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

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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 climate 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...

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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 bioclimatic variables (see §3c). 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) Bioclimatic 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 bioclimatic 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 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 use the annual mean value of MTCO (MTCO), for 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 bioclimatic variables, as described previously (Huntley et al. 2007). We then used these models and the annual values of the bioclimatic 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 the resulting estimates were applied to the total area to calculate the long-term annual mean probability of occurrence and year. We refer to this slope as the species' climate suitability trend (CST).
which is correlated with many of these variables. We wished to avoid including in our analysis of 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 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 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. To perform this, we fitted 32 models with the main effects of either CST or LAT 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 (AICc) values and AICc weights, following Burnham & Anderson (2002). We calculated, using AICc weights, the weighted average multiple regression coefficient 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'.

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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 model with the lowest AICc or the multi-model weighted average using AICc weights. The nuisance variables included in the model with the lowest AICc are shown.

<table>
<thead>
<tr>
<th>variable</th>
<th>species included</th>
<th>type of estimate</th>
<th>β</th>
<th>p</th>
<th>nuisance variables</th>
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<tr>
<td>CST</td>
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<td>0.0573</td>
<td>LMS, PRX</td>
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<tr>
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<td>0.0017</td>
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<tr>
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<td>0.0006</td>
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<td>multi-model</td>
<td>−0.502</td>
<td>0.0015</td>
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</table>

Table 1. Standardized regression coefficients β and one-tailed p-values denoting the statistical significance of the influence 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 AICc and the multi-model weighted average using AICc weights. The nuisance variables included in the model with the lowest AICc are shown.)

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).

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