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RESEARCH PAPER

Latitudinal gradients in the productivity of European migrant warblers have not shifted northwards during a period of climate change

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ABSTRACT

Aim As global temperatures have increased, many species distributions have exhibited polewards shifts, a trend that is predicted to continue in future decades. However, the mechanisms underlying such shifts are not well understood. Here we quantify the impact of large-scale variation in temperature on reproductive output within a group of migratory birds to assess the potential for future range changes.

Location Western Europe.

Methods We use data from captures of 350,000 individual birds, collected under constant effort ringing protocols from 1994–2006, to estimate productivity (percentage of juveniles caught) for seven species of migrant warblers (family Sylviidae) breeding in Europe in relation to spring temperature and latitude by fitting generalized linear mixed models.

Results Productivity was highest at mid-latitudes for six of our seven study species and did not change significantly over the study period. Only one species (reed warbler, *Acrocephalus scirpaceus*) showed increased productivity at northern sites as expected. Six of the seven species also showed evidence for local adaptation, with productivity decreasing as temperatures diverged from the local mean. However, for three of these species the 'optimum' temperature was greater than the local mean temperature at the majority of sites.

Main conclusions These results indicate that latitudinal gradients in productivity are likely to influence large-scale abundance patterns, but that adaptation to local climate conditions has the potential to constrain the rate of northward range shifts in many species.

Keywords
***Acrocephalus*, constant effort ringing, demography, *Phylloscopus*, population dynamics, range distribution, *Sylvia*, Sylviidae, temperature.**

INTRODUCTION

Within a species' range, populations tend to occur at low densities at the range margins, with higher population densities towards the centre (Brown, 1984; Gaston, 2000; Rodrigues & Gaston, 2002). Species distributions are at least partly determined by temperature (Huntley *et al.*, 2007; Boucher-Lalonde *et al.*, 2014) and one of the most notable 'fingerprints' of global climate change has been a poleward shift in species distributions across a wide range of taxa (e.g. Parmesan & Yohe, 2003; Walther *et al.*, 2005; Hickling *et al.*, 2006), which can be related to the magnitude of warming experienced (Chen *et al.*, 2011). In particular, such shifts have been documented for both breeding (Thomas & Lennon, 1999) and wintering (Maclean *et al.*, 2008) populations of birds. However, little work exists documenting the mechanisms underpinning these changes, and that which

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does (e.g. Both *et al*., 2006; Frederiksen *et al*., 2006; Pearce-Higgins *et al*., 2010) tends to focus on individual areas and so, generally, does not quantify the variation across the occupied range that would be necessary to drive such changes in distributional pattern.

Large-scale spatial variation in productivity (the number of juvenile birds raised per adult) and the processes generating it have long been of interest to ecologists (Lack, 1947; Ashmole, 1963). There remains debate as to whether productivity increases linearly with latitude, reflecting seasonality in primary production and energy requirements, as originally suggested by Ricklefs (1980) and more recently demonstrated by Cooper *et al*. (2005) and Evans *et al.* (2009), or nonlinearly (Sanz, 1997, 1998; Fargallo, 2004). Such nonlinear relationships would arise if breeding conditions are more ‘optimal’ near the centre of a range than towards its periphery. Thus, as thermal isoclines are generally shifting northwards (e.g. Loarie *et al*., 2009), we might expect similar latitudinal shifts in patterns of productivity. This would provide a demographic mechanism for observed shifts in species distributions, but the process remains untested. We address this issue by modelling latitudinal variation in the relative productivity of seven migrant bird species (order Passeriformes, family Sylviidae). These species have similar life-history traits with the exception of the distance migrated to their non-breeding grounds (Simms, 1985). They exhibit a degree of variation in recent population trend, in part related to their migratory status, which makes them ideal for testing for the impact of changes in demographic rates (Ockendon *et al*., 2012; Morrison *et al*., 2013). In particular, we find that population trends are generally positive among short-distance migrating species, at least in part in response to warming temperatures, but negative in the longer-distance migrants (Jones & Cresswell, 2010).

The rate of population change in migratory warblers has been shown to vary with latitude and temperature such that southern populations, near the species thermal maximum, generally have lower growth rates than northern populations near the thermal minimum (e.g. Jiguet *et al*., 2010; Morrison *et al*., 2013). This trend is predicted to continue (Huntley *et al*., 2007), although rates of population change may be lagging behind those of temperature change (Devictor *et al*., 2008, 2012; Visser, 2008). Recent studies of the impacts of climate change have tended to investigate correlates of change in population numbers (or even just an index of them) and then inferred the reasons for change rather than directly assessing the underlying demographic mechanisms (e.g. Møller *et al*., 2008; Both *et al*., 2010; Jiguet *et al*., 2010). Quantifying such mechanisms will be necessary in order to properly understand the impacts of climate warming.

We used constant-effort ringing data from western Europe collected as part of the European Constant Effort Sites (EuroCES) programme to quantify the relationship between temperature and productivity at an extensive spatial scale from the Mediterranean to northern Scotland. By encompassing such a broad latitudinal range we are able to examine the response to temperature over much of the species ranges, something that would be impossible with data from only a single country. Although data on bird abundance in Europe have been analysed previously at a continental scale, this is the first time that demographic data for these species have been collated at such large spatial extents, facilitating a more direct examination of the mechanisms of population change. Firstly, we assessed the extent to which productivity varies with temperature, predicting a peak at intermediate temperatures, and that a similar relationship should then exist between reproductive output and latitude. We then tested whether productivity has increased at more northern latitudes (or, conversely, decreased in the south), thus providing a demographic mechanism whereby observed range shifts might occur. Changes in distribution may be pre-figured by local responses to temperature, so we also tested for the strength of adaptation to local temperatures by quantifying the impact on reproductive output of variation in site-specific annual temperature anomalies. If climate warming is to influence distributional shifts through productivity, we would predict that productivity would be higher in years that were warmer than the site mean, independently of the absolute temperature.

MATERIALS AND METHODS

Productivity data

We measured productivity as the ratio of juvenile to adult birds caught during standardized mist-netting sessions as part of the EuroCES monitoring programme (Peach *et al*., 1996; Julliard *et al*., 2004; Robinson *et al*., 2009) for the period 1994–2006 (the longest period for which data were available from all the schemes included in this study). Only sites that had been operated in at least two years (though 75% of sites were operated for four or more years) and only years in which at least 10 individuals of any given species were caught at a site were included. This provided a dataset with 426 sites from five countries: Great Britain (220 sites), France (111), Ireland (13), the Netherlands (54) and Spain (28). Our sites are typically in more or less open habitats, such as reedbed, shrubland and open woodland, which generally do not exhibit a narrow seasonal peak in food availability (Both *et al*., 2010).

We calculated productivity indices for seven species of closely related, and ecologically similar, migrant passerine birds: chiffchaff, *Phylloscopus collybita* (occurring on 285 sites, Table S1 in Supporting Information); willow warbler, *Phylloscopus trochilus* (257); sedge warbler, *Acrocephalus schoenobaenus* (167); reed warbler, *Acrocephalus scirpaceus* (191); whitethroat, *Sylvia communis* (175); blackcap, *Sylvia atricapilla* (335); and garden warbler *Sylvia borin* (162). The latitudinal range of these sites (40–58° N, Fig. 1) occupied the majority of the geographical breeding range of these species, which for most is from 35–40° N in the south to 65–70° N in the north, though the reed warbler has a more southerly range (30–63° N) and the willow warbler a more northerly range (45–72° N). Populations of each species from these countries follow a common migratory trajectory to wintering grounds in Africa, although the distance migrated differs between species:

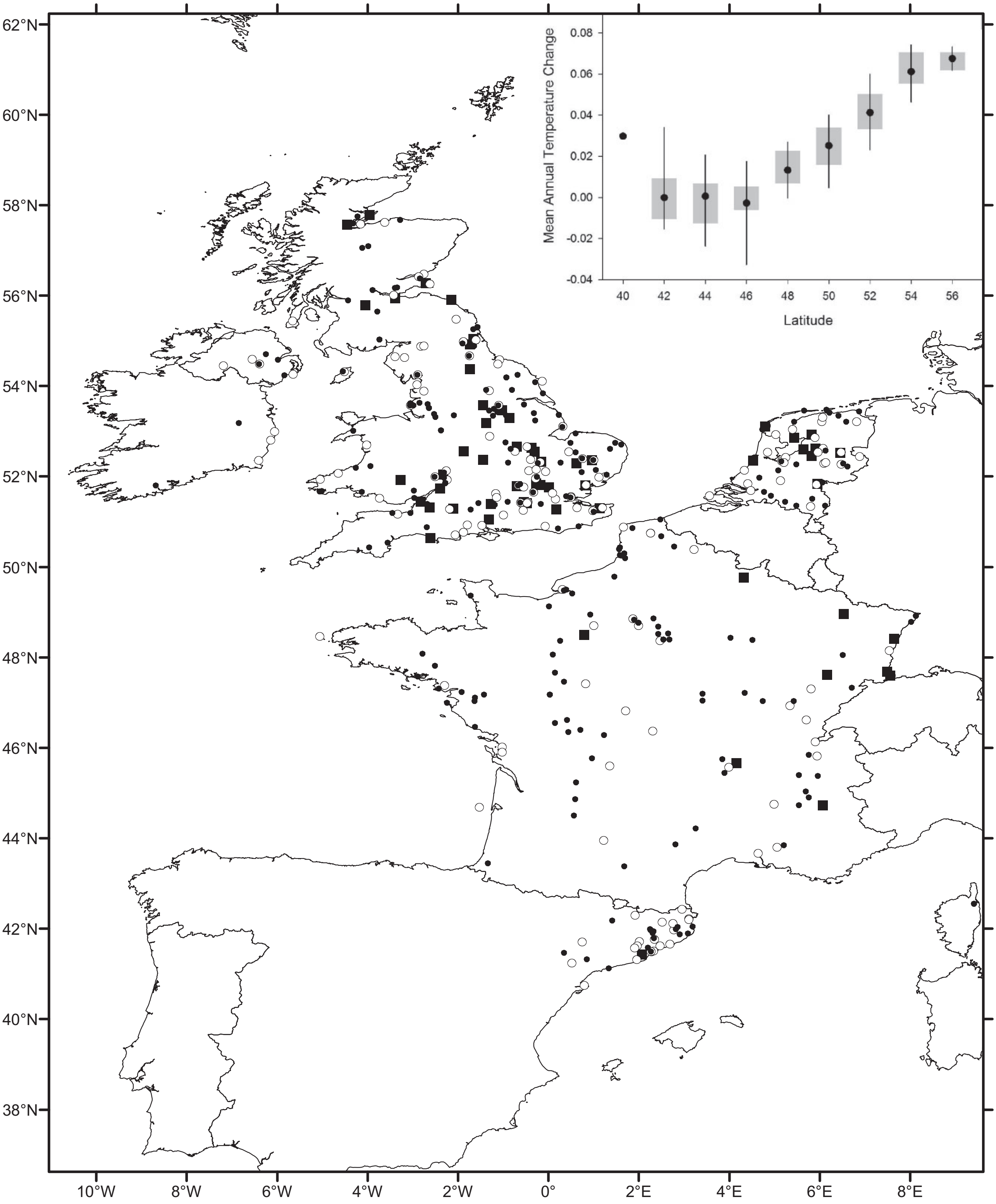

Figure 1 Location of EuroCES sites ($n = 426$). Sites indicated by small filled dots operated for 2–5 years; open circles for 5–10 years and filled squares for > 10 years. The inset graph shows the site-specific mean rate of warming (°C year^{-1}) by 2° latitude bands (dot, mean; box, inter-quartile range; bar, 5th and 95th percentile).

chiffchaff and blackcap winter in southern Europe/northern Africa; sedge warbler and whitethroat mostly in western Africa; reed and garden warblers in central Africa and willow warbler in southern Africa (Wernham *et al*., 2002).

Although our data span only 13 years, this matches the period over which significant variation in population trends in European birds (Gregory *et al*., 2009) and population declines in migrants have been linked to increasing temperatures (Møller *et al*., 2008; Both *et al*., 2010) and also for which evidence for climate-driven latitudinal trends in population change has been collated (Jiguet *et al*., 2010). It is also a period in which warming has occurred, especially at northern latitudes (Fig. 1). Furthermore, Kampichler & van der Jeugd (2011) used a resampling approach to show that for the 20 most abundant species, including all seven species considered here, the effort invested in the Dutch CES programme (a subset of the data used here) provides sufficient power to detect temporal trends in productivity during the period 1994–2009. We therefore conclude that the number of sites in the present study should be adequate to detect spatial and temporal trends in productivity.

The CES schemes in Britain, Ireland, the Netherlands and Spain follow a protocol based on that described by Peach *et al*. (1996). Briefly, the breeding season, generally taken to be May to August, is divided into 10–12 equal periods of *c.* 10 days' duration, with ringers operating a catching session in each period. Mist-nets are usually erected from sunrise for up to 6 h per visit, but different patterns are allowed provided they are adhered to consistently between years. In France, a reduced effort scheme is operated with three to five visits completed between May and mid July at each site (Julliard *et al*., 2004). Each newly captured individual is fitted with a uniquely numbered metal ring, then age and other biometric characters are determined before the bird is released. Our measure of productivity then, is the proportion of individual birds, caught across all visits in a season at a site, that are juveniles. Juveniles in these species are readily identifiable on the basis of plumage characteristics. This provides only a relative measure of productivity, but one that is integrative, by incorporating the number of breeding attempts made, clutch size, hatching and fledging success and early post-fledging mortality, and so provides a useful index of overall reproductive output at that locality (Peach *et al*., 1996).

For the schemes requiring 10–12 visits over the season, a few individual visits are inevitably missed in some years due to, for example, adverse weather conditions or shortage of ringers. Usually only one or two visits are missed in any year at a given site and more than four missing visits cause the site to be treated as not covered in that year. The influence of missed visits at the sites included in the calculated indices is generally not large (Miles *et al*., 2007; Cave *et al*., 2009); however, we included an offset in our analyses to correct for any effect of missing visits (see below).

Climate data

We extracted monthly estimates of mean March, April and May temperatures for the period 1994–2006 from the CRU TS3.0 dataset (Mitchell & Jones, 2005) and averaged these to provide a measure of spring temperature. These data are provided on a 0.5° × 0.5° grid, so we assigned temperatures to each CE site based on the grid cell in which it was located (with an average of two CE sites per grid cell). These three months broadly cover the main period of arrival and initiation of first breeding attempts of each of the study species across Europe, and temperatures in this period are likely to be correlated with the abundance of insect prey (Buse *et al*., 1999; Smith *et al*., 2011). We did not use more specific measures of temperature since the necessary understanding of how variation in temperature (both spatially and temporally) drives resource abundance across the geographical range of our sites is lacking.

Statistical analysis

Because we were interested in common patterns across all species, we present a multispecies analysis in a single model whereby we modelled productivity (the number of juvenile birds caught at a site in a year as a proportion of the total number of birds caught) as a generalized linear mixed model (GLMM) with a logit link and binomial errors using the events/trials syntax of the SAS GLIMMIX procedure with the default residual pseudo-likelihood estimation technique (SAS Institute Inc, 2008). We first examined the relationship between productivity and mean annual spring temperature across species by including the following variables in the GLMM: species (categorical), temperature, temperature^2 (to account for any non-linearity in the response) and year (continuous, to account for any variation in population size) and interactions between these terms and species (Table 1). Although there was a moderate correlation between temperature and latitude of the CE sites ($r = -0.73$), controlling for latitude (by including this term in the GLMM) resulted in a very similar pattern; thus we did not include it in the model. We accounted for the structured nature of the data by including the CES site identifier (nested within country) and year (as a factor nested within species) as random intercepts and a residual variance term (grouped by site) to represent over-dispersion. We included country as a fixed factor to account for the methodological differences between the national schemes (and it is difficult to estimate a random effect from a variable with only five levels). We further included a correction factor (as an offset) to account for the reduced number of captures caused by missing visits following Robinson *et al*. (2007). We tested for the significance of each term (partial increase in amount of deviance explained) with a χ^2 statistic after adjusting the degrees of freedom of the denominator using the Kenward–Rogers option. We next examined the effect of latitude on productivity by fitting a similar GLMM with latitude and latitude^2 replacing temperature and its square in the list of independent variables. To test whether variation in productivity changed systematically over time we also included interaction terms between latitude and year in this model (Table 2).

As productivity may be more sensitive to deviations in local temperature (i.e. colder or warmer than average years) rather than absolute temperature, we calculated site-specific

Table 1 Parameter estimates of generalized linear mixed models estimating the effect of temperature on productivity. For simple linear fixed and random effect terms we give the parameter estimate ± 1 standard error; for terms involving an interaction with species we give the mean of the species-specific slopes as the main effect and the range of these for the interaction term. We then give the numerator and denominator degrees of freedom (d.f., as determined by the Kenward–Rogers algorithm), the χ^2 value for the reduction in deviance attributable to the term and their approximate significance (*P*).

Parameter	Estimate	d.f.	χ^2	*P*
Fixed effects				
Country	–	3, 490	435	< 0.0001
Species	–	6, 4730	39.6	< 0.0001
Temperature	−0.001	1, 3441	< 0.01	0.99
Species × temperature	−0.42, 0.59	6, 5992	28.5	< 0.0001
Temperature^2	0.0036	1, 5109	0.61	0.44
Species × temperature^2	−0.0298, 0.0357	6, 6588	35.2	< 0.0001
Year	0.0013	1, 109	0.08	0.77
Year × species	−0.0095, 0.0123	1, 84.6	2.14	0.91
Random effects				
Site	0.277 ± 0.025			
Year	0.017 ± 0.004			
Residual	3.60 ± 0.06			

Table 2 Parameter estimates of generalized linear mixed models estimating the effect of latitude on productivity. For details see Table 1.

Parameter	Estimate	d.f.	χ^2	*P*
Fixed effects				
Country	–	3, 453	335	< 0.0001
Species	–	6, 6704	25.9	0.0004
Latitude	1.13	1, 1439	8.36	0.004
Species × latitude	0.22, 2.28	6, 6781	22.5	0.001
Latitude^2	−0.0112	1, 1443	8.73	0.003
Species × latitude^2	−0.023, −0.002	6, 6886	21.3	0.002
Year	1.80 ± 0.75	1, 7590	5.70	0.017
Year × latitude	−0.068	1, 7613	5.35	0.021
Year × latitude × species	−0.075, −0.064	6, 7528	6.07	0.42
Year × latitude^2	0.0007	1, 7633	5.02	0.025
Year × latitude^2 × species	0.0006, 0.0008	1, 7695	6.59	0.36
Random effects				
Site	0.259 ± 0.023			
Year	0.019 ± 0.004			
Residual	3.54 ± 0.06			

temperature anomalies by subtracting the mean temperature (over the period during which the site was operated) from the annual temperatures. We constructed a binomial GLMM with temperature anomaly (and its square) as the independent variables. We included site as a fixed effect as, in this case, we were interested in the differences in productivity relative to the site mean. As before, we included a species-specific intercept (country is subsumed within the site effects), an offset to account for missing visits and a residual random term (grouped by site) to account for any over-dispersion.

RESULTS

The proportion of juveniles in catches varied between species (ranging from a mean of 0.33 for reed and garden warblers to 0.66 for chiffchaff), but there was no consistent relationship between productivity and temperature over the range experienced at our sites (main effects of temperature were non-significant; Table 1). Three species did show increased productivity with warmer temperatures; however, willow warbler productivity decreased at warmer temperatures and three species showed little change over most of the temperature space they occupied (Figs 2a & S1).

Despite the species-specific responses to temperature, there was a consistent relationship among species between latitude and productivity (main effects significant; Table 2). Sites at intermediate latitudes tended to exhibit the highest proportion of juveniles in catches, as indicated by the significant quadratic term (Fig. 2b), although the latitude of sites having the highest productivity varied between species (significant interaction between species and latitude^2; Table 2). Productivity showed a tendency to increase in the warmer, more southerly, sites but only for the reed warbler was there a significant change in productivity in northern sites (Figs 3 & S2). These patterns remained after two extreme observations (for sedge and willow warblers; Fig. S2) were excluded (Table S2, Fig. S3).

There was a strong curvilinear response to site-specific temperature anomalies (significant squared terms; Table 3). Productivity (relative to the site-specific average) was increasingly reduced with greater deviation in the annual temperature from the site-specific average; significantly so for four species (blackcap, chiffchaff, reed warbler and whitethroat) and non-significantly for a further two (sedge warbler and garden warbler; Fig. 4). For three species (blackcap, reed warbler and sedge warbler) the maximum of this curve did not occur at the average temperature but above it, indicating that, on this measure at least, the occupied sites tended to be below the species thermal optimum.

DISCUSSION

These results demonstrate relationships between temperature and the number of juveniles produced each season that underpin strong latitudinal gradients in productivity across western Europe. Although these gradients differed between species, most

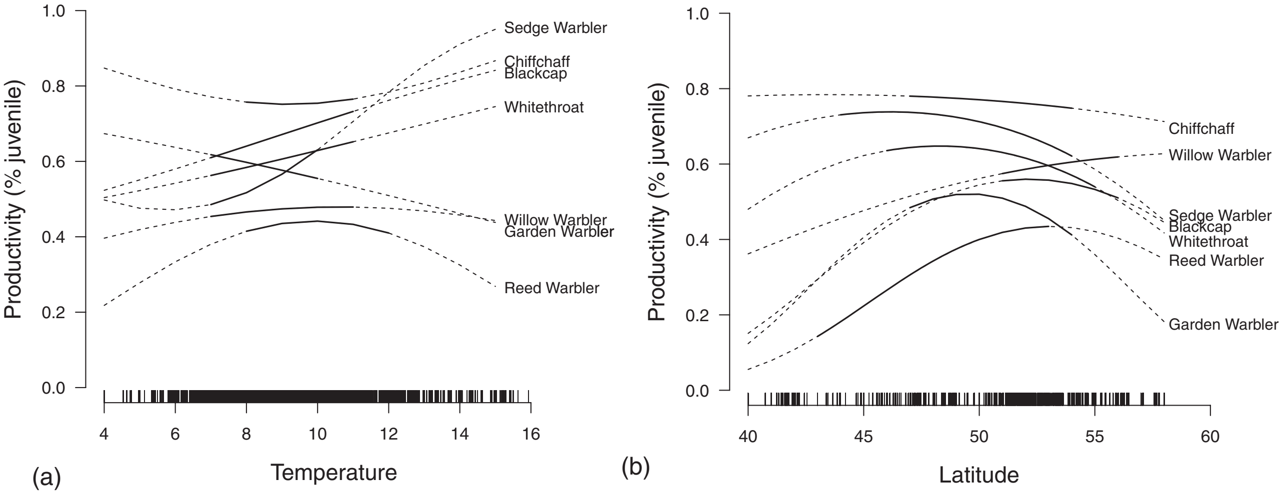

Figure 2 The relationship between productivity and (a) temperature and (b) latitude for seven migrant warbler species. Lines are predicted estimates of productivity for each species. The solid portion of each line indicates the range over which the central 90% of data occur for each species, the rug plots the incidence of sites.

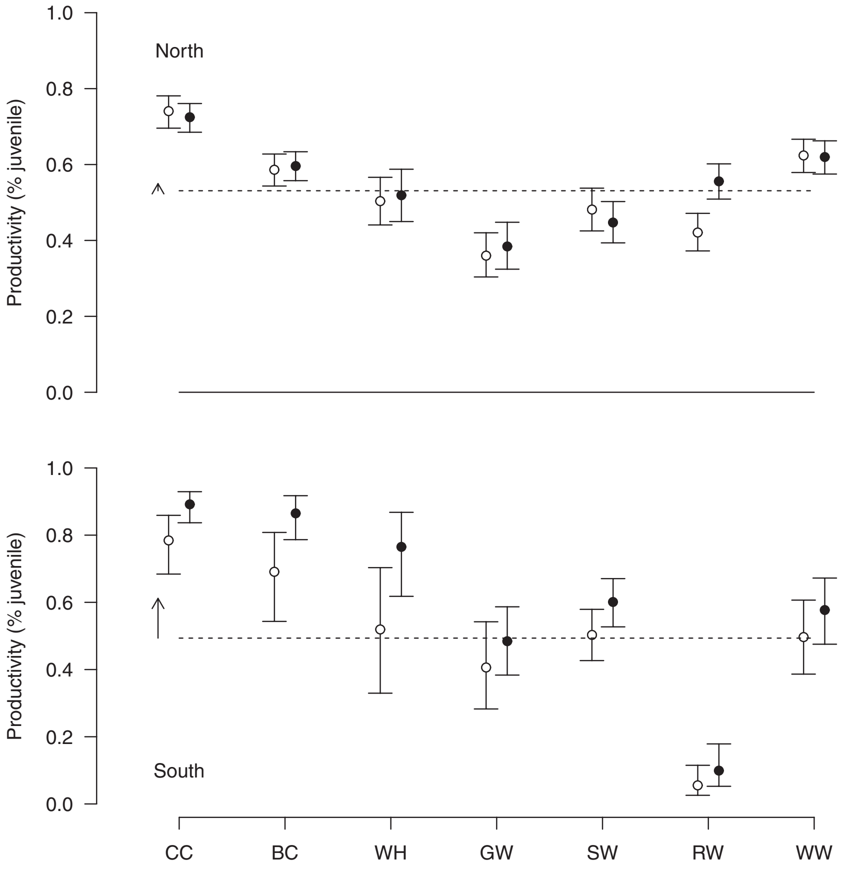

Figure 3 Fitted productivity in the first (open symbols) and last (closed symbols) years of the study at the northern (top) and southern (bottom) range margins; bars represent the 83% prediction interval (which overlap with *c.* 95% probability) and species are ordered by the latitude at which predicted peak productivity occurs. The dotted line indicates the mean productivity across all species in the first year and the arrow the change in this over the period of study. Species are: BC, blackcap; CC, chiffchaff; GW, garden warbler; RW, reed warbler; SW, sedge warbler; WH, whitethroat; WW, willow warbler.

exhibited a mid-latitude peak in productivity as predicted, with only the northerly breeding willow warbler having peak predicted productivity outside our study range. Previous studies of latitudinal variation in reproductive output have focused on clutch size (Sanz, 1997, 1998; Fargallo, 2004). We show that such curvilinear gradients persist when an integrative measure of reproductive output is used, i.e. one that incorporates nesting success, number of breeding attempts and survival during the immediate post-fledging period. In this group of annual migrants, survival is often regarded as the primary driver of annual variation in population size (Peach *et al.*, 1991; Baillie & Peach, 1992); however, our results suggest that spatial variation

Table 3 Parameter estimates of generalized linear mixed models estimating the effect of temperature anomaly on productivity. For details see Table 1.

Parameter	Estimate	d.f.	χ^2	*P*
Fixed effects				
Site	–	425, 7386	7216	< 0.0001
Species	–	6, 7386	2064	< 0.0001
Anomaly	0.022	1, 7386	2.33	0.13
Species × anomaly	–0.034, 0.096	6, 7386	12.9	0.045
Anomaly^2	–0.068	1, 7386	19.8	< 0.0001
Species × anomaly^2	–0.120, 0.020	6, 7386	14.9	0.021
Random effects				
Residual	3.83 ± 0.06			

in productivity may be a key determinant of spatial patterns of abundance and range limits. Indeed, the importance of breeding season conditions for the population status of these species more generally is being increasingly recognized (Morrison *et al.*, 2013; Ockendon *et al.*, 2013).

We cannot directly infer the mechanism by which spring temperature influences productivity, though it seems plausible that the availability of food is a likely mediating factor since it is known that spring temperatures influence insect abundance. For example, Smith *et al.* (2011) showed a close correlation between mean April/May temperature in Britain and peak caterpillar frass fall, a measure of resource abundance for woodland passerines. In this regard, it is notable that the two species most associated with wetlands (reed and sedge warbler) show an asymmetric response to temperature anomalies, with lower temperatures resulting in reduced productivity (Fig. 4). Primary productivity in reedbeds is thermally limited and lacks a strong seasonal peak, so current temperatures may be food limiting for birds in such habitats (McKee & Richards, 1996; Halupka *et al.*, 2008). Recent increases in reed warbler productivity in both the Netherlands (Kampichler & van der Jeugd, 2011) and the UK (Baillie *et al.*, 2012) may thus be explained by thermally induced increases in resource availability.

Given the widely observed poleward shift in distributions (e.g. Thomas & Lennon, 1999; Hickling *et al.*, 2006), we predicted increased productivity at northern latitudes as a result of higher temperatures; however, only one species (reed warbler) showed the predicted pattern. This suggests that, despite the observed relationships between productivity and temperature and variation in the population status of these species, there is not yet a clear link between warming and changes in productivity through time. Six species (four significantly) showed a degree of local adaptation with deviations away from the local mean temperature being associated with reductions in productivity in most species, indicating either that the mechanisms underpinning large-scale variation in productivity are not the same as those determining shorter-term fluctuations or that changes are restricted to the geographical vicinity of the northern range margin outside our study area. For three species (blackcap, sedge and reed warblers), highest productivity was reached at temperatures above the local mean, indicating that the majority of sites where these species occurred were below the species thermal optimum and thus potentially a precursor to a northwards range shift (for example, both blackcap and reed warbler are substantially increasing their breeding range within Britain; Balmer *et al.*, 2013). Thus, while short-term temporal variation in productivity may be directly related to temperature (Julliard *et al.*, 2004), spatial variation is probably determined more by the indirect effects of temperature on habitat quality and resource availability (Smith *et al.*, 2011; Ferger *et al.*, 2014). Our results suggest that the population changes and range shifts detected over a similar time-frame to our study (Jiguet *et al.*, 2010; Devictor *et al.*, 2012) are not underpinned by equivalent changes in productivity because local adaptation constrains species responses.

In the last couple of decades, populations towards the cool north of a species' range have been more likely to increase than those in the warmer south (Julliard *et al.*, 2004; Gregory *et al.*, 2009; Jiguet *et al.*, 2010). Significant uncertainty remains, however, about the likely impacts of climate change on species populations and distributions, and there is much more still to learn, particularly about the demographic mechanisms that drive such changes (Knudsen *et al.*, 2011). We have identified strong latitudinal gradients in productivity which may underpin large-scale abundance and distribution patterns. However, changes in these gradients do not appear to have responded to recent warming in the manner expected, at least among the species we studied, suggesting that relationships between temperature and productivity may be complex.

Although we considered only seven species, their responses are likely to be representative of a wider range of migratory species, since nearly half (23/53) of migratory European passerines belong to the Sylviidae, and many of the remainder (pipits, chats, flycatchers) are also small-bodied insectivores inhabiting a range of open scrub and wooded habitats. It has previously been suggested that differential northward shifts in isotherms have resulted in widespread declines in the populations of Palaearctic migrants, particularly those migrating longer distances (Jones & Cresswell, 2010). Our results, although based on a limited number of species, indicate that responses to climate change may not be universal, presumably at least in part because any such changes are also likely to interact with ongoing changes in land use which affect resource availability (Warren *et al.*, 2001; Barbet-Massin *et al.*, 2012), and because some species may be able to 'adapt' by exploiting new resources (e.g. Berthold, 1995). Characterization of demographic, rather than population, responses to climate will be required to help understand these differences.

It is likely that different mechanisms underlie large-scale patterns and short-term fluctuations; understanding such relationships will be important in assessing the potential for effective climate change adaptation (Pearce-Higgins & Gill, 2010). Clearly, the existence of national and continent-wide monitoring schemes that not only record abundance (Gregory *et al.*, 2009) but also productivity and survival, such as CE ringing schemes (e.g. Saracco *et al.*, 2008; Robinson *et al.*, 2009), provide

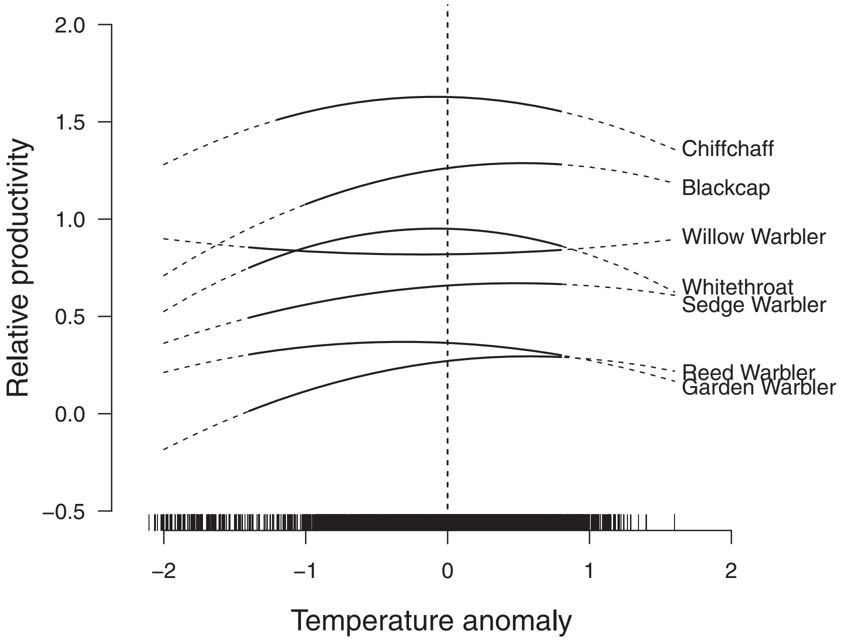

Figure 4 The relationship between productivity and temperature anomaly for seven migrant warbler species. Lines are predicted estimates of productivity (on the logit-scale) for each species; the dashed vertical line represents the site-specific mean temperature. The solid portion of each line indicates the range over which the central 90% of data occur for each species and the rug plot shows the incidence of sites.

an important tool for understanding such processes, a necessary prerequisite if future changes in biodiversity are to be assessed with confidence.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 Relationship between temperature and productivity for seven warbler species.

Figure S2 Relationship between latitude and productivity for seven warbler species.

Figure S3 Relationship between latitude and productivity for seven warbler species, excluding outlying points.

Table S1 Summary statistics for the number of sites and birds caught in each country.

Table S2 Parameter estimates of generalized linear mixed models estimating the effect of latitude on productivity, excluding outlying points.

BIOSKETCH

Sarah Eglington was a research ecologist at the BTO with a particular interest in lowland waders. The EuroCES initiative is a collaboration of national ringing schemes, through the umbrella of Euring (http://www.euring.org/research/ces_in_europe), aimed at monitoring the demography of birds across Europe. It relies on the enthusiasm and dedication of thousands of ringers.

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