run.

Table S3. Mean estimated probability across all sites of a captured bird being a transient.

Table S4. Mean estimated probability of capturing a resident bird at least twice in the first year of capture.

Table S5. Final recapture models. Blank cells represent models which were not run.

Table S6. Mean estimated annual recapture rate across all sites.

Table S7. Mean estimated annual percentage population change (and standard error) by species and breeding region.

Table S8. Estimates and standard errors of coefficients from the model of population change as a function of species and breeding region and survival.