

Drivers of climate change impacts on bird communities

James W. Pearce-Higgins^{1*}, Sarah M. Eglinton¹, Blaise Martay¹ and Dan E. Chamberlain²

¹British Trust for Ornithology, The Nunnery Thetford, Norfolk IP24 2PU, UK; and ²Dipartimento di Scienze della Vita e Biologia dei Sistemi, Università di Torino, Via Accademia Albertina 13, 10123 Torino, Italy

Summary

1. Climate change is reported to have caused widespread changes to species' populations and ecological communities. Warming has been associated with population declines in long-distance migrants and habitat specialists, and increases in southerly distributed species. However, the specific climatic drivers behind these changes remain undescribed.
2. We analysed annual fluctuations in the abundance of 59 breeding bird species in England over 45 years to test the effect of monthly temperature and precipitation means upon population trends.
3. Strong positive correlations between population growth and both winter and breeding season temperature were identified for resident and short-distance migrants. Lagged correlations between population growth and summer temperature and precipitation identified for the first time a widespread negative impact of hot, dry summer weather. Resident populations appeared to increase following wet autumns. Populations of long-distance migrants were negatively affected by May temperature, consistent with a potential negative effect of phenological mismatch upon breeding success. There was evidence for some nonlinear relationships between monthly weather variables and population growth.
4. Habitat specialists and cold-associated species showed consistently more negative effects of higher temperatures than habitat generalists and southerly distributed species associated with warm temperatures. Results suggest that previously reported changes in community composition represent the accumulated effects of spring and summer warming.
5. Long-term population trends were more significantly correlated with species' sensitivity to temperature than precipitation, suggesting that warming has had a greater impact on population trends than changes in precipitation. Months where there had been the greatest warming were the most influential drivers of long-term change. There was also evidence that species with the greatest sensitivity to extremes of precipitation have tended to decline.
6. Our results provide novel insights about the impact of climate change on bird communities. Significant lagged effects highlight the potential for altered species' interactions to drive observed climate change impacts, although some community changes may have been driven by more immediate responses to warming. In England, resident and short-distance migrant populations have increased in response to climate change, but potentially at the expense of long-distance migrants, habitat specialists and cold-associated species.

Key-words: birds, climate change, community specialization index, community temperature index, migrants, population trends, precipitation, temperature

Introduction

Climate change is projected to have a significant effect upon the future rate of biodiversity loss, the first consequences of

which have already been detected (e.g. Parmesan & Yohe 2003; Thomas *et al.* 2004). There is mounting evidence for widespread changes to the distribution of species as a result of warming, with ranges spreading polewards and upwards (Hickling *et al.* 2006; Chen *et al.* 2011). Impacts of climate change have been detected on individual populations (e.g. Conrad, Woiwod & Perry 2002; Both *et al.* 2006; Foden

*Correspondence author. E-mail: james.pearce-higgins@bto.org

et al. 2007; Wake 2007), although few studies have demonstrated increased risk of extinction in response to climate change (Cahill *et al.* 2013). Some of the strongest signals of climate change have been apparent at the community level (Morecroft & Speakman 2013), indicative of differential impacts of climate change on populations of different species. These may be used to infer potential variation in the sensitivity of different populations and species to future climate change and therefore are worthy of further investigation.

Many of these studies have been conducted on well-monitored bird populations, where three main trends in community change have been described. First, long-distance migrants have declined more than resident or short-distance migrant species (Holmes & Sherry 2001; Sander-son *et al.* 2006; Yamaura *et al.* 2009). This has been attributed to a range of factors, but there is evidence that climate change may have driven at least some of this variation. For example, long-distance migrants now arrive later relative to spring temperatures on the breeding grounds than they used to, which may have population consequences (Both & Visser 2001; Møller, Rubolini & Lehikoinen 2008; Saino *et al.* 2011; although see Johansson & Jonzén 2012), whilst their populations may also be affected by climate change on the wintering grounds (Newson *et al.* 2009a). Variation in population trends have been attributed to differences in wintering (Jones & Creswell 2010; Thaxter *et al.* 2010), breeding location (Ockendon *et al.* 2012; Morrison *et al.* 2013) and habitat (Both *et al.* 2010), each of which may be interpreted in relation to potential effects of climate change, as well as other factors.

Secondly, communities have become increasingly similar to each other (homogenized) as a result of populations of generalist species increasing relative to those of habitat specialists (Devictor *et al.* 2008a; Davey *et al.* 2012; Le Viol *et al.* 2012), findings that are apparent across a wide range of taxa (Spear & Chown 2008; Winter *et al.* 2009). Whilst this may be attributable to a range of drivers associated with land-use and management change (e.g. Devictor *et al.* 2008a; Doxa *et al.* 2012), there is increasing evidence that generalist species with a broader niche breadth may respond more positively to warming than specialists (Davey *et al.* 2012, 2013).

Thirdly, variation in population trends between species at individual locations has been linked to the spatial association of each species to temperature. Populations associated with warmer temperatures (which tend to have southerly distributions) have increased in abundance relative to more northerly distributed species associated with cooler temperatures (Devictor *et al.* 2008b; Jiguet *et al.* 2010; Lindström *et al.* 2013). This has led to detectable changes in communities of both birds and butterflies across Europe, as measured by the community temperature index (Devictor *et al.* 2012a), although some of the changes observed may also be linked to land-use change (Clavero, Villero & Brotons 2011; Barnagaud *et al.* 2012).

Combined, there is good evidence that populations of long-distance migrants, specialists and cold-associated bird species have declined in Europe (Sanderson *et al.* 2006; Devictor *et al.* 2012a; Le Viol *et al.* 2012). However, there is a lack of understanding about the extent to which such changes may be directly attributable to climate change in Europe, or precisely which components of climate change may be responsible. Given differential patterns of warming and precipitation change in different seasons of the year (see Fig. 5), there is a clear need to understand more precisely to which components of climate change species' populations are responding, the likely ecological mechanisms driving these population responses, and how these mechanisms vary between species.

To do this, we analysed long-term national population time-series data of birds in England, in relation to variation in both temperature and precipitation measures through the year. Importantly, this is an avifauna where both distribution and community changes have previously been attributed to warming (e.g. Thomas & Lennon 1999; Davey *et al.* 2012; Devictor *et al.* 2012a). Specifically, we examined the extent to which the observed community changes of declining long-distance migrants, community homogenization and increasing community temperature index may be driven by variation in species' sensitivity to the weather variables. We did this by testing whether species' population responses to temperature and precipitation varied with respect to migratory strategy, habitat specialization and thermal association. In order to identify the seasons where long-term climate change is most likely to have driven recent changes in bird populations, we then regressed long-term population trend against species' sensitivity to temperature and precipitation in each month.

Materials and methods

DATA

Data from the British Trust for Ornithology's (BTO) Common Bird Census (CBC) and the BTO/Joint Nature Conservation Committee/Royal Society for the Protection of Birds, Breeding Bird Survey (BBS) were used to generate annual indices of population change for England from 1966 to 2011. The CBC provided data from 1966 until 2000. Within the CBC, bird territories were mapped from observations made on seven to ten visits per year to self-selected sites (Marchant *et al.* 1990). Starting in 1994, the BBS involves two parallel 1-km line-transects in 1-km squares being surveyed during two early morning surveys between early April and late June (Gregory & Baillie 1998; Risely *et al.* 2012). These two methods produce differently structured data at the site level, making combined analysis at this resolution across the entire time period very difficult. However, at the national level, despite the switch in methodology, the data from the two surveys can be combined to produce joint trends for most species using a loglinear model with a Poisson error distribution (Freeman *et al.* 2007). We therefore analysed data for 59 species (listed in Appendix S1, Sup-

porting information) with comparable trends for England from both CBC and BBS that can be used to generate robust annual estimates of abundance using well-established analytical protocols developed specifically for this purpose (e.g. Gregory *et al.* 2005; Newson *et al.* 2009b). Trends were fixed to one in the first year (1966) and indicate relative population changes across species, so that each species contributes equally to the analysis.

Variation in the weather was described by monthly averages of temperature and precipitation for England (<http://www.metoffice.gov.uk/climate/uk/datasets/>). For the purposes of analyses, we focussed on mean monthly temperature (°C) and total monthly precipitation (mm), although equivalent patterns in the data for temperature were also produced using mean minimum and mean maximum monthly temperatures (Appendix S2, Supporting information).

Given the strong spatial autocorrelations in weather variables and our use of national summaries of bird populations, this study describes large-scale population responses to large-scale climatic variation. We do not consider how variation in the conditions experienced at individual sites (e.g. Newson *et al.* 2014), or local adaptation, might influence specific population responses.

STATISTICAL ANALYSIS

Annual variation in the population (n) growth rate of each species from year t to year $t+1$ ($\ln(n_{t+1}/n_t)$) was modelled as a function of each of the monthly weather variables, using a single model combining data from all species. Count (n_{t+1}) was modelled using a Poisson error distribution and a log link function, with $\ln(n_t)$ specified as an offset in order to generate the log-ratio of change. Count in year t (n_t) was also included as a predictor variable to account for potential density dependence and survey error (Freckleton *et al.* 2006). Thus populations at carrying capacity are less likely to increase further in response to warmer temperatures than those starting at a low level. Similarly, populations at high levels are more likely to 'crash' in response to severe weather events, whilst in those at a low level, density dependence may lead to compensatory increases in other demographic parameters, reducing the impact of any such crash (e.g. Siriwardena *et al.* 2000). Species identity was specified as a random effect, and a first-order autoregressive function accounted for potential temporal autocorrelation in the data. The Kenward–Rogers correction was applied to ensure the correct estimation of the degrees of freedom. This model was run for temperature and rainfall separately.

We considered also correcting for relatedness amongst species in our analysis, to reduce the possibility of type I errors arising from phylogenetic autocorrelation. The inclusion of family identity as an additional random effect accounted for a negligible amount of covariance (mean across all models = $2.98E^{-20} \pm 5.41E^{-21}$) compared to that attributed to species (mean across all models = $0.011 \pm 7.99E^{-5}$). To further examine similarity of response between species as a function of relatedness, we repeated all analysis, but with species included as a fixed effect instead of a random effect, and then conducted a Moran's I test on the species effects in relation to their phylogenetic similarity. In only three cases out of 54 was this test significant, models of the interaction between species temperature index (STI) and temperature in April _{$t-1$} ($P = 0.022$), July _{$t-1$} ($P = 0.025$) and April _{t} ($P = 0.049$). Given this lack of evidence for species population responses to temperature and precipitation being phylogenetically

conserved, and given the statistical difficulties of accounting for phylogenetic independence within a single model that includes multiple observations from the same species that are temporally autocorrelated, we have not formally corrected for relatedness (see Kunin 2008).

For 11% of tests, the inclusion of the autoregressive function led to a failure of model convergence, in which case the function was deleted. To assess the extent to which this may have reduced the comparability of these models with the remainder, we repeated the analysis without the autoregressive function for all models and correlated the parameter estimates and standard errors from the two models for all cases where both were estimated. Parameter estimates and standard errors were virtually identical and highly correlated ($r > 0.993$ and 0.986 respectively), demonstrating that the model outputs were comparable. Nevertheless, we highlight these cases to the reader in case they are more susceptible to type I error.

Whilst we used the mixed-model framework to estimate mean responses to each weather variable across all species, it was necessary to account for species-specific variation in the strength of density dependence. Each model therefore included the species $\times n_t$ interaction. The final model was specified as follows, with w as the weather variable of interest and a , b_0 and b_1 as modelled estimates of the intercept, species-specific effect of density dependence and mean weather effect size across all species, respectively.

$$\ln\left(\frac{n_{t+1}}{n_t}\right) = a + b_0 n_t + b_1 w + \varepsilon$$

We tested the effect of monthly weather variables from April in the year before the first survey (April _{$t-1$}) to June at the end of the second survey (June _{$t+1$}); a spread of 2 years plus 3 months of the second survey that allowed for some investigation of potential lagged effects of weather variables upon populations which have been shown to be important for some species (e.g. Pearce-Higgins *et al.* 2010), without over-inflating the number of variables considered (Fig. 1). These models provide a description of the mean sensitivity of the bird community as a whole to weather at different times of the year, and although not the main focus of this study, are reported in Appendix S3 (Supporting information), alongside additional models that test for potential nonlinear relationships between weather variables and population growth through the inclusion of an additional term $b_2 w^2$ in the model.

Factors affecting variation in the sensitivity of different species

The effect of these weather variables is likely to differ between species in a manner that can account for the observed changes in community composition. The focus of this study was to test the extent to which species-specific responses to the weather varied with migratory strategy, habitat specialization (niche breadth) and thermal association. The pattern of these results indicates the likely processes underpinning each of the observed community responses to climate change. Species were classified as resident, short- and long-distance migrants from Thaxter *et al.* (2010). Niche breadth was measured using the species specialization index (SSI), calculated from the coefficient of variation of species' density across habitats (Davey *et al.* 2012). Thermal

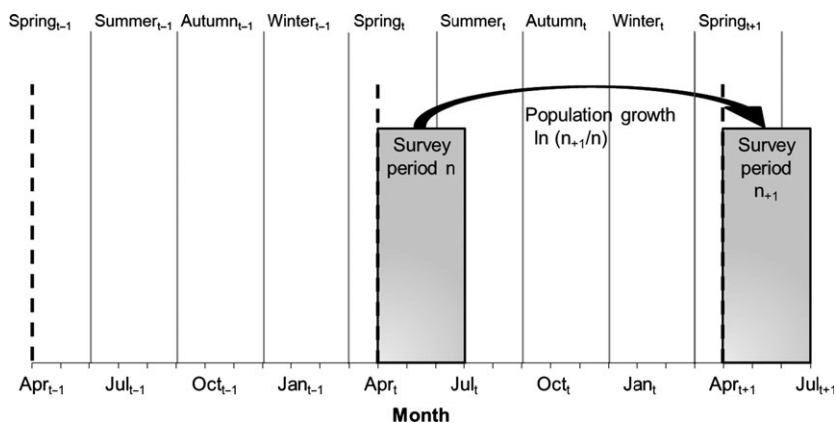


Fig. 1. Schematic illustration of the months and seasons over which weather data were collated (only every third month is shown for reasons of space) against the survey periods used to generate the population growth data. Vertical dashed lines indicate census years.

association was summarized using the STI, calculated as the mean temperature across each species European breeding range (from Devictor *et al.* 2012a), which shows the extent to which species are associated with warmer (high STI values) or colder (low values) climates across their European range. This test was achieved by separately adding to each model the trait variable (T) plus its interaction with the relevant weather variable as follows.

$$\ln\left(\frac{n_{t+1}}{n_t}\right) = a + b_0sn_t + b_1w + b_2T + b_3Tw + \varepsilon$$

The three traits were independent (correlation between SSI and STI values across species, $r = -0.20$, $n = 59$, $P = 0.11$; relationship between migratory strategy and both STI, $F_{2,55} = 0.82$, $P = 0.44$, and SSI, $F_{2,55} = 1.08$, $P = 0.35$).

Variation in population trend with species' sensitivity to weather variables

In order to assess the extent to which species population trends may be related to their sensitivity to weather variables, and to directional shifts in those weather variables through time (climatic change), we estimated linear national population trends from the 45 years covered (1966–2011), from the slope of n_t against year. The interaction of this trend with species-specific responses to weather in each month was then tested, in the same way as described for other ecological traits above. For example, a positive interaction between population trend and temperature in a particular month would show that species with a positive relationship between temperature and population growth in that month have generally shown a long-term increase. Similarly, species for which temperature had a negative impact on population growth will have tended to decline in abundance. In other words, we are testing the extent to which the effect of weather upon population fluctuations results in long-term population trends as a result of climate change.

All analyses were undertaken using PROC GLIMMIX in SAS 9.2 (Littell *et al.* 1996). Given the number of tests performed, we applied Bonferroni correction to highlight those which are most likely to be statistically significant and meaningful ($P < 0.00185$), and focus primarily on those in the discussion of the results, although record all of the weaker relationships for completeness. All parameter estimates, standard errors and significance values

of relationships shown graphically are presented to the reader in Appendix S4 (Supporting information).

Results

FACTORS AFFECTING VARIATION IN THE SENSITIVITY OF DIFFERENT SPECIES

Monthly variation in the mean temperature effect upon populations was generally similar between residents and short-distance migrants (Fig. 2a,b). Significant interactions between migratory strategy and winter temperature were apparent in February_{t-1} ($P = 0.0021$), December_t ($P = 0.0065$) and January_t ($P = 0.0005$), although only the latter was below the Bonferroni threshold. These interactions are indicative of a strong positive effect of winter temperature upon populations of resident species counted in the following spring, the significance of which exceeded the Bonferroni threshold for residents for December_t, January_t and February_t (Appendix S4). The same relationships were apparent, but weaker, in short-distance migrants, and not apparent in long-distance migrants (Fig. 2c). The strongest interaction between temperature and migratory strategy was with May_t temperature ($P = 0.0003$), which was positively related to population growth in resident species (0.00915 ± 0.0035), but negatively in long-distance migrants (-0.0203 ± 0.0066), although neither effect achieved Bonferroni significance alone. There were significantly different responses to June_{t+1} temperature between long-distance migrants (positive effect) and short-distance migrants (negative effect), neither of which achieved Bonferroni significance in isolation. Across species, in addition to these spring and winter temperature effects, there was also evidence of a strong negative effect of summer temperature with a one-year lag (July_{t-1} and August_{t-1}) upon population growth (Appendix S3), which was below the Bonferroni significance level for both short-distance and long-distance migrants for July_{t-1}. Variation in the response of populations to precipitation did not differ strongly with respect to migratory strategy (Fig. 2d–f) and broadly reflected the general patterns across species of positive effects of wet spring

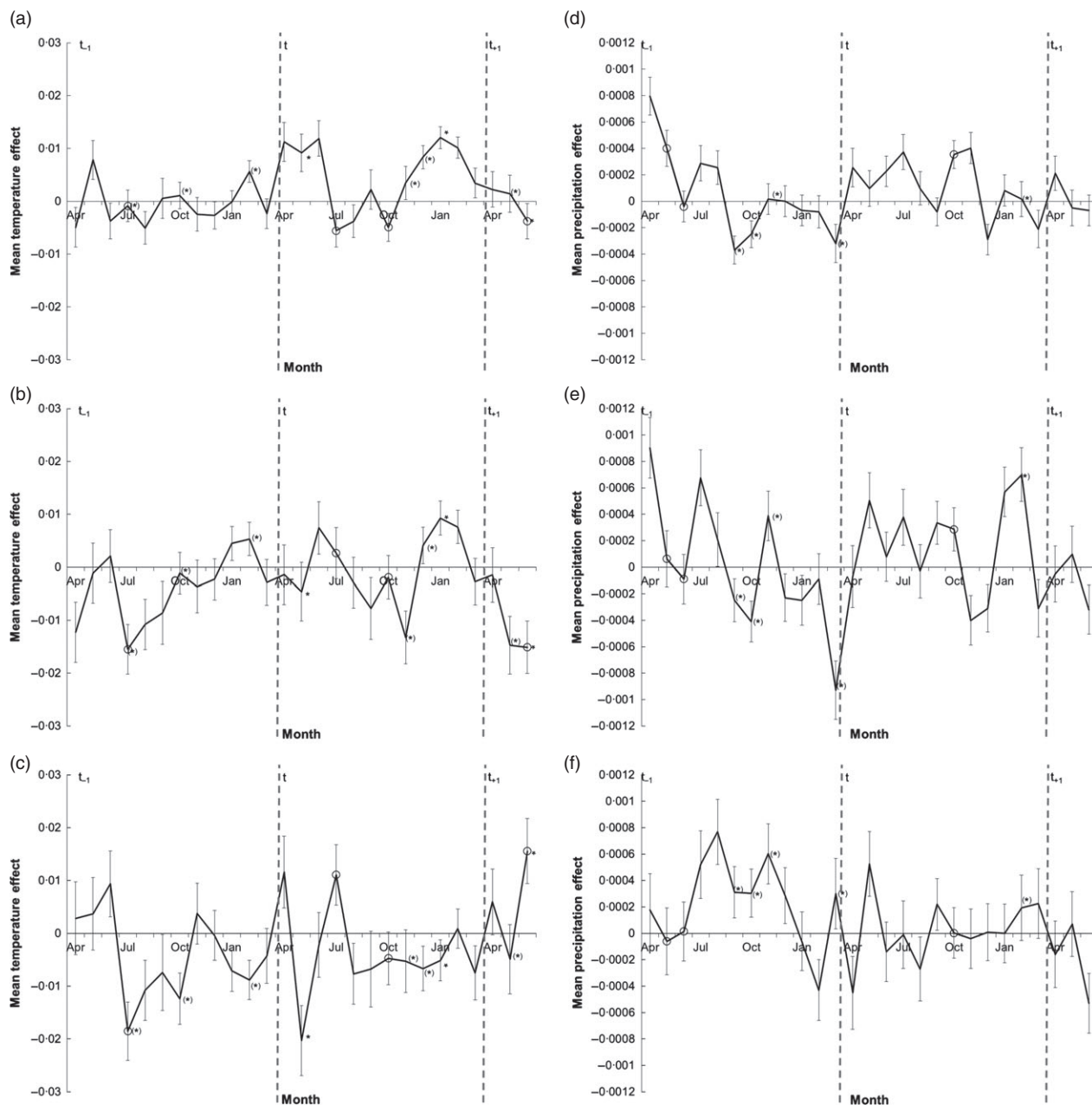


Fig. 2. Monthly variation in the mean effect of temperature (a–c) and precipitation (d–f) upon the population growth of bird species plotted separately for resident (a, d), short-distance migrants (b, e) and long-distance migrants (c, f). Statistically significant ($P < 0.05$) interactions between weather variable effect and migratory status are indicated by an asterisk, with those outside of parenthesis achieving the Bonferroni threshold for significance. The significance of individual effects is given in Appendix S4. Estimates from models in which the autoregressive function failed to converge are circled as they may be more prone to type I error.

weather in year t_{-1} (Appendix S3), particularly for resident and short-distance migrants in April $_t$, and of precipitation in July and August in year $_{t-1}$ upon population growth. Precipitation in October $_t$ and November $_t$ also had a strong positive effect on resident population growth (Appendices S3 and S4).

The interaction between mean monthly temperature and SSI was statistically significant ($P < 0.05$) for eight months, of which three remained significant after applying the Bonferroni correction (Fig. 3a). All of these significant

effects, and the results for the majority of other months, were for negative interactions between temperature and SSI, indicating that habitat specialists experience greater negative impacts of warming than generalists. Although there was some evidence that the previously detected lagged negative effects of summer warming were more severe for specialists (July $_{t-1}$ $P = 0.003$, August $_{t-1}$ $P = 0.019$), the strongest contrasts were with respect to spring temperature (March $_{t-1}$ $P = 0.0007$, April $_t$ $P = 0.047$, March $_t$ $P = 0.0002$, May $_{t+1}$ $P = 0.0006$).

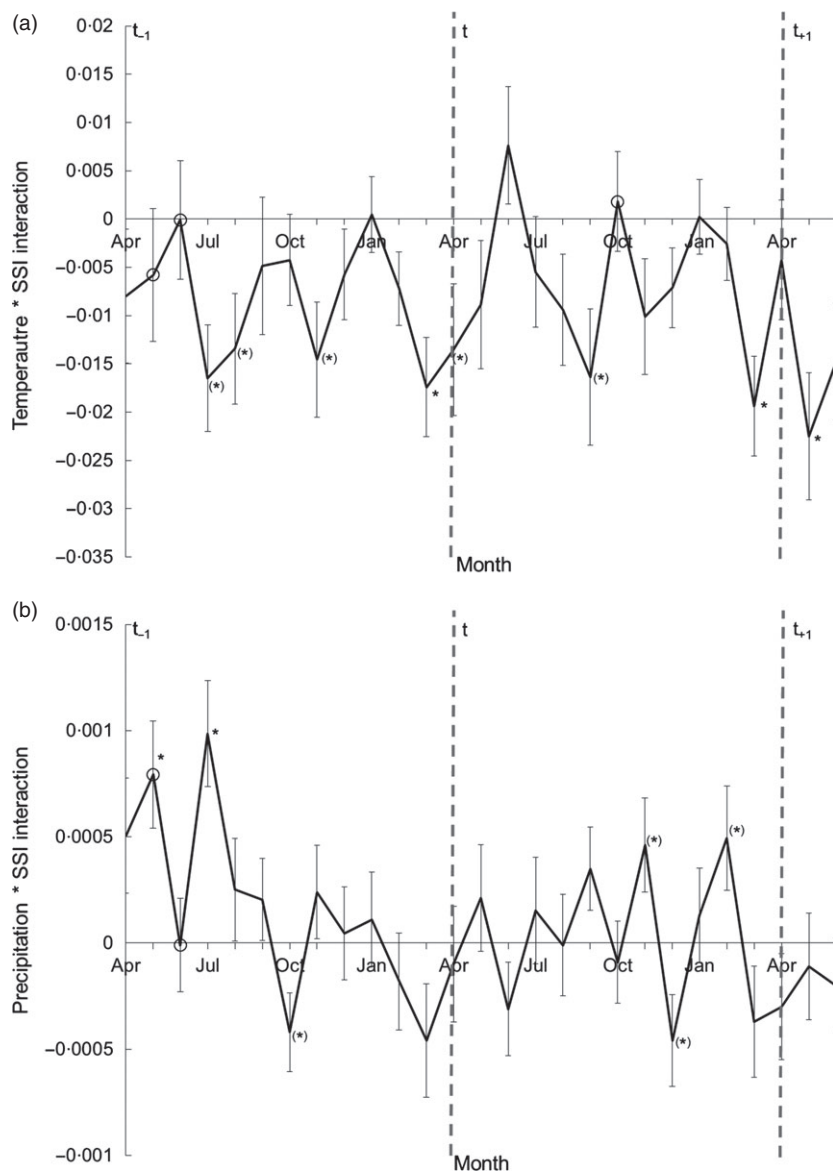


Fig. 3. Monthly variation in the mean interaction (\pm SE) between temperature (a) or precipitation (b) and niche breadth (measured by the species specialization index; SSI), upon the population growth of bird species. A negative interaction means that weather variables had a more negative, or less positive, impact on specialist than generalist species. Statistically significant interactions ($P < 0.05$) are indicated by an asterisk, with those outside of parenthesis achieving the Bonferroni threshold for significance. Estimates from models in which the autoregressive function failed to converge are circled as they may be more prone to type I error.

Warmer spring weather tended to increase populations of generalists relative to specialists, both with and without a time-lag. With respect to monthly precipitation, correlations between population growth and the interaction with SSI were significant for 6 months (Fig. 3b), of which those with May_{t-1} ($P = 0.0006$) and $July_{t-1}$ ($P < 0.0001$) precipitation remained significant after applying the Bonferroni correction. The latter re-enforces the suggestion that the negative effects of hot, dry summer weather most strongly affect specialists.

The effect of STI on population responses to temperature was largely positive, such that species with a high STI were more likely to have more positive relationships between temperature and population growth (Fig. 4a). Thus, as expected, the population change of species associated with warm climates was positively correlated with warmer temperatures. Thirteen of the interactions were significant ($P < 0.05$), including five which remained after

applying the Bonferroni correction. All of these related to spring or early summer temperature ($April_{t-1}$ $P < 0.0001$, $April_t$ $P = 0.0002$, $March_t$ $P \leq 0.0001$, May_{t+1} $P \leq 0.0001$, $June_{t+1}$ $P \leq 0.0001$) and indicate that a greater number of individuals from species with a high STI were recorded both in and following warm breeding seasons. Ten of the interactions between STI and precipitation also reached significance ($P < 0.05$), with negative correlations with $April_{t-1}$ ($P < 0.0001$), May_t ($P < 0.0001$) and $September_t$ ($P < 0.0001$), and a positive correlation with $March_{t-1}$ ($P < 0.0001$) remaining significant after applying the Bonferroni correction (Fig. 4b).

VARIATION IN POPULATION TREND WITH SPECIES' SENSITIVITY TO WEATHER VARIABLES

There were strong and largely positive correlations between species' sensitivity to temperature and population

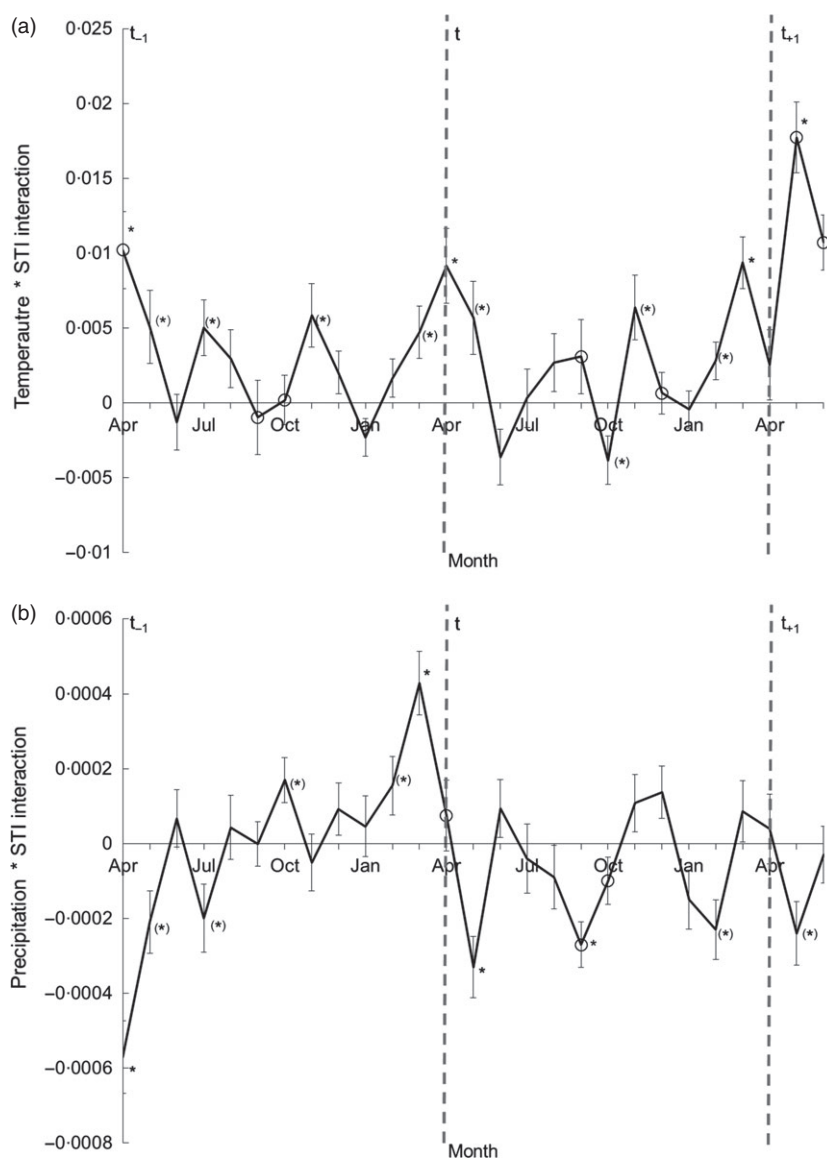


Fig. 4. Monthly variation in the mean interaction (\pm SE) between temperature (a) or precipitation (b) and thermal association (measured by the species temperature index; STI), upon the population growth of bird species. A negative interaction means that weather variables had a more negative, or less positive, impact on warm-associated than cold-associated species. Statistically significant interactions ($P < 0.05$) are indicated by an asterisk, with those outside of parenthesis achieving the Bonferroni threshold for significance. Estimates from models in which the autoregressive function failed to converge are circled as they may be more prone to type I error.

trend (Fig. 5a). A total of 16 of 27 relationships were significantly positive, and a further two negative, whilst 11 positive interactions remained significant after Bonferroni correction. The most consistent positive relationships occurred in spring (April $_{t-1}$, March $_{t-1}$ to May $_t$ and March $_t$ to June $_{t+1}$), although positive effects of summer (July $_{t-1}$ and to a lesser extent August $_{t-1}$), autumn (November $_{t-1}$, November $_t$) and late winter (February $_t$) temperature upon population growth were also apparent. The months where there was the strongest interaction between species' sensitivity to temperature and population trend were not those where temperature appeared to have the strongest mean impact across species (correlation between y-axes of Figs S3ai in Appendix S3 and 5a; $r = -0.20$, $P = 0.31$), but were those where the amount of warming had been greatest (correlation between y-axis and z-axis of Fig. 5a; $r = 0.65$, $P = 0.00024$).

Species sensitivity to precipitation was correlated with population trend across 11 of the months covered,

although for only two of these (April $_{t-1}$ and March $_{t-1}$) did these achieve Bonferroni-corrected significance. Unlike temperature, there was no correlation between the trend in precipitation and the interaction between population growth and species' sensitivity to precipitation ($r = 0.14$, $P = 0.49$). Instead, mean species' sensitivity to precipitation in that month (Fig. S3aai in Appendix S3) was negatively correlated with the relationship between precipitation sensitivity and long-term trend ($r = -0.66$, $P = 0.00017$). This indicates that in months where species responses to precipitation were largely positive, species with the most positive relationship between precipitation and population growth tended to decline. Similarly, in months where precipitation had largely negative effects upon population growth, species with the most negative relationship between precipitation and population growth tended to decline. In other words, species most sensitive to precipitation extremes were those with the most negative population trends.

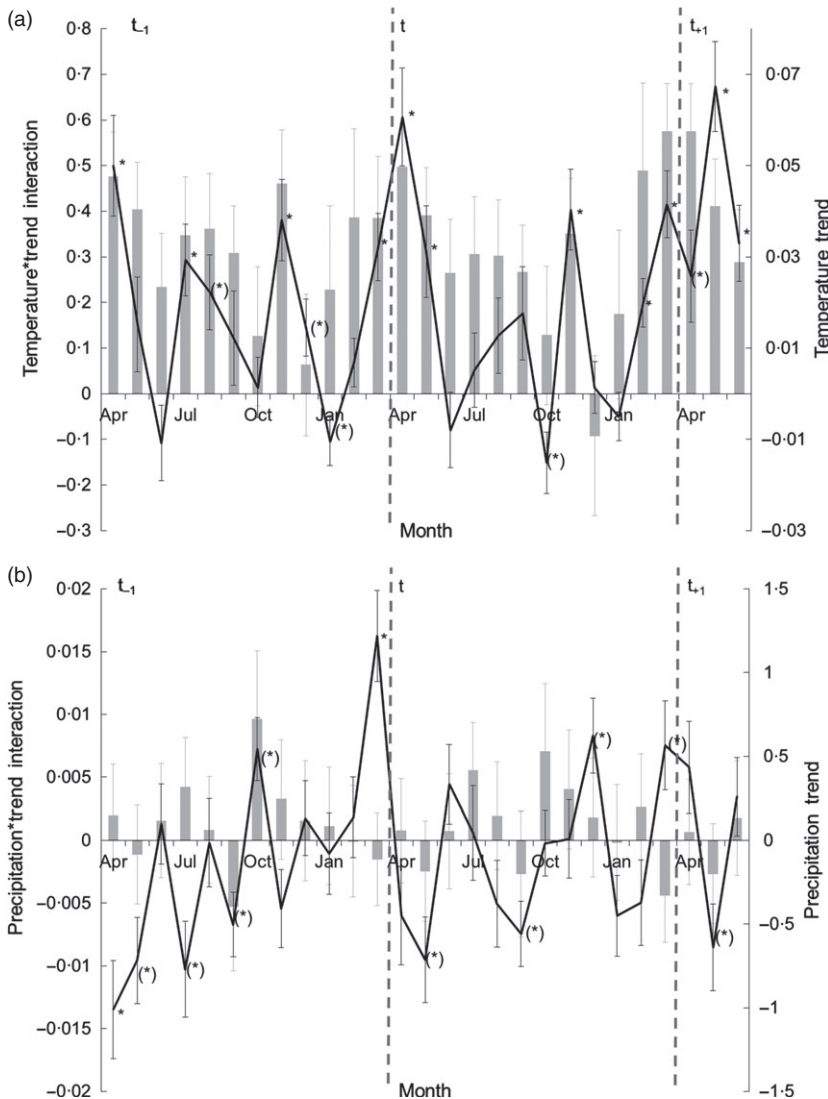


Fig. 5. Monthly variation in the interaction between the relationship between weather variables and population growth and 45-year population trends (solid line). Statistically significant interactions ($P < 0.05$) are indicated by an asterisk, with those outside of parenthesis achieving the Bonferroni threshold for significance. The temperature*trend interaction for May_{t+1} is from a model in which the autoregressive function failed to converge and may be more prone to type I error. These are overlaid above the long-term trend in weather variables (z -axis) for each month over the same period (grey bars). Values vary slightly for the same month, depending on which year they refer to. Error bars give standard errors.

Discussion

We have presented important evidence identifying the key periods of the year in which bird populations in England are affected by the weather, and how climate change may have driven recent changes in bird communities.

First, three main periods of sensitivity were apparent across species: the breeding season (particularly June_t), winter (December_t to February_t) and summer (July_{t-1} and August_{t-1}), although the importance of different months varied between species groups. Positive relationships between winter temperature and population growth of resident and short-distance migrants reflect negative effects of cold winter weather on survival rates of many species, from small passerines, such as winter wren *Troglodytes troglodytes* and treecreeper *Certhia familiaris* (Peach, du Feu & McMeeking 1995; Robinson, Baillie & Crick 2007), to waders such as northern lapwing *Vanellus vanellus* and Eurasian golden plover *Pluvialis apricaria* (Peach, Thompson & Coulson 1994; Piersma *et al.* 2005). Although for individual species, the duration of snow

cover or the number of frost days may provide better predictors of survival or population change (e.g. Greenwood & Baillie 1991; Robinson, Baillie & Crick 2007), our results suggest that at the large scale, cold winters have a consistent negative impact upon resident and short-distance migrant breeding bird populations in England. Unsurprisingly, populations of long-distance migrants were unaffected by winter temperature during year_t, but instead are strongly correlated with rainfall on their wintering grounds (Peach, Baillie & Underhill 1991; Newson *et al.* 2009a; Pearce-Higgins & Green 2014).

Positive effects of June breeding season temperature are probably mediated through increased invertebrate food abundance, reduced thermoregulatory requirements and increased foraging time (Pearce-Higgins & Green 2014) associated with warm weather. These were most apparent in resident species, with strong relationships close to the Bonferroni threshold apparent also in April_t and May_t. The strong significant negative effect of May_t temperature on long-distance migrant population trends, in contrast to the positive effect on resident species, accounts for the less

positive effect of May_{*t*} temperature overall on bird populations (Fig. S3ai in Appendix S3). This contrast is consistent with the proposed vulnerability of long-distance migrants to climate change on the breeding grounds, as a result of phenological mismatch. Late arriving long-distance migrants that have failed to advance their arrival time have tended to decline in abundance, particularly in seasonal habitats (Møller, Rubolini & Lehikoinen 2008; Saino *et al.* 2011; Both *et al.* 2010). Although the empirical evidence in support of detrimental impacts of mismatches on migrant populations in the UK is so far weak (reviewed in Pearce-Higgins & Green 2014), we would nevertheless expect May temperature to have positive impacts on resident species likely to be feeding chicks, but a negative impact on long-distance migrants likely to be incubating their eggs at this time, and therefore unable to further adjust their breeding phenology to compensate for accelerated environmental conditions.

Detrimental impacts of hot, dry summers on bird populations, were apparent, but appeared to operate with a 1-year lag. Thus, such conditions in year_{*t-1*} will result in a population decline, not from year_{*t-1*} to year_{*t*}, but between year_{*t*} and year_{*t+1*}. This is the effect previously identified for some upland birds as a result of negative impacts of summer temperature upon their invertebrate prey (Pearce-Higgins *et al.* 2010; Fletcher *et al.* 2013) and appears greatest in species that prey upon subsurface invertebrates whose larvae are vulnerable to desiccation, such as Diptera, and invertebrates that become less accessible in dry weather, such as Lumbricidae (Pearce-Higgins 2010; Carroll *et al.* 2011). Our results suggest that lagged negative impacts of hot, dry summer weather may affect more than just upland birds and may be ecologically more important than more direct effects of summer drought that appear to affect post-fledging survival of thrushes (Robinson *et al.* 2004; Robinson, Baillie & King 2012). These conclusions emphasize the importance of research to identify the precise mechanisms that underpin these lagged effects, particularly as it is likely to be through such lagged impacts affecting ecological interactions that climate change may have the greatest impact on species' extinction risk (Cahill *et al.* 2013; Ockendon *et al.* 2014). The positive lagged relationship between precipitation in April_{*t-1*} and population growth is less clearly related to a specific mechanism, but may also occur through altered trophic interactions, such as changes in plant growth. The mechanisms underlying the positive effect of autumn, precipitation upon population growth, particularly apparent in October and November for resident species, were also unclear, but may again occur through effects on other species, such as by influencing prey availability during the winter.

Davey *et al.* (2012) suggested for Great Britain that increasing temperatures have resulted in a reduction in community specialization, a finding subsequently replicated in Sweden (Davey *et al.* 2013). Our results are consistent with this observation, with a generally negative

interaction between mean monthly temperature and SSI (Fig. 3a). Although these effects were not strongly tied to a particular month or season, combined with the interactions for precipitation, they do suggest that negative effects of hot, dry summers (July_{*t-1*} and August_{*t-1*}) may be most apparent in habitat specialists, whilst the positive effects of spring temperature (March_{*t-1*}, April_{*t*}) may be greatest for generalist species. Interestingly, the strongest interactions were for March_{*t+1*} and May_{*t+1*} temperatures, suggestive of a differential effect of breeding season temperature upon the settlement or detectability of generalist and specialist species in that year. This is consistent with the observation that the strongest correlations between temperature and community change are with breeding season temperature during the year of the second survey (Davey *et al.* 2012, 2013). The meaning of more positive effects of lagged May_{*t-1*} precipitation upon specialists than generalists (Fig. 3b) is uncertain, but may be attributed to potential changes in vegetation growth and habitat quality following wet springs that could enhance their breeding success and survival (e.g. Robinson *et al.* 2004).

The analysis of interactions between species' responses to weather and thermal association produced similar findings to those just described for habitat specialization. Thus, as expected from the large-scale increase in CTI observed across Europe (Devictor *et al.* 2012a), there was a tendency for positive interactions between STI and temperature effects on population growth across a range of months (Fig. 4a). Effects were strongest during the spring of the first survey (March_{*t-1*} to May_{*t*}, although phylogenetic autocorrelation signalled the potential for a type I error in the positive interaction in April_{*t*}). This suggests that warmer breeding seasons tend to increase the productivity of warm-adapted species, whilst warming during the spring of the second survey (March_{*t*}, May_{*t+1*} and June_{*t+1*}) may lead such warm-adapted species either to settle further north, or to be more detectable. Despite concerns over the role of land-use change in also influencing changes in STI (Clavero, Villero & Brotons 2011; Barnagaud *et al.* 2012) and uncertainties associated with the precision of STI estimates (Rodríguez-Sánchez, De Frenne & Hampe 2012), observed trends in CTI seem largely robust to these issues (Devictor *et al.* 2012b; Lindström *et al.* 2013). Our results are consistent with the concept that changes in CTI track avian population responses to warming.

Finally, our results highlighted widespread correlations between long-term population trends and species' sensitivity to temperature, compared to precipitation. Thus, recent warming trends appear likely to have contributed to the observed changes in bird communities previously described, including declines in long-distance migrants, habitat specialists with a narrow niche breadth and cold-adapted species (Sanderson *et al.* 2006; Davey *et al.* 2012; Devictor *et al.* 2012a). Although there was no match between the main periods of sensitivity to weather across species, and the periods of greatest correlation between

sensitivity and population trend, it did appear that species whose populations had increased tended to be those with positive relationships between temperature and population growth in periods of greatest warming. In particular, late winter and spring warming appear to have caused increases in populations with significant positive relationships between February_t, March_t, May_{t+1} and June_{t+1} temperatures and population growth. This potentially accounts for the apparent effects of conditions during spring_{t+1} upon changes in both community specialization and CTI. Long-term population trends did not appear significantly related to the periods of greatest contrast between species with differing migratory strategies, including May_t and February_t. In addition, the effect of precipitation upon long-term population trends was negatively correlated with mean precipitation effect, such that species which showed the greatest sensitivity to precipitation (having the most positive effects of precipitation upon population growth during periods where most species respond positively to precipitation, or the most negative effects of precipitation upon growth in months when most species respond negatively to precipitation) were also those which tended to decline. Although further work is required to fully attribute long-term population changes to climate change, our results suggest that both warming and changes in precipitation extremes may have influenced long-term avian population trends in the UK.

It is worth emphasizing that the results presented here are for relatively common and widespread bird species monitored by extensive surveys. Although these data have previously formed the basis for assessing community-level changes in response to climate change (e.g. Davey *et al.* 2012; Devictor *et al.* 2012a), no very rare species, and few upland species, are sufficiently well covered by these surveys to be included in our analysis. Thus, as these other species may be particularly sensitive to climate change (Pearce-Higgins 2010), the results presented here may present a potentially more positive overall assessment of climate change than would be apparent were the entire avifauna assessed. In addition, we have also not considered other potentially confounding non-climatic drivers of change that may also affect long-term population trends. Although these may be more responsible for some of the long-term trends observed than climate change (e.g. Eglinton & Pearce-Higgins 2012), by including a first-order autoregressive function in our models, we significantly reduced the risk that our results may be due to type I errors caused by other potential drivers of change being correlated with the precipitation and temperature variables.

To conclude, we have found good evidence that increasing winter and spring temperatures are likely to have improved climatic conditions for resident and short-distance migrant species in England, accounting for some of the observed long-term population increases in these species. A component of long-distance migrant population declines may also have been caused by warming in the UK, such as through increasing May temperatures, potentially

through detrimental effects of phenological mismatch upon breeding success (e.g. Both & Visser 2001; Both *et al.* 2006) and lagged effects of hot, dry summers. The effects of such summer conditions were relatively widespread across species, particularly also affecting habitat specialists with a narrow niche breadth (Fig. 3a), and cold-adapted species (Fig. 4a), and may have been mediated through impacts on food resources reducing breeding success in year_t, as has previously been observed in upland habitat specialists (Pearce-Higgins 2010; Pearce-Higgins *et al.* 2010; Fletcher *et al.* 2013). Thus, our results add weight to the increased recognition of the need to consider potential lagged effects of climate change on species' interactions (Cahill *et al.* 2013; Ockendon *et al.* 2014). Positive effects of autumn precipitation on resident populations may also be mediated through changes in food resources, although this hypothesis does not appear supported by the same degree of published evidence as that for summer drought effects. Finally, our results are consistent with previous work demonstrating negative impacts of warming on habitat specialists with a narrow niche breadth (Davey *et al.* 2012, 2013) and northerly distributed species associated with cold climates (Devictor *et al.* 2012a). These community-level changes appear to represent the accumulation of consistent differential impacts of summer and spring warming. In summary, our analysis has provided novel insights about the climatic drivers of recently observed changes in bird communities in England and strengthens the assertion that such changes are indeed at least partially a response to climate change.

Acknowledgements

This work was carried out under the BICCO-Net partnership, a joint research initiative sponsored by Defra, CCW, NIEA, NE and SNH and managed by JNCC. We are grateful to members of the steering group and the project group, for their comments on the methodology and previous drafts of this manuscript. Thanks also to Marco Girardello (CEH) for the extraction of the climate data. We are grateful to Vincent Devictor for comments on a draft of the manuscript, and to further comments from two anonymous reviewers and Ben Sheldon.

Data accessibility

The annual population trend estimates for England used in this study can be viewed at <http://www.bto.org/about-birds/birdtrends> and are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.m0nh6> (Pearce-Higgins *et al.* 2015). This also includes monthly temperature and precipitation data for England from <http://www.metoffice.gov.uk/climate/uk/datasets/> and species trait data listed in Appendix S1.

References

- Barnagaud, J.-Y., Devictor, V., Jiguet, F., Barbet-Massin, M., Le Voil, I. & Archaux, F. (2012) Relating habitat and climatic niches in birds. *PLoS One*, **7**, e32819.
- Both, C. & Visser, M.E. (2001) Adjustment to climate change is constrained by arrival date in a long-distance migratory bird. *Nature*, **411**, 296–298.
- Both, C., Bouwhuis, S., Lessells, C. & Visser, M. (2006) Climate change and population declines in a long-distance migratory bird. *Nature*, **441**, 81–83.
- Both, C., Van Turnhout, C.A.M., Bijlsma, R.G., Sipel, H., Van Strien, A.J. & Foppen, R.P.B. (2010) Avian population consequences of climate

- change are most severe for long-distance migrants in seasonal habitats. *Proceedings of the Royal Society of London, Series B*, **277**, 1259–1266.
- Cahill, A.E., Aiello-Lammens, M.E., Fisher-Reid, M.C., Hua, X., Karanewsky, C.J., Ryu, H.Y. *et al.* (2013) How does climate change cause extinction? *Proceedings of the Royal Society of London, Series B*, **280**, 21231890.
- Carroll, M.J., Dennis, P., Pearce-Higgins, J.W. & Thomas, C.D. (2011) Maintaining northern peatland ecosystems in a changing climate: effects of soil moisture, drainage and drain blocking on craneflies. *Global Change Biology*, **17**, 2991–3001.
- Chen, I.-C., Hill, J.K., Ohlemüller, R., Roy, D.B. & Thomas, C.D. (2011) Rapid range shifts of species associated with high levels of climate warming. *Science*, **333**, 1024–1026.
- Clavero, M., Villero, D. & Brotons, L. (2011) Climate change or land use dynamics: do we know what climate change indicators indicate? *PLoS One*, **6**, e18581.
- Conrad, K.F., Woiwod, I.P. & Perry, J.N. (2002) Long-term decline in abundance and distribution of the garden tiger moth (*Arctia caja*) in Great Britain. *Biological Conservation*, **106**, 329–337.
- Davey, C.M., Chamberlain, D.E., Newson, S.E., Noble, D.G. & Johnston, A. (2012) Rise of the generalists: evidence for climate driven homogenization in avian communities. *Global Ecology and Biogeography*, **21**, 568–578.
- Davey, C.M., Devictor, V., Jonzén, N., Lindström, Å. & Smith, H.G. (2013) Impact of climate change on communities: revealing species' contribution. *Journal of Animal Ecology*, **82**, 551–561.
- Devictor, V., Julliard, R., Clavel, J., Jiguet, F., Lee, A. & Couvet, D. (2008a) Functional biotic homogenization of bird communities in disturbed landscapes. *Global Ecology and Biogeography*, **17**, 252–261.
- Devictor, V., Julliard, R., Couvet, D. & Jiguet, F. (2008b) Birds are tracking climate warming, but not fast enough. *Proceedings of the Royal Society of London, Series B*, **254**, 2743–2748.
- Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J. *et al.* (2012a) Differences in the climate debts of birds and butterflies at a continental scale. *Nature Climate Change*, **2**, 121–124.
- Devictor, V., van Swaay, C., Brereton, T., Brotons, L., Chamberlain, D., Heliölä, J. *et al.* (2012b) Uncertainty in thermal tolerances and climatic debt. Reply. *Nature Climate Change*, **2**, 638–639.
- Doxa, A., Paracchini, M.L., Pointereau, P., Devictor, V. & Jiguet, F. (2012) Preventing biotic homogenization of farmland bird communities: the role of High Nature Value farmland. *Agriculture Ecosystems and the Environment*, **148**, 83–88.
- Eglington, S.M. & Pearce-Higgins, J.W. (2012) Disentangling the relative importance of changes in climate and land-use intensity in driving recent bird population trends. *PLoS One*, **7**, e30407.
- Fletcher, K., Howarth, D., Kirby, A., Dunn, R. & Smith, A. (2013) Effect of climate change on breeding population, clutch size and chick survival of an upland bird. *Ibis*, **155**, 456–463.
- Foden, W., Midgley, G.F., Hughes, G., Bond, W.J., Thuiller, W., Hoffmann, M.T. *et al.* (2007) A changing climate is eroding the geographical range of the Namib Desert tree *Aloe* through population declines and dispersal lags. *Diversity & Distributions*, **13**, 645–653.
- Freckleton, R.P., Watkinson, A.R., Green, R.E. & Sutherland, W.J. (2006) Census error and the detection of density dependence. *Journal of Animal Ecology*, **75**, 837–851.
- Freeman, S.N., Noble, D.G., Newson, S.E. & Baillie, S.R. (2007) Modelling population changes using data from different surveys: the Common Birds Census and the Breeding Bird Survey. *Bird Study*, **54**, 61–72.
- Greenwood, J.D. & Baillie, S.R. (1991) Effects of density-dependence and weather on population changes of English passerines using a non-experimental paradigm. *Ibis*, **133**(Suppl. 1), 121–133.
- Gregory, R.D. & Baillie, S.R. (1998) Large-scale habitat use of some declining British birds. *Journal of Animal Ecology*, **35**, 785–799.
- Gregory, R., Van Strien, A., Vorisek, P., Meyling, A., Noble, D., Foppen, R. *et al.* (2005) Developing indicators for European birds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **360**, 269–288.
- Hickling, R., Roy, D.B., Hill, J.K., Fox, R. & Thomas, C.D. (2006) The distributions of a wide range of taxonomic groups are expanding polewards. *Global Change Biology*, **12**, 450–455.
- Holmes, R.T. & Sherry, T.W. (2001) Thirty-year bird population trends in an unfragmented temperate deciduous forest: importance of habitat change. *The Auk*, **118**, 589–609.
- Jiguet, F., Gregory, R.D., Devictor, V., Green, R.E., Vorisek, P., Van Strien, A. *et al.* (2010) Population trends of European common birds are predicted by characteristics of their climatic niche. *Global Change Biology*, **16**, 497–505.
- Johansson, J. & Jonzén, N. (2012) Game theory sheds new light on ecological responses to current climate change when phenology is historically mismatched. *Ecology Letters*, **15**, 881–888.
- Jones, T. & Creswell, W. (2010) The phenology mismatch hypothesis: are declines of migrant birds linked to uneven climate change? *Journal of Animal Ecology*, **79**, 98–108.
- Kunin, W.E. (2008) On comparative analyses involving non-heritable traits: why half a loaf is sometimes worse than none. *Evolutionary Ecology Research*, **10**, 787–796.
- Le Viol, I., Jiguet, F., Brotons, L., Herrando, S., Lindström, Å., Pearce-Higgins, J.W. *et al.* (2012) More and more generalists: two decades of changes in the European avifauna. *Biology Letters*, **8**, 780–782.
- Lindström, Å., Green, M., Paulson, G., Smith, H.G. & Devictor, V. (2013) Rapid changes in bird community composition at multiple temporal and spatial scales in response to recent climate change. *Ecography*, **36**, 313–322.
- Littell, R.C., Milliken, G.A., Stroup, W.W. & Wolfinger, R.D. (1996) *SAS System for Mixed Models*. SAS Institute, Cary, North Carolina, USA.
- Marchant, J.H., Hudson, R., Carter, S.P. & Whittington, P.A. (1990) *Population Trends in British Breeding Birds*. BTO, Tring.
- Møller, A.P., Rubolini, D. & Lehikoinen, E. (2008) Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences*, **105**, 16195–16200.
- Morecroft, M. & Speakman, L. (eds.) (2013) *Terrestrial Biodiversity Climate Change Impacts*. Summary Report, Living With Environmental Change, ISBN 978-0-9928679-0-4.
- Morrison, C.A., Robinson, R.A., Clark, J.A., Risely, K. & Gill, J.A. (2013) Recent population declines in Afro-Palaearctic migratory birds: the influence of breeding and non-breeding seasons. *Diversity & Distributions*, **19**, 1051–1058.
- Newson, S.E., Mendes, S., Crick, H.Q.P., Dulvy, N.K., Houghton, J.D.R., Hays, G.C. *et al.* (2009a) Indicators of the impact of climate change on migratory species. *Endangered Species Research*, **7**, 101–113.
- Newson, S.E., Ockendon, N., Joys, A., Noble, D.G. & Baillie, S.R. (2009b) Comparison of habitat-specific trends in the abundance of breeding birds in the UK. *Bird Study*, **56**, 233–243.
- Newson, S.E., Oliver, T.H., Gillings, S., Crick, H.Q.P., Morecroft, M.D., Duffield, S.J. *et al.* (2014) Can site and landscape-scale environmental attributes buffer bird populations against weather events? *Ecography*, **37**, 872–882.
- Ockendon, N.O., Hewson, C.M., Johnston, A. & Atkinson, P.W. (2012) Declines in Afro-Palaearctic migrant birds are linked to bioclimatic wintering zone, possibly via constraints in arrival time advancement. *Bird Study*, **59**, 111–125.
- Ockendon, N., Baker, D.J., Carr, J.A., Almond, R.E.A., Amamo, T., Bertram, E. *et al.* (2014) Mechanisms underpinning climatic impacts on natural populations: altered species interactions are more important than direct effects. *Global Change Biology*, **20**, 2221–2229.
- Parnesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Peach, W., Baillie, S. & Underhill, L. (1991) Survival of British sedge warblers *Acrocephalus schoenobaenus* in relation to west African rainfall. *Ibis*, **133**, 300–305.
- Peach, W.J., du Feu, C. & McMeeking, J. (1995) Site tenacity and survival rates of Wrens *Troglodytes troglodytes* and Treecreepers *Certhia familiaris* in a Nottinghamshire wood. *Ibis*, **137**, 497–507.
- Peach, W.J., Thompson, P.S. & Coulson, J.C. (1994) Annual and long-term variation in the survival rates of British Lapwings *Vanellus vanellus*. *Journal of Animal Ecology*, **63**, 60–70.
- Pearce-Higgins, J.W. (2010) Using diet to assess the sensitivity of northern and upland birds to climate change. *Climate Research*, **45**, 119–130.
- Pearce-Higgins, J.W., Dennis, P., Whittingham, M.J. & Yalden, D.W. (2010) Impacts of climate on prey abundance account for fluctuations in a population of a northern wader at the southern edge of its range. *Global Change Biology*, **16**, 12–23.
- Pearce-Higgins, J.W., Eglington, S.M., Martay, B. & Chamberlain, D.E. (2015) Data from: drivers of climate change impacts on bird communities. *Dryad Digital Repository*, <http://dx.doi.org/10.5061/dryad.m0nh6>.
- Pearce-Higgins, J.W. & Green, R.E. (2014) *Birds and Climate Change: Impacts and Conservation Solutions*. Cambridge University Press, Cambridge.
- Piersma, T., Rogers, K.G., Boyd, H., Bunschoke, E.J. & Jukema, J. (2005) Demography of Eurasian Golden Plovers *Pluvialis apricaria* staging in The Netherlands, 1949–2000. *Ardea*, **93**, 49–64.

- Risely, K., Massimino, D., Johnston, A., Newson, S.E., Eaton, M.A., Musgrove, A.J. *et al.* (2012) *The Breeding Bird Survey 2011*. BTO Research Report 624, British Trust for Ornithology, Thetford.
- Robinson, R., Baillie, S.R. & Crick, H. (2007) Weather-dependent survival: implications of climate change for passerine population processes. *Ibis*, **149**, 357–364.
- Robinson, R.A., Baillie, S.R. & King, R. (2012) Population processes in European blackbirds *Turdus merula*: a state-space approach. *Journal of Ornithology*, **152**, 419–433.
- Robinson, R.A., Green, R.E., Baillie, S.E., Peach, W.J. & Thomson, D.L. (2004) Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain. *Journal of Animal Ecology*, **73**, 670–682.
- Rodríguez-Sánchez, F., De Frenne, P. & Hampe, A. (2012) Uncertainty in thermal tolerances and climatic debt. *Nature Climate Change*, **2**, 636–637.
- Saino, N., Ambrosini, R., Rubolini, D., von Hardenberg, J., Provenzale, A., Huppoc, K., *et al.* (2011) Climate warming, ecological mismatch at arrival and population decline in migratory birds. *Proceedings of the Royal Society of London, Series B*, **278**, 835–842.
- Sanderson, F., Donald, P., Pain, D., Burfield, I. & van Bommel, F. (2006) Long-term population declines in Afro-Palaearctic migrant birds. *Biological Conservation*, **131**, 93–105.
- Siriwardena, G.M., Baillie, S.R., Crick, H.Q.P. & Wilson, J.D. (2000) The importance of variation in the breeding performance of seed-eating birds in determining their population trends on farmland. *Journal of Applied Ecology*, **37**, 128–148.
- Spear, D. & Chown, S.T. (2008) Taxonomic homogenization in ungulates: patterns and mechanisms at local and global scales. *Journal of Biogeography*, **35**, 1962–1975.
- Thaxter, C., Joys, A., Gregory, R., Baillie, S. & Noble, D. (2010) Hypotheses to explain patterns of population change among breeding bird species in England. *Biological Conservation*, **143**, 2006–2019.
- Thomas, C.D. & Lennon, J.J. (1999) Birds extend their ranges northwards. *Nature*, **399**, 213.
- Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C. *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Wake, D.B. (2007) Climate change implicated in amphibian and lizard declines. *Proceedings of the National Academy Science, USA*, **104**, 8201–8202.
- Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andropoulos, P., Ariannoutsou, M. *et al.* (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy Science, USA*, **106**, 21721–21725.
- Yamaura, Y., Amano, T., Koizumi, T., Mitsuda, Y., Taki, H. & Okabe, K. (2009) Does land-use change affect biodiversity dynamics at a macroecological scale? A case study of birds over the past 20 years in Japan. *Animal Conservation*, **12**, 110–119.

Received 13 January 2014; accepted 7 October 2014

Handling Editor: Christiaan Both

Supporting Information

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

Appendix S1. Species names and traits.

Appendix S2. Relationships with other temperature measures.

Fig. S2. Monthly variation in the mean effect of mean (solid line), minimum (dotted line) or maximum (dashed line) daily temperature upon the population growth of 59 bird species.

Appendix S3. Effects across all species.

Fig S3a. Monthly variation in the mean effect (\pm SE) of temperature (i) and precipitation (ii) upon the population growth of 59 bird species.

Fig. S3b. The form of relationships between mean monthly temperature (i) and total precipitation (ii) and population growth in cases where there was a significant quadratic term (b_2) after applying the Bonferroni correction.

Appendix S4. Coefficient estimates and significance levels from figures.