

Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change

Rhys E. Green^{1,2,*}, Yvonne C. Collingham³,
Stephen G. Willis³, Richard D. Gregory²,
Ken W. Smith² and Brian Huntley^{3,†}

¹Conservation Science Group, Department of Zoology,
University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK
²Conservation Science Department, Royal Society for the Protection of
Birds, The Lodge, Sandy, Bedfordshire SG19 2DL, UK

³Institute of Ecosystem Science, School of Biological and Biomedical
Sciences, University of Durham, South Road, Durham DH1 3LE, UK

*Author and address for correspondence: Conservation Science Group,
Department of Zoology, University of Cambridge, Downing Street,
Cambridge CB2 3EJ, UK (reg29@hermes.cam.ac.uk).

†Author for correspondence (brian.huntley@durham.ac.uk).

Twenty-five-year population trends of 42 bird species rare as breeders in the UK were examined in relation to changes in climatic suitability simulated using climatic envelope models. The effects of a series of potential 'nuisance' variables were also assessed. A statistically significant positive correlation was found across species between population trend and climate suitability trend. The demonstration that climate envelope models are able to retrodict species' population trends provides a valuable validation of their use in studies of the potential impacts of future climatic changes.

Keywords: Rare Breeding Birds Panel; climate envelope models; climate response surface models; population trends; climate suitability

1. INTRODUCTION

Climate envelope models of static observed geographical distributions are frequently used to assess potential future effects of climatic change on plant and animal distributions (e.g. Araujo *et al.* 2006; Thuiller *et al.* 2006), but their use for this purpose is difficult to validate. Frequently, only validation in terms of model performance in describing overall range is attempted (but see Beerling *et al.* 1995), although some studies have used hindcasts of recent range boundary shifts (Hill *et al.* 1999). The latter studies, however, may give misleading negative results if species' range boundary adjustments lag climatic changes, perhaps as a result of dispersal or habitat

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2008.0052> or via <http://journals.royalsociety.org>.

One contribution of 12 to a Special Feature on 'Global change and biodiversity: future challenges'.

limitations. In this paper, we compare trends in breeding populations of bird species at the edge of their European range in the UK over a recent 25-year period, with trends in the suitability of the climate for each species obtained by making annual estimates of probability of occurrence in 50 km squares in the UK using climate envelope models of the recent European breeding distribution. Population trends (POPTs) are expected to parallel climatic suitability trends more closely because they do not suffer from lags to the same extent as range adjustments.

2. MATERIAL AND METHODS

(a) Bird population data

We used a database maintained by the Rare Breeding Birds Panel, which contains the numbers of pairs (or equivalent; see the electronic supplementary material, table S1) reported annually for 1970–2004 from the UK for 61 bird species that breed there in small numbers. We restricted our analysis to the period 1980–2004 because this is a period of a reasonably uniform trend in bioclimate variables (see §2c). For reasons described in the electronic supplementary material, we restricted our analysis to 42 species.

(b) Estimation of population trends

We fitted linear regression models to the data for each species for the period 1980–2004, with the count of pairs, or equivalent, as the dependent variable and calendar year as the independent variable, assuming Poisson errors and a log link function. We took the regression coefficient as the measure of POPT in subsequent analyses. The data for years with poor coverage (see electronic supplementary material) were excluded from the analysis, as were years of abnormally good coverage, if there was only one such year in the series. For the six species with more than 1 year of good coverage, mainly those with repeated national surveys, the presence or absence of abnormally good coverage in each year was included in the model, in addition to the calendar year, as a binary independent variable (good=1 and normal=0). The modelled effect of good coverage was positive, the increase in numbers recorded in such years, estimated by back-transforming the regression coefficient, ranging from 8 to 67%. We calculated the average number of pairs (or equivalent) recorded per year for the period 1980–2004, excluding any years for which coverage was considered abnormally poor or good.

(c) Bioclimate variables

For each 50 km Universal Transverse Mercator (UTM) square in the UK, we calculated annual values (1970–2002), as described previously for 1961–1990 means in Huntley *et al.* (2007), for three bioclimate variables: coldest-month mean temperature (MTCO, °C); annual temperature sum above 5°C (GDD5, degree-days); and annual ratio of actual to potential evapotranspiration (AET/PET). The UK annual mean values were then obtained by averaging across all squares.

Inspection of graphs of the annual mean values indicated that, following a possible decline during 1970–1980, MTCO increased fairly steadily after 1980 (figure 1). GDD5 increased over the whole period, although with indications of a more rapid rate of increase after ca 1980. AET/PET showed no clear evidence of a trend. Given the indication of consistent upward trends in both MTCO and GDD5 since ca 1980, we elected to calculate trends in climate suitability for bird species for the period 1980–2002 and to compare these trends with observed trends in bird numbers over a similar period.

(d) Climate suitability trends

We fitted climatic response surface (CRS) models relating each species' European breeding distribution in the late 1980s, recorded by 50 km UTM square (Hagemeijer & Blair 1997), to the 1961–1990 mean values of the three bioclimate variables, as described previously (Huntley *et al.* 2007). We then used these models and the annual values of the bioclimate variables to calculate the probability of occurrence of each species in each of the years 1980–2002 for every 50 km UTM square in the UK. The probabilities for each year were then averaged across all squares to obtain the annual mean probability of occurrence and ordinary least-squares linear regression was used to calculate the slope of the regression between logit annual mean probability of occurrence and year. We refer to this slope as the species' climate suitability trend (CST).

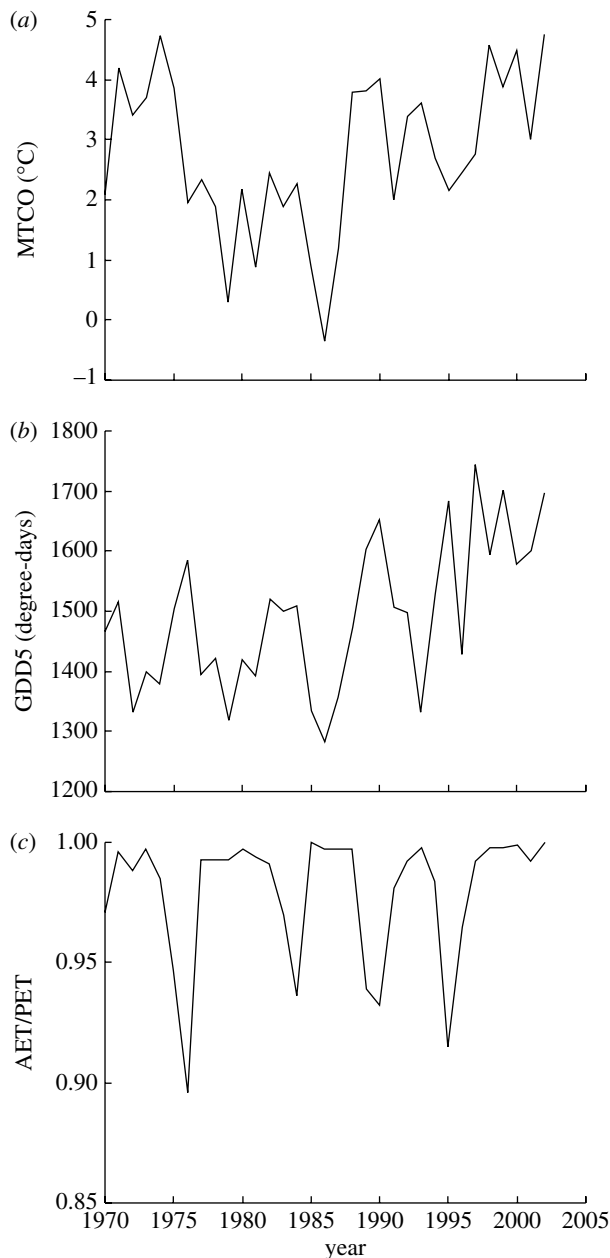


Figure 1. Annual values of three bioclimate variables, (a) MTCO, (b) GDD5 and (c) AET/PET, averaged over all 50 km UTM grid squares in the UK during the period 1970–2002.

(e) Other covariates of population trend

We obtained, for each species, the mean latitude of its European range (LAT), a measure of proximity to the UK of other parts of the European breeding range (PRX), its mean body mass and classifications of breeding habitat (HAB) and migratory behaviour (MIG). Details are presented in the electronic supplementary material and variable values are listed in table S2.

(f) Analysis of population trends in relation to CST, mean latitude of range and other variables

We used ordinary least-squares regression to relate variation in POPT among species to CST and LAT. We performed univariate regressions of POPT on CST or LAT and multiple regressions in which other potentially confounding variables that might influence POPT were included. There is evidence from other studies that POPTs of European birds vary according to breeding habitat (Gregory *et al.* 2007) and migratory status (Sanderson *et al.* 2006). We supposed that proximity to the UK of other parts of a species' European range might also influence POPT. POPT might also vary with life-history characteristics. We wished to avoid including in our models the many different life-history variables that could be assessed, so we used the natural logarithm of mean body mass (LMS) which is correlated with many of these variables.

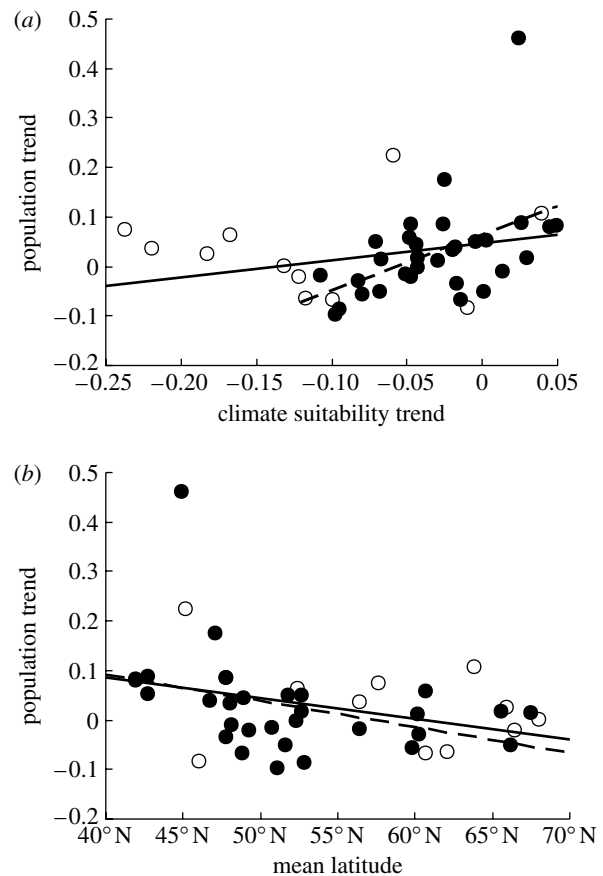


Figure 2. (a) Average annual population trend of 42 rare breeding bird species in the UK during the period 1980–2004 in relation to the CST (see text) for each species derived from climate envelope models and annual meteorological data from the UK for the period 1980–2002. (b) Population trends in relation to the mean latitude of the European distribution in the 1980s. The solid line shows the linear regression fitted to all points. Open symbols denote species with a mean annual population in the UK of less than five pairs. The dashed line is the regression fitted only to those 31 species (filled symbols) with an average population of more than five pairs.

For the purposes of our analysis, HAB, MIG, PRX and LMS were nuisance variables, our interest being in the effects of CST and LAT upon POPT. We therefore performed separate model-averaging analyses for CST and LAT to estimate the average effect of each on POPT in a set of multiple regression models that included combinations of the variable of interest with the nuisance variables present or absent, together with the nuisance variables present or absent, in all possible combinations, including the null model with no effects. We calculated, for each model, log-likelihoods, corrected Akaike information criterion (AIC_c) values and AIC_c weights, following Burnham & Anderson (2002). We calculated, using AIC_c weights, the weighted average multiple regression coefficient of POPT on CST or LAT and the relative importance of each independent variable as the sum of its AIC_c weights across all models in the set. We standardized univariate and multiple regression coefficients of POPT on CST or LAT by multiplying the crude coefficient by the standard deviation of CST or LAT and dividing by the standard deviation of POPT. We had a clear *a priori* expectation that the effect of CST on POPT would be positive and that of LAT would be negative, so we used one-tailed *t*-tests of the null hypothesis of no effect.

To allow for the potential effects of statistical non-independence of species' data points caused by similarity of characteristics due to common descent, analyses were also performed using a phylogenetic method, CAIC v. 2.6.9 (Purvis & Rambaut 1995). We followed the phylogenetic classification of Sibley & Monroe (1990), updated according to Møller (2006) and references therein. Independent contrasts were obtained using the option 'crunch',

Table 1. Standardized regression coefficients β and one-tailed p -values denoting the statistical significance of the effects of climate suitability trend (CST) and mean latitude of the European range (LAT) on the observed population trend of all species ($n=42$) and species with an average number of more than five pairs in the UK ($n=31$). (Results are shown for the simple univariate regression, the multiple regression model with the lowest AIC_c and the multi-model weighted average using AIC_c weights. The nuisance variables included in the model with the lowest AIC_c are shown.)

variable	species included	type of estimate	β	p	nuisance variables
CST	all	simple	0.242	0.0573	
CST	all	lowest AIC _c	0.303	0.0143	LMS, PRX
CST	all	multi-model	0.192	0.1405	
CST	more than five pairs	simple	0.478	0.0017	
CST	more than five pairs	lowest AIC _c	0.514	0.0006	LMS, PRX
CST	more than five pairs	multi-model	0.414	0.0247	
LAT	all	simple	-0.335	0.0122	
LAT	all	lowest AIC _c	-0.587	<0.0001	LMS
LAT	all	multi-model	-0.586	<0.0001	
LAT	more than five pairs	simple	-0.373	0.0153	
LAT	more than five pairs	lowest AIC _c	-0.490	0.0006	PRX
LAT	more than five pairs	multi-model	-0.502	0.0015	

with the assumption that all branch lengths in the phylogeny were equal. We used linear univariate and multiple regressions through the origin to examine relationships between contrasts in POPTs and independent variables.

3. RESULTS

As expected, there was a positive correlation between variation among species in their observed POPT and CST (figure 2a). Statistical significance varied according to whether simple univariate regression, the multiple regression with the lowest AIC_c or the model-averaged multiple regression was used, and was greater if 11 species with the mean annual UK population size less than five pairs were excluded (table 1). Because the UK is in the middle latitudes of Europe, we expected that recent climatic warming would favour species with ranges located in the south of Europe and adversely affect northern species. The negative correlation between POPT and LAT supports this expectation (figure 2b) and was consistently statistically significant and less affected by the exclusion of the rarest species (table 1).

Of the four nuisance variables included in the multiple regression models, the relative importance scores of PRX and LMS were consistently higher than those of MIG and HAB (0.717, 0.773, 0.311 and 0.110, respectively, for the model set with CST as the variable of interest; 0.996, 0.875, 0.239 and 0.094, respectively, for the LAT model set). The effects of LMS and PRX on POPT were positive. The analyses that allowed for phylogenetic relationships led to very similar conclusions (table 2).

HAB, MIG, PRX and LMS might affect the strength of the relationship between POPT and the expected effect of recent climatic change. We tested the statistical significance of the two-way interaction between each of these variables and CST in regression models that included one of the variables and CST. None of the interactions approached significance (F -tests, $p > 0.27$). Equivalent tests revealed no significant two-way interactions between LAT and HAB, MIG, PRX or LMS ($p > 0.18$).

Table 2. One-tailed p -values obtained using the phylogenetic method CAIC, denoting the statistical significance of the effects of CST and mean latitude of the European range (LAT) on the observed population trend of all species ($n=41$ contrasts) and species with an average number of more than five pairs in the UK ($n=30$ contrasts). (The nuisance variables included in the multiple regression models are shown.)

variable	sign of effect	nuisance variables included	all species p	more than five pairs p
CST	+	none	0.059	0.0005
CST	+	LMS	0.030	0.0005
CST	+	PRX	0.039	0.0015
CST	+	LMS+PRX	0.033	0.0020
LAT	-	none	0.023	0.0065
LAT	-	LMS	0.010	0.0065
LAT	-	PRX	<0.0001	0.0005
LAT	-	LMS+PRX	<0.0001	0.0005

4. DISCUSSION

CSTs derived from CRS models of static recent European breeding distributions of birds showed the expected correlation with observed population trends. Although there was considerable unexplained variation, and not all effects were statistically significant, there was no indication that the strength of the relationship between observed and expected trends was affected by habitat, migratory status, proximity of parts of the geographical range outside the UK or mean body mass. The effect of CST was most apparent when the rarest species were excluded, probably owing to the vulnerability of very small populations to stochastic effects. The mean latitude of a species' European range was also a good predictor of its POPT; much simpler to calculate than CST, LAT acts as a proxy for the species' thermal preference.

Unfortunately, the proportion of species expected to show positive and negative POPTs that are actually showing trends in the expected direction could not be assessed reliably from the data used because the apparent trends were probably positively biased, albeit

to a comparable extent across species, as a result of increasing recording effort across the period examined (see electronic supplementary material).

Our results represent a valuable independent validation of the CRS models and provide support for their use to simulate potential impacts of future climatic changes (Huntley *et al.* 2007, 2008). They also indicate the potential to use CRS, and perhaps other climate envelope models, in more sophisticated ways than have been explored to date; in particular, these results indicate the potential to explore potential impacts of climatic change on species' populations as well as ranges. Furthermore, these results provide useful evidence of the potential to apply such models in the development of policy-relevant indicators of the impacts of climatic change on biodiversity (Gregory *et al.* 2005).

We thank Mark Holling and the Rare Breeding Birds Panel for access to data and assistance, and the many ornithologists without whom these data could not have been collected. Simon Wotton assisted in data preparation. We thank Ward Hagemeyer and the EBCC for access to data recording European breeding distributions of birds. Development of the climate response models was supported by grants from the Natural Environment Research Council and the Royal Society for the Protection of Birds. The manuscript was completed during a period of research leave granted to B.H. by the University of Durham, during which he benefited from the financial support of a Royal Society–Wolfson Foundation 'Research Merit Award'.

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