Journal of Biogeography (*J. Biogeogr.*) (2009) **36**, 1194–1208

ORIGINAL ARTICLE

Potential impacts of climatic change on the breeding and non-breeding ranges and migration distance of European *Sylvia* warblers

Nathalie Doswald[1], Stephen G. Willis[1*], Yvonne C. Collingham[1], Deborah J. Pain[2†], Rhys E. Green[2,3] and Brian Huntley[1]

[1]Centre for Ecosystem Science, School of Biological and Biomedical Sciences, University of Durham, Durham, UK, [2]Royal Society for the Protection of Birds, The Lodge, Sandy, Bedfordshire, UK and [3]Conservation Science Group, Department of Zoology, University of Cambridge, Cambridge, UK

ABSTRACT

Aim To explore the potential impacts of climatic change on species with different migratory strategies using *Sylvia* warblers breeding in Europe as a 'model' species group.

Location Europe and Africa.

Methods Climate response surfaces and generalized additive models (GAMs) were used to model relationships between species recorded breeding and non-breeding ranges and recent climate. Species potential future breeding and non-breeding ranges were simulated for three scenarios of late 21st-century climate. The simulated potential future and present ranges were compared in terms of their relative extent and overlap, as well as their location. The impact of any shifts in potential range location on migration distance were quantified.

Results Potential breeding ranges consistently showed a shift northwards, whereas potential non-breeding ranges showed no consistent directional shift, even when trans-Saharan migrants were considered separately from resident/short-distance or partial migrants. Future potential range extent relative to simulated recent range extent varied considerably among species, although on average range extent increased. Overlap between future and recent simulated range was generally low, averaging < 36% for both breeding and non-breeding ranges. Overlap was consistently less for range-restricted than for widespread species. Migration distance increased generally, by about twice as much in the case of trans-Saharan migrant species than for short-distance migrants. In many cases potential future non-breeding areas were simulated in regions far from the species present non-breeding area, suggesting that new migration strategies and routes may need to be developed in response to climatic change.

Main conclusions Migratory species can be expected to suffer greater negative impacts from climatic change than species that are resident or undertake only short-distance or partial migrations. Trans-Saharan migrants face the greatest potential increases in migration distances, whereas range-restricted species are expected to experience major population reductions because of the limited, or in some cases lack of, overlap between their present and potential future ranges.

Keywords

Climate change, climate envelope model, climate response surface, distribution, generalized additive models, migratory birds, Palaearctic, species range change, *Sylvia*.

*Correspondence: Stephen G. Willis, Centre for Ecosystem Science, School of Biological and Biomedical Sciences, University of Durham, South Road, Durham DH1 3LE, UK.
E-mail: s.g.willis@durham.ac.uk
†Present address: Wildfowl and Wetlands Trust, Slimbridge, Gloucestershire GL2 7BT, UK.

www.blackwellpublishing.com/jbi
doi:10.1111/j.1365-2699.2009.02086.x

INTRODUCTION

Migration is a common strategy among birds, particularly those breeding in temperate regions, for coping with seasonal variability in daylength and the abundance of food. Amongst bird species breeding in the Western Palaearctic about 70% are migratory, with 30% undertaking long-distance migrations to sub-Saharan Africa (Snow & Perrins, 1998). Successful migration depends upon complex behaviour, physiology and endogenous programmes, suitably located stopover habitats between breeding and non-breeding areas, and synchronization of migration times with seasons in different geographical areas (Berthold & Helbig, 1992; Berthold, 2001; Alerstam *et al.*, 2003). It is often strongly linked with seasonal changes in temperature and availability of prey (Berthold, 2001; Robinson *et al.*, 2005). Recent and forecast future climatic changes (Christensen *et al.*, 2007; Meehl *et al.*, 2007) may thus have important effects on migratory birds, especially long-distance migrants (Robinson *et al.*, 2008).

There is evidence that migratory species are already responding to recent climatic changes (Both & Visser, 2001; Jonzén *et al.*, 2002; Walther *et al.*, 2002; Cotton, 2003; Jenni & Kéry, 2003; Lemoine & Böhning-Gaese, 2003; Marra *et al.*, 2005; Robinson *et al.*, 2005; Both *et al.*, 2006; Zalakevicius *et al.*, 2006). Warmer winters have probably encouraged more frequent over-wintering of some migrants in the British Isles, notably blackcap (*Sylvia atricapilla*) from central European breeding populations (Bearhop *et al.*, 2005). The breeding ranges of many species have expanded northwards (Parmesan & Yohe, 2003) and some species' non-breeding distributions have also changed and are now closer to their breeding areas (Austin & Rehfisch, 2005). Some of these responses to climatic change may make migration easier to accomplish, although there are indications that extensions or shifts of the breeding range are often accompanied by retention of established migration routes and non-breeding ranges, which may make migration more difficult (Sutherland, 1998; Ruegg *et al.*, 2006). It has also been suggested that partial migrants may become increasingly resident if warmer conditions permit over-wintering on the breeding grounds (Berthold, 2001), as has been observed for chiffchaff (*Phylloscopus collybita*) in Britain and Ireland (Lack, 1986). Widespread, unexplained population declines have been reported recently for many European long-distance migrants, although populations of related short-distance migrants have remained relatively stable (Sanderson *et al.*, 2006). Warmer winters in temperate regions may result in increased over-winter survival of residents and consequent population increases, perhaps adding increased competition to other factors contributing to declines in long-distance migrants, including habitat loss and mis-timing of migration and breeding (Both & Visser, 2001; Lemoine & Böhning-Gaese, 2003; Böhning-Gaese & Lemoine, 2004; Both *et al.*, 2006). Earlier arrival in breeding areas and/or earlier egg laying have been reported for many short- to medium-distance migrants and some long-distance migrants, these shifts in timing being considered to represent responses to climatic change (Crick *et al.*, 1997; Gordo *et al.*, 2005).

Climatic envelope models have been used to simulate the potential impacts of climatic change on breeding ranges of birds (Erasmus *et al.*, 2002; Thuiller, 2003; Huntley *et al.*, 2006, 2007, 2008), including long-distance migrants, although few studies have modelled species non-breeding ranges (e.g. Martínez-Meyer *et al.*, 2004). Positive relationships have been shown between interspecific variation in recent population trends and retrodicted trends in the suitability of climate based upon observed climatic change and climate envelope models (Green *et al.*, 2008). However, despite the recognition that climatic change may have more deleterious effects upon migrants than upon residents, we are aware of no previous study examining potential impacts of climatic change on both breeding and non-breeding ranges of migrants. Weather conditions in their non-breeding areas influence population fluctuations and trends in several trans-Saharan migrants (Baillie & Peach, 1992; Jones *et al.*, 1996; Saino *et al.*, 2004a,b; Gordo *et al.*, 2005), so changes in the extent or location of their non-breeding range are likely also to have important impacts. Large decreases in extent of their non-breeding range, increased migratory distances or altered migration routes with reduced access to, or suitability of, stopover sites, could all result in population declines in species whose breeding range extent and suitability were little affected by climatic change.

In this paper we use climate envelope models to assess potential effects of climatic change upon the ranges of species within a genus of migratory birds. We examine the degree to which modelling supports the following propositions about expected impacts of climatic change.

(1) Climatic change is expected to have effects on the non-breeding ranges of trans-Saharan migrants that are largely independent of effects on the breeding range; this independence is less likely for short-distance and partial migrants.

(2) Migration distance between potential breeding and non-breeding ranges is expected to increase for trans-Saharan migrants.

(3) Potential impacts of climatic change upon resident/short-distance or partial migrants will be less than upon trans-Saharan migrants, because breeding and non-breeding ranges of the former species are within the same hemisphere and general climatic zone, and thus likely to be affected in a similar manner.

(4) The impacts of climatic change will be greater for species with breeding or non-breeding ranges of limited geographical extent, because there is likely to be less overlap between their present and potential future ranges.

Here we present an assessment of these propositions using the European *Sylvia* warblers as a model group. We selected the *Sylvia* warblers because: (1) they include partial residents, short-distance migrants and trans-Saharan migrants; (2) they have a diversity of range extents; (3) they mainly breed wholly within the Western Palaearctic; and (4) members of the group breed from the Mediterranean region to Arctic Europe. They are also well studied in terms of their ecology (e.g. Shirihai *et al.*, 2001), their range (e.g. Böhning-Gaese *et al.*, 2006) and migratory behaviour (e.g. Berthold, 1988). We fit models relating the breeding and non-breeding ranges of each European breeding *Sylvia* species to bioclimatic variables and use these models to simulate species' potential future ranges for a series of alternative future climate scenarios.

MATERIALS AND METHODS

Species' distribution and climatic data

Böhning-Gaese *et al.* (2003) recognize 25 *Sylvia* species globally. We included in our study those 17 species that breed in Europe, the Mediterranean region and/or northern Africa, whose breeding ranges lie wholly or mostly in the Western Palaearctic (Shirihai *et al.*, 2001) and whose non-breeding ranges are in Europe or Africa (Table 1). The eight species excluded comprise five sub-Saharan African residents (*Sylvia layardi*, *Sylvia subcaeruleum*, *Sylvia boehmi*, *Sylvia abyssinica*, *Sylvia lugens*) and three primarily Arabian species (*Sylvia buryi*, *Sylvia leucomelaena*, *Sylvia mystacea*) (taxonomy follows Böhning-Gaese *et al.*, 2003).

Data for the European breeding ranges primarily follow those of Hagemeijer & Blair (1997), who record presence/absence of breeding in the *c.* 50 × 50 km (*c.* 0.5° longitude × latitude) cells of a Universal Transverse Mercator (UTM) grid. Species' breeding ranges in North Africa or parts of the Mediterranean region outside the area covered by Hagemeijer & Blair (1997) were gridded at 0.5° longitude × 0.5° latitude from range maps held in the BirdLife International 'World Bird Database' (see http://www.birdlife.org/datazone/) and made available to us by Birdlife International, Cambridge. Non-breeding ranges were gridded from the same source, at 0.5° resolution north of 20° N and at 1° for more southerly areas. The lower resolution used for sub-Saharan Africa reflects greater uncertainties with respect to species' range margins in parts of that region.

Climatic data for 1961–1990 were from a 0.5° longitude × 0.5° latitude global compilation (New *et al.*, 1999). Soil water capacity data were derived following the methods of Prentice *et al.* (1992). Inverse distance weighted bilinear interpolation was used to interpolate these data to the grids used to record breeding (8216 cells – Europe, the Mediterranean region and Africa north of 20° N) and non-breeding (10,178 cells – Europe, the Mediterranean region and all of Africa) ranges. Four bioclimatic variables were derived from the climatic variables: annual temperature sum above 5°C (GDD5); mean coldest month temperature (MTCO); mean warmest month temperature (MTWA); and annual actual to potential evapotranspiration ratio (APET) following the formulation of Prentice *et al.* (1992). These variables were selected because they reflect known direct or indirect determinants of species distributions; they have also previously been used successfully to model breeding ranges in Europe and Africa (Huntley *et al.*, 2004, 2006, 2007, 2008; Thomas *et al.*, 2004).

Model construction and evaluation

Climate response surface models (CRS) and generalized additive models (GAMs), two robust modelling approaches that are widely utilized, were used to model the relationship between probability of occurrence of species and the bioclimatic variables. CRS models were fitted using locally weighted regression (Cleveland & Devlin, 1988; Huntley *et al.*, 1995). GAMs were fitted using a spline smoother, binomial error distribution and a logistic link function in R (R Development Core Team, 2006) using the GAM package (Hastie, 2006; R Development Core Team, 2006). Both approaches simulate the probability of occurrence of a species for a given combination of values of the bioclimatic variables. Simulated probability of occurrence is transformed into simulated presence/absence using a threshold probability of occurrence value. Following Huntley *et al.* (1995), threshold values selected were those that optimized model fit as assessed using Cohen's kappa (Cohen, 1960).

Each species' breeding and non-breeding range was modelled separately. Model performance was assessed using the area under the curve (AUC) for a receiver operating characteristic (ROC) plot (Fielding & Bell, 1997). AUC values ≥ 0.7 indicate 'useful' models whilst values ≥ 0.9 indicate models with a 'high' performance (Swets, 1988; Fielding, 2002). Model robustness was assessed using a stringent *k*-fold partitioning approach, rather than the frequently applied jackknife technique using single randomly selected 'training' and 'test' subsets of the data (e.g. Araújo *et al.*, 2006). Each study area was partitioned into 'panels' (6° longitude × 8° latitude) using major UTM grid divisions; the area used to model breeding ranges comprised 98 panels and that used to model non-breeding ranges 148. A series of models was fitted, in each case omitting data from one panel and using the resulting model to simulate the probability of occurrence of a species in cells of the omitted panel. An overall grid of species' probability of occurrence values was constructed by combining values simulated by each of the series of models for the relevant omitted panel. The AUC was calculated for this overall grid to provide an assessment of performance of the *k*-fold partitioned model. This approach is more stringent than the widely used jackknife approach and substantially reduces, although does not entirely remove, non-independence arising from spatial autocorrelation in both distribution and climatic data. The *k*-fold partitioning was not possible for two of the species (*Sylvia melanothorax*, *Sylvia balearica*), however, because their entire breeding range lay in one panel.

Areas of overlap between simulated breeding and non-breeding ranges were considered areas of 'residency', although we recognize that in some cases these areas are used by different populations in the two seasons (Bearhop *et al.*, 2005). The performance of models in simulating areas of residency was assessed by calculating AUC values using the product of the probabilities of occurrence simulated for each cell by the breeding and non-breeding range models with 1961–90

Table 1 Species traits and model performance for *Sylvia* warblers in Europe and Africa.

Species	Common name	Breeding range	Non-breeding range	Migratory strategy	AUC breeding	AUC non-breeding
S. sarda	Marmora's warbler	S. Europe	S. Europe and N. Africa	Partial and short distance	0.960	0.953
S. balearica	Balearic warbler	Balearic Islands	Balearic Islands	Resident	0.999*	0.999*
S. undata	Dartford warbler	S. Europe and N. Africa	S. Europe and N. Africa	Partial and short distance	0.968	0.952
S. deserticola	Tristram's warbler	N. Africa	N. Africa	Resident and dispersive	0.956	0.918
S. conspicillata	Spectacled warbler	S. Europe and N. Africa	N. Africa	Partial and short distance	0.927	0.910
S. cantillans	Subalpine warbler	S. Europe	Sub-Saharan Africa	Long distance	0.953	0.964
S. melanocephala	Sardinian warbler	S. Europe and N. Africa	S. Europe and N. Africa	Partial and short distance	0.955	0.901
S. melanothorax	Cyprus warbler	Cyprus	Cyprus and N. Africa	Partial and short distance	0.999*	0.979*
S. rueppelli	Rüppell's warbler	SE Europe	E. sub-Saharan Africa	Long distance	0.963	0.918
S. nana	Desert warbler	N. Africa	N. Africa	Resident	0.904	0.904
S. hortensis†	Western Orphean warbler	S. Europe and N. Africa	Sub-Saharan Africa	Long distance	0.927	0.981†
S. crassirostris†	Eastern Orphean warbler	S. Europe and N. Africa	Sub-Saharan Africa	Long distance	0.930	
S. nisoria	Barred warbler	C. Europe	E. sub-Saharan Africa	Long distance	0.959	0.947
S. curruca	Lesser whitethroat	Widespread Europe	E. sub-Saharan Africa	Long distance	0.972	0.924
S. communis	Whitethroat	Widespread Europe and N. Africa	Widespread sub-Saharan Africa	Long distance	0.979	0.970
S. borin	Garden warbler	Widespread Europe	Widespread Sub-Saharan Africa	Long distance	0.971	0.980
S. atricapilla	Blackcap	Widespread Europe and N. Africa	Europe and N. Africa and sub-Saharan Africa	Partial and short and long distance	0.981	0.898

AUC, area under the curve. Values are from the *k*-fold partitioned generalized additive models (GAMs) except where otherwise indicated.

*AUC values from full data GAMs because *k*-fold partitioning could not be performed for these restricted-range species.

†AUC value for GAM fitted to the combined non-breeding range of these two species as they have not been separately mapped in their non-breeding area.

climatic data and the observed area of overlap between breeding and non-breeding ranges.

Simulating potential future ranges

Future climate scenarios were interpolated from the TYN SC 2.0 0.5° longitude × latitude global compilation (Mitchell *et al.*, 2004) for 2001–2100, in which mean monthly values for 1961–90 (New *et al.*, 1999) have been adjusted using annual anomalies derived from transient simulations made using various general circulation models (GCMs). Scenarios for 2071–2100 were derived from simulations made for the SRES B2 emissions scenario (Nakicenovic & Swart, 2000) using three GCMs: HadCM3 (H) (Gordon *et al.*, 2000); ECHAM4/OPYC3 (E) (Roeckner *et al.*, 1996); and CSIRO Mk2 (C) (Hirst *et al.*, 1996). Future scenario values for bioclimatic variables were calculated and used to simulate species' potential future ranges.

Analyses of simulated ranges

Paired *t*-tests on arcsine square root transformed AUC values were used to compare the performance of CRS and GAM models for: (1) breeding range; (2) non-breeding range; and (3) areas of residency.

Differences between simulated recent and potential future breeding and non-breeding ranges were expressed using two quantities: relative range extent (R, potential future range extent expressed as a percentage of simulated present range extent) and range overlap (O, overlap of potential future and simulated present ranges expressed as a percentage of simulated present range extent). Potential changes in the extent of areas of residency were also examined. Comparisons were made of both R and O between long-distance (i.e. trans-Saharan) migrants and residents/short-distance or partial migrants (Table 1), and also between species with limited range extent and those with more extensive ranges.

Geodesic distance (km) was calculated between centroids of simulated breeding and non-breeding ranges. This is referred to as 'migration distance', although we recognize that in reality migration distance is, for various reasons including nonlinear migration routes and leap-frog migration, highly variable within species. Minimum and maximum 'migration distance' were calculated as the minimum and maximum of the geodesic distances between all grid cells in each of the simulated breeding and non-breeding ranges. In a few cases, non-breeding range simulations for present climate indicated climatically suitable areas in southern Africa where a species does not currently occur. When calculating present simulated range centroids and migration distances such areas were excluded by removing grid cells with simulated presence beyond the known southern latitudinal limit for these species. Similarly, some species' potential future (but not current) non-breeding ranges included areas in southern Africa distant from any part of the present range. Such areas were excluded when calculating species' potential future range centroids. Simulated present and potential future breeding ranges of some species currently restricted to either the eastern or western Mediterranean region (e.g. *Sylvia rueppelli*, *Sylvia melanothorax*, *Sylvia deserticola*, *Sylvia nana*) included a few climatically suitable cells in the opposite part of the region. These simulated presences were excluded from analyses because they are unlikely to be realized. *Sylvia atricapilla* is the only species in the genus with a mixed migratory strategy. Its non-breeding range includes sub-Saharan Africa as well as Europe and North Africa. The centroid of its simulated non-breeding range was calculated separately for areas north and south of 20° N. Migration distance was calculated separately for its short-distance and trans-Saharan migrant populations. Potential changes in migration distance were expressed both as differences, subtracting present from potential future distance, and as ratios of potential future to present distance, and were compared between long-distance migrants and resident/short-distance or partial migrants.

RESULTS

Breeding and non-breeding range models

CRS models performed slightly but significantly better than GAMs when fitted to the full dataset (breeding range, $t_{16} = 5.502$, $P < 0.001$; non-breeding range, $t_{14} = 3.41$, $P < 0.01$; area of residency, $t_8 = 3.88$, $P < 0.01$). Their performance was uniformly 'high' ($\mathrm{AUC}_{\mathrm{breeding}}$ 0.948–0.999; $\mathrm{AUC}_{\mathrm{non\text{-}breeding}}$ 0.925–0.999; $\mathrm{AUC}_{\mathrm{residency}}$ 0.945–0.999; see Table S1). The *k*-fold partitioning results showed that both modelling methods were robust in terms of their predictive power (Table S1). GAMs built by *k*-fold partitioning performed slightly but significantly better than equivalent CRS models (breeding range, $t_{14} = 5.403$, $P < 0.001$; non-breeding range, $t_{12} = 3.94$, $P < 0.01$; area of residency, $t_7 = 4.73$, $P < 0.01$). GAMs were selected to simulate present and potential future ranges for subsequent analyses because of this aspect of their performance.

Breeding range

Simulated potential future breeding range centroids shifted consistently north relative to simulated present range centroids, by a mean of 3.8–4.4° latitude depending upon the GCM scenario considered (paired *t*-test on centroid latitudes, d.f. = 16, $P < 0.0001$ for all three scenarios). Areas near species' present southern margins were simulated as no longer suitable, whereas areas beyond present northern margins were simulated as newly suitable (Figs 1 and 2). For all three GCM scenarios, the magnitude of the northward shift was greater for trans-Saharan migrants than for resident/short-distance or partial migrants, although the difference was not significant in the case of the E scenario (two-sample *t*-test, assuming unequal variance, on difference in centroid latitude: H, d.f. = 14.312, $t = 2.901$, $P = 0.011$; E, d.f. = 12.794, $t = 1.525$, $P = 0.152$; C, d.f. = 14.998, $t = 2.266$, $P = 0.039$).

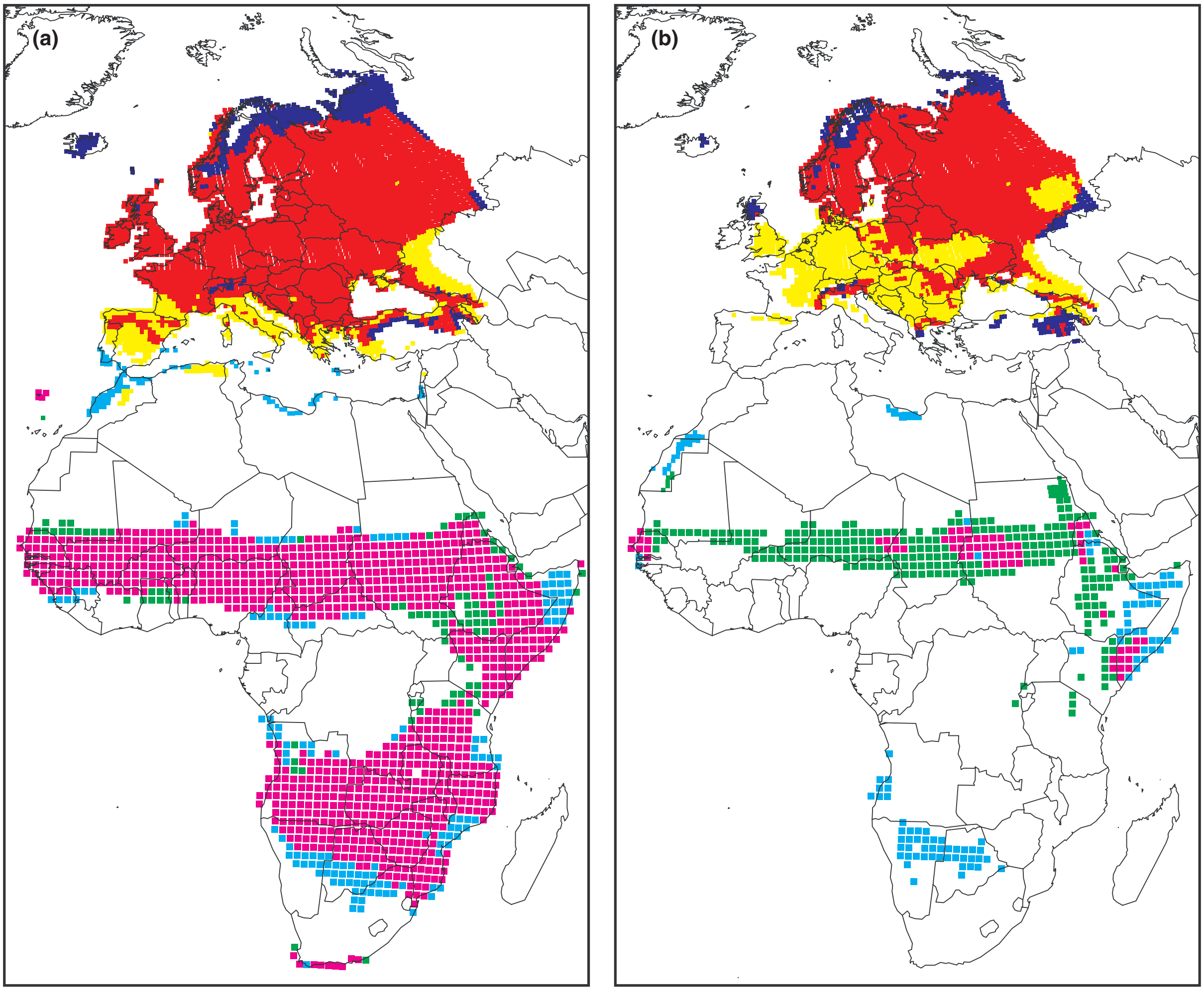

Figure 1 Simulated potential range changes between 1961–90 and 2071–2100 for two widespread trans-Saharan migrants: (a) *Sylvia communis* (whitethroat); (b) *Sylvia curruca* (lesser whitethroat). Results shown are for the ECHAM4 general circulation model scenario. Red, yellow and blue indicate the breeding range and magenta, green and cyan the non-breeding range. Red/magenta shading indicates areas simulated as suitable in both periods; yellow/green shading indicates areas simulated as suitable only for 1961–90 (i.e. areas of potential future range contraction); and blue/cyan shading indicates areas simulated as suitable only for 2071–2100 (i.e. areas of potential future range expansion).

Across the three GCM scenarios, relative breeding range extent R was consistently ≤ 100% for eight species (mean 68%) and consistently > 100% for four species (mean 382%, median 168%) (Table 2). *Sylvia deserticola*, the present range of which is limited in extent and southern, showed the most marked potential range reduction (mean R 22%), whilst *S. melanothorax*, with a present range limited to Cyprus, showed the greatest potential increase (mean R 1039%). Neither R nor breeding range overlap O exhibited any consistent difference between trans-Saharan migrants and resident/short-distance or partial migrants for any GCM scenario (t-test on log R, d.f. = 16 in all cases; H, $t = 0.328$, $P = 0.747$; E, $t = -1.05$, $P = 0.309$; C, $t = -0.471$, $P = 0.644$; t-test on arcsine square root transformed O, d.f. = 16 in all cases; H, $t = 1.791$, $P = 0.092$; E, $t = 1.988$, $P = 0.064$; C, $t = 1.715$, $P = 0.105$). However, O was consistently greater for widespread species than for species with a restricted range (t-test on arcsine square root transformed O, allowing for unequal variance, d.f. = 7 in all cases; H, $t = 3.86$, $P < 0.01$; E, $t = 4.15$, $P < 0.01$; C, $t = 3.3$, $P < 0.05$).

Non-breeding range

Simulated potential future non-breeding range centroids shifted substantially compared with those of the simulated present ranges, although they did not show a consistent directional shift, especially amongst trans-Saharan migrant species. The mean shift was northwards by 1.8–2.3° depending upon the GCM scenario considered (paired t-tests on changes in centroid latitude among species, d.f. = 17 in all cases, H, $t = -1.936$, $P = 0.070$; E, $t = -2.656$, $P = 0.017$; C, $t = -2.591$, $P = 0.019$). There were no significant differences between the mean centroid shifts for trans-Saharan migrants, as opposed to resident/short-distance or partial migrants, for

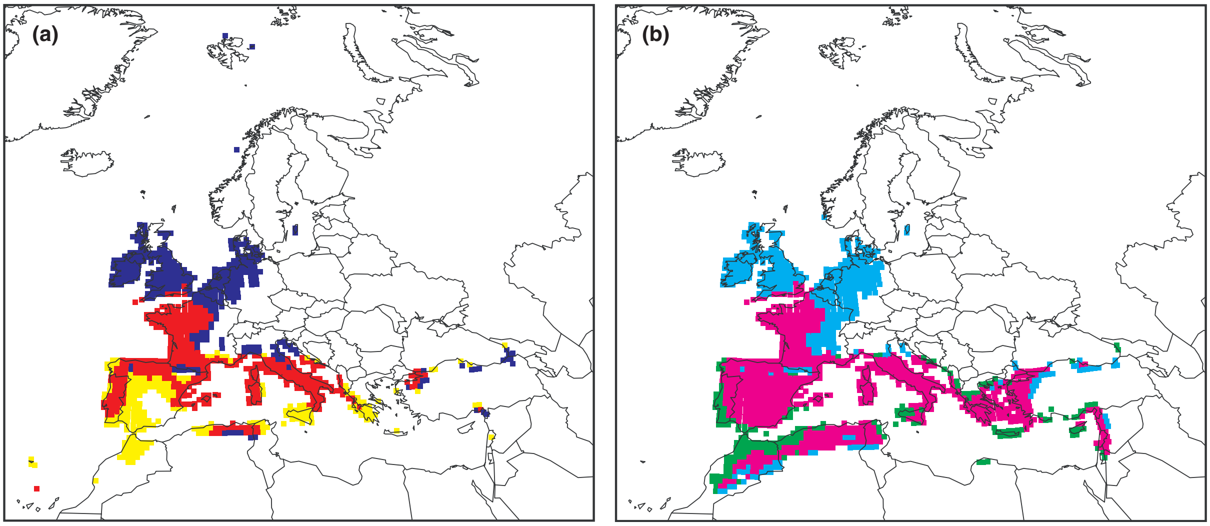

Figure 2 Simulated potential range changes between 1961–90 and 2071–2100 for the resident/short-distance migrant *Sylvia undata* (Dartford warbler): (a) breeding range; (b) non-breeding range. Results shown are for the ECHAM4 general circulation model scenario. For key to shading colours see caption to Fig. 1.

any of the GCM scenarios (two-sample *t*-test, assuming unequal variance, on difference in centroid latitude, H, d.f. = 13.370, $t = -0.476$, $P = 0.642$; E, d.f. = 12.478, $t = -0.304$, $P = 0.766$; C, d.f. = 14.528, $t = -0.031$, $P = 0.976$). However, southward shifts of simulated non-breeding range were more frequent among trans-Saharan migrants, although only *S. atricapilla* showed a shift in this direction that was consistent across GCMs (mean shift across the three GCMs 7.5° S).

Relative non-breeding range extent *R* was consistently ≤ 100% for four species (mean 72%) and > 100% for six (mean 154%) (Table 2). As with breeding ranges, neither *R* nor *O* exhibited any consistent difference between trans-Saharan migrants and resident/short-distance or partial migrants for any GCM scenario (*t*-test on log *R*, d.f. = 14 in all cases, H, $t = 0.227$, $P = 0.823$; E, $t = -0.352$, $P = 0.723$; C, $t = -0.946$, $P = 0.360$; *t*-test on arcsine square root transformed *O*, d.f. = 14 in all cases, H, $t = 1.08$, $P = 0.296$; E, $t = 1.735$, $P = 0.104$; C, $t = 1.240$, $P = 0.235$). However, amongst the long-distance migrants, *O* was consistently greater for widespread than for restricted range species (*t*-test on arcsine square root transformed *O*, d.f. = 4 in all cases, H, $t = 4.62$, $P < 0.01$; E, $t = 4.20$, $P < 0.01$; C, $t = 3.65$, $P = 0.01$), the latter all being those with non-breeding ranges in east Africa (*Sylvia curruca*, *Sylvia nisoria*, *S. rueppelli*).

Comparisons among species

Although *R* differed for individual species across the GCM scenarios, species showed a high level of consistency across scenarios in their value of *R* (Table 2), both for breeding range (Kendall coefficient of concordance, $W = 0.828$, $P < 0.001$) and non-breeding range ($W = 0.792$, $P = 0.003$). However, positive correlations between inter-specific variation in *R* for the breeding and non-breeding ranges were weak and non-significant, except for the C scenario (Pearson correlation between log relative range extent for breeding and wintering ranges, H, $r = 0.219$, $P = 0.433$; E, $r = 0.459$, $P = 0.060$; C, $r = 0.543$, $P = 0.037$).

The overlap percentage *O* represents a worst-case scenario of potential range extent change where species fail to colonize newly climatically suitable areas but are lost from areas where climate becomes potentially unsuitable. Values of *O* were low both for breeding and non-breeding ranges (mean *O*, breeding range/non-breeding range: H 32/37%; E 32/33%; C 35/36%; Table 2). As for *R*, values of *O* differed considerably amongst species, although species' values of *O* showed very high consistency across scenarios, both for their breeding ($W = 0.959$, $P < 0.001$) and non-breeding ranges ($W = 0.952$, $P < 0.001$).

Migration distance

For all three future scenarios, migration distance potentially increased for most species, mean migration distance being significantly increased for two scenarios (Wilcoxon's signed rank tests, $n = 14$ in all cases, H, $z = -2.103$, $P < 0.05$; E, $z = -2.166$, $P < 0.05$; C, $z = -1.161$, $P < 0.245$). Across all three scenarios, mean increase in migration distance was greater for trans-Saharan migrants (413 km) than for resident/short-distance or partial migrants (201 km) (Table 3), although the variability amongst species was such that this difference was not significant for any scenario (Mann–Whitney *U*-tests, $n = 14$, H, $U = 15$, $P = 0.259$; E, $U = 17$, $P = 0.383$; C, $U = 17$, $P = 0.383$). Given the generally shorter migration distance for the latter group of species, potential increases as a proportion of the present distance were also examined, but again the variability amongst species was such that there was

Table 2 Relative extent and overlap for simulated present and potential future ranges of *Sylvia* warblers in Europe and Africa based on generalized additive models and IPCC third assessment report general circulation models (HadCM3, ECHAM4 and CSIRO Mk2).

	Relative range extent (%)			Range overlap (%)		
Species	HadCM3	ECHAM4	CSIRO Mk2	HadCM3	ECHAM4	CSIRO Mk2
(a) Breeding range						
S. sarda	58	180	85	0	0	4
S. balearica	106	324	224	0	0	0
S. undata	58	120	104	35	43	47
S. deserticola	10	39	16	1	0	0
S. conspicillata	58	65	74	44	36	51
S. cantillans	94	155	115	36	31	40
S. melanocephala	93	164	117	40	42	52
S. melanothorax	1217	983	917	5	0	9
S. rueppelli	78	57	61	1	1	6
S. nana	71	67	68	19	22	22
S. hortensis	107	109	108	32	32	36
S. crassirostris	96	100	97	17	18	16
S. nisoria	179	155	156	53	47	57
S. curruca	75	76	56	62	61	45
S. communis	92	97	99	72	75	77
S. borin	61	69	54	58	64	49
S. atricapilla	93	104	100	70	76	75
(b) Non-breeding range						
S. sarda	61	63	99	4	1	9
S. balearica	106	324	224	0	0	0
S. undata	70	106	95	54	54	58
S. deserticola	144	79	79	73	17	27
S. conspicillata	98	93	123	41	37	48
S. cantillans	176	232	143	39	40	42
S. melanocephala	120	160	137	60	50	59
S. melanothorax	152	128	120	7	5	8
S. rueppelli	103	89	81	8	14	8
S. nana	71	67	68	19	22	22
*S. hortensis** *S. crassirostris**	135*	170*	130*	39*	49*	39*
S. nisoria	95	83	114	50	46	53
S. curruca	73	54	47	11	16	16
S. communis	102	107	102	76	79	75
S. borin	82	88	86	79	83	82
S. atricapilla	138	162	131	51	46	56

*Value based on the combined non-breeding range of these two species that have not been separately mapped in their non-breeding area.

no significant difference between trans-Saharan migrants and residents/short-distance or partial migrants for any scenario (Mann–Whitney *U*-tests, $n = 14$, H, $U = 22$, $P = 0.749$; E, $U = 21$, $P = 0.655$; C, $U = 19$, $P = 0.482$). Potential changes in migratory distance were in most cases more a consequence of shifts in the breeding rather than the non-breeding range; the trans-Saharan migratory population of *S. atricapilla* was the main exception, its non-breeding range being potentially shifted south by more than twice the potential northward shift of the species' breeding range.

Potential maximum migration distance increased for trans-Saharan migrants under all three scenarios (Wilcoxon's signed ranks test, $n = 7$ in all cases, H, $z = -2.03$, $P < 0.05$; E, $z = -2.40$, $P < 0.05$; C, $z = -2.37$, $P < 0.05$), but showed no consistent pattern for residents/short-distance or partial migrants (Wilcoxon's signed ranks test, $n = 7$ in all cases, H, $z = -0.845$, $P = 0.398$; E, $z = -1.18$, $P = 0.237$; C, $z = -1.18$, $P = 0.237$). Minimum migration distance showed no consistent pattern of potential change, either across all species (Wilcoxon's signed ranks test, $n = 14$ in all cases; H, $z = -0.664$, $P = 0.507$; E, $z = -0.664$, $P = 0.507$; C, $z = -0.941$, $P = 0.347$), or when trans-Saharan migrants and resident/short-distance or partial migrants were considered separately.

Using the flight-range equation from Alerstam & Lindström (1990) and parameters from Erni *et al.* (2005), the potential increases in mean migration distance for trans-Saharan migrants and for residents/short-distance or partial migrants

Table 3 Simulated current and future migration distances and range shifts of *Sylvia* warblers in Europe and Africa.

	Migration distance (km)						Potential range shift (km)	
	Mean		Minimum		Maximum			
Species	Present	Potential future	Present	Potential future	Present	Potential future	Breeding range	Non-breeding range
S. sarda	400	450–1200	0	0	2400	2850–3550	150–650	100–300
S. balearica	–	–	–	–	–	–	970–990	–
S. undata	200	100–150	0	0	5000	5800–5850	400–650	500–800
S. deserticola	350	600–1400	0	150–800	2100	2800–3300	550–900	200–650
S. conspicillata	700	800–1250	0	0	5050	5300–5650	250–800	800–950
S. cantillans	2600	3050–3350	400	0	7200	9350–9600	700–950	200–250
S. melanocephala	500	700–800	0	0	7200	6350–6550	700–850	650–950
S. melanothorax	1050	200–250	0	0	2050	1400–1650	150–300	100–1000
S. rueppelli	1950	1350–2200	350	800–2050	6400	5400–8850	350–450	1350–1650
S. nana	–	–	–	–	–	–	200–300	–
*S. hortensis**	2700*	3100–3250*	1000*	0–100*	6600*	9300–9550*	700–800	250–350*
*S. crassirostris**							350–450	
S. nisoria	4800	5600–5750	2300	2150–2550	8500	11100–12150	800–1050	900–1350
S. curruca	4450	4350–4400	1750	850–1000	7600	11400–11500	500–600	850–950
S. communis	5500	5700–6050	1550	0	10800	12200–12500	350–450	350–500
S. borin	6550	6550–6650	1200	0–700	11700	12150–12500	400–550	300–550
S. atricapilla	–	–	–	–	–	–	450–450	–
Short-distance	1700	1500–1650	0	0	7050	7050–7100	–	500–650
Trans-Saharan	4550	5500–5800	1900	2200–2500	8950	11900–12200	–	720–1200

Distances are rounded to the nearest 50 km; the ranges of potential future values represent the range across the three general circulation model scenarios examined. Potential range shifts represent potential shifts in position of the range centroids. Figures for *S. atricapilla* are separated into those that undertake short distance versus trans-Saharan migration (see main text).

*Value based on the combined non-breeding range of these two species that have not been separately mapped in their non-breeding area.

equate to extra fuel loads of about 9% and about 5% of lean body mass, respectively. Assuming that such increases in fuel requirements for migration can be physiologically accommodated, they are likely to require birds to spend more time feeding prior to migration and/or to make additional stopovers.

Migration strategy

Potential new short-distance migratory strategies were identified for all three GCMs in four species of trans-Saharan migrant (*Sylvia communis*, *S. curruca*, *Sylvia cantillans*, *S. rueppelli*). Regions simulated as newly suitable for occupation in the non-breeding season, albeit of limited extent for each species, were in areas of Egypt, Libya, Morocco and Western Sahara (Fig. 1). In the case of *Sylvia conspicillata*, currently a short-distant migrant to North Africa, potential future non-breeding areas were simulated in mainland Europe. A potential increase was simulated in the proportion of populations of *S. atricapilla* adopting a short-distance or partial migratory strategy and spending the non-breeding season in areas used also in the breeding season; the mean extent of its 'resident' range for the three scenarios was 21% greater than at present.

For several species with non-breeding ranges that do not currently extend into the Southern Hemisphere, areas climatically suitable for use in the non-breeding season were simulated south of the equator under the future climate scenarios (Fig. 1b). Although the future use of such disjunct areas seems unlikely in most cases, if a species did utilize such areas in the future then migration distance would be substantially increased for at least part of its population.

DISCUSSION

Models relating breeding and non-breeding ranges to climate built using two modelling techniques all fitted well and were shown to be robust when tested using a stringent *k*-fold partitioning procedure. Although similarly well-fitting models have been constructed for the ranges of various plant and non-migratory animal species in several regions (e.g. Huntley *et al.*, 1995, 2004; Sykes, 1997; Erasmus *et al.*, 2002; Williams *et al.*, 2005; Araújo *et al.*, 2006; Thuiller *et al.*, 2006) and for the breeding ranges of migratory birds (e.g. Huntley *et al.*, 2006, 2007, 2008), models of the non-breeding ranges of migratory species have rarely been fitted (Martínez-Meyer *et al.*, 2004; Walther *et al.*, 2007). Whilst fit was generally poorer for models of non-breeding ranges, this may well reflect the poorer quality data available for species' non-breeding ranges, especially in sub-Saharan Africa, rather than a systematic difference in strength of the relationship between range and climate in the non-breeding and breeding seasons. Strong similarities between simulations of potential future ranges made for three GCM scenarios further increase confidence in our conclusions.

Most species' breeding ranges were simulated as potentially shifting northwards in response to climate scenarios for the end of the present century, whereas there was no consistent directional shift in non-breeding ranges, even when trans-Saharan migrants and resident/short-distance or partial migrants were considered separately. For many trans-Saharan migrants, parts of North Africa, especially around the Mediterranean, were simulated to be suitable for occupation in the future during the non-breeding season, whilst for some short-distance or partial migrants (e.g. *S. conspicillata*) such potential future suitability was newly simulated for areas in Europe. These potential northern additions to species' non-breeding ranges may be important in ensuring optimal migration timing under future changed climates. For some trans-Saharan migrants, a few areas within or on the southern borders of the Sahara are simulated as potentially newly suitable in future for occupation in the non-breeding season; realization of such potential range changes may be facilitated by ongoing 'greening' of the Sahel (Herrmann *et al.*, 2005; Olsson *et al.*, 2005). For some species the extent of the overlap between their breeding and non-breeding ranges will potentially increase, favouring increased adoption of a resident strategy in future by some partial migrants (e.g. *S. conspicillata*, *Sylvia undata*, *S. atricapilla*). In the case of *S. atricapilla*, however, short-distance and trans-Saharan migratory populations potentially face opposite pressures in future, with mean 'migration distance' simulated to decrease by 50–250 km for short-distance migrant populations but to increase by 950–1250 km for trans-Saharan migrant populations. The latter increase principally reflects simulated potential southward expansion of the species' non-breeding range, to include large areas of the southern tropics that are not currently used, and retraction from the east of the northern tropics.

Our results thus support our first proposition, that climatic change is expected to affect breeding and non-breeding ranges independently, especially for trans-Saharan migrants. They also support our second proposition, that migration distance between breeding and non-breeding areas is expected to increase for trans-Saharan migrants. Averaged across the three scenarios, migration distances for trans-Saharan migrants potentially increased by 421 km. The greatest contribution to these increases comes in most cases from the potential northward shift of species' breeding ranges.

All species were simulated potentially to lose some southern parts of their breeding range. However, anthropogenic activities, such as irrigated agriculture, may locally reduce the impacts on some species of projected future reductions in moisture availability, especially in Southern Europe (Böhning-Gaese & Lemoine, 2004). Northern parts of the species' present ranges are expected to become of increasing importance, potentially supporting the populations that will be vital to species' realization of their simulated range expansions to the north of their present northern limits. In some cases, species' northern populations are already exhibiting such increases, for example *S. undata* in southern Britain, apparently in response to recent climatic change (Crick, 2004).

For six species (*S. conspicillata*, *S. deserticola*, *Sylvia melanocephala*, *S. rueppelli*, *Sylvia sarda*, *S. undata*), isolated small regions suitable for occupation during the non-breeding season were simulated in southern Africa, far beyond the present non-breeding range of these species. Although these areas support two endemic resident *Sylvia* species (*S. subcaeruleum*, *S. layardi*) that use habitats similar to those favoured by the Mediterranean species (Shirihai *et al.*, 2001), it is considered unlikely, given their geographical isolation from the remainder of the species' ranges, that these areas will be colonized by the European breeding species, even if their extent is in future increased.

Simulated potential future range extents were on average increased for both breeding (154%) and non-breeding (113%) ranges. However, these mean figures obscure potentially severe negative impacts upon some individual species. Future breeding ranges were potentially reduced in extent for 47–76% of species, and non-breeding ranges for 46–53%, depending upon the scenario examined. More significantly, for five species (*Sylvia borin*, *S. curruca*, *S. nana*, *S. rueppelli*, *S. undata*) both their breeding and non-breeding range were on average simulated to decrease in extent; in three cases (*S. curruca*, *S. borin*, *S. nana*) both ranges were simulated to decrease in extent for all three scenarios. This further highlights the importance of examining both breeding and non-breeding ranges when considering the potential impacts of climatic change on migratory species. Even those species simulated in the future potentially to increase their range extent may not realize these increases if newly climatically suitable areas do not offer appropriate habitat and/or if other ecosystem components upon which they depend are less mobile and as a result lag in their response to climatic change. Responses of human land-use to climatic change may exacerbate this problem if they further reduce habitat availability (Erasmus *et al.*, 2002; Jetz *et al.*, 2007).

In addition to potential changes in range extent, it is also important to examine the extent to which potential future and current ranges overlap. Averaged across the three scenarios, overlaps between potential future and present breeding and non-breeding ranges were 33% and 36%, respectively. Although most birds are highly mobile and able to adjust their ranges so as to occupy areas where conditions are suitable, time is needed for the discovery and exploitation of newly suitable areas. In cases where a species is unable to persist in areas that have become climatically unsuitable, the extent of the area of overlap may determine the population that can be sustained until such time as newly suitable areas are located and colonized. In the case of migrants, genetically determined migration routes can be conserved even in the face of substantial climatic changes (Ruegg & Smith, 2002; Ruegg *et al.*, 2006), rendering the discovery of newly suitable areas unlikely. Sutherland (1998) reports evidence that several species that have expanded their breeding range retain suboptimal migration routes and non-breeding areas. Even after they have started to be used, newly suitable areas, and the associated new migration routes, may need further time for the genetic adaptations required to use them to become established amongst the species' populations (Berthold & Helbig, 1992; Sutherland, 1998). Site fidelity of populations (Markovets & Yosef, 2005) and potential lags in habitat availability in newly suitable areas (Bensch, 1999; Alerstam *et al.*, 2003) will further constrain future range changes.

Overlaps between potential future and present ranges were significantly less for species with restricted ranges than for widespread species. The most restricted overlaps were simulated for four resident/short-distance or partial migrant species of the Mediterranean region and North Africa (*S. balearica, S. deserticola, S. melanothorax*, *S. sarda*), along with *S. rueppelli*, a trans-Saharan migrant with a restricted European breeding range. All five species had breeding range overlaps of < 10% for all three scenarios, and three of the species (*S. balearica*, *S. melanothorax*, *S. sarda*) also had non-breeding range overlaps of < 10% for all three scenarios. In the case of *S. balearica*, overlap was zero percent for both breeding and non-breeding ranges for all three scenarios. In many studies of the potential impacts of climatic change on species' ranges, greater relative range displacements, and hence lower overlaps, are simulated for species with restricted ranges, leading to inferences that such species face greater additional extinction risks as a result of climatic change than do widespread species (Schwartz *et al.*, 2006). This pattern has been ascribed to poorer model fits for range-restricted species (Schwartz *et al.*, 2006); however, this was not the case in the present study (Table 1). Nonetheless, there may be other constraints to such species' distributions apart from climate. These may include behavioural constraints, resident island endemics apparently being adapted not to be dispersive and having unchanged ranges since they originated (Böhning-Gaese *et al.*, 2006), or morphological constraints, some resident species being poor fliers and hence having limited dispersal ability (Böhning-Gaese *et al.*, 2003). Such species thus may have greater climatic tolerances than are modelled, although it is more likely that these tolerances extend to include conditions experienced during the climatic fluctuations of the Quaternary, which was predominantly cooler than the recent past (Jansen *et al.*, 2007), rather than to the warmer conditions projected for the future (Meehl *et al.*, 2007). Only experimental investigations of the climatic tolerances of these species might provide greater insight into how they may be affected by potential future climatic changes.

Our results provide some support for our third proposition, that the impacts of climatic change upon resident/short-distance or partial migrants are expected to be less than upon trans-Saharan migrants, because breeding and non-breeding ranges of the former species are within the same hemisphere and general climatic zone, and thus likely to be affected in a similar manner. Although the simulated impacts upon range extent and overlap were similar for the two groups of species, the simulated impacts upon migration distances differed. This was consistent with our expectation that the impacts of climatic change will be greater upon species having widely separated breeding and non-breeding ranges lying, respectively, in parts of the temperate and tropical climatic zones, and especially upon those species whose breeding and non-breeding ranges lie north and south of the equator. Our fourth proposition, that the impacts of climatic change will be greater for species with breeding or non-breeding ranges of limited geographical extent, because there is likely to be less overlap between their present and potential future ranges, is also strongly supported by our results. Given the importance of the area of overlap for the persistence of species in the face of rapid climatic change and resulting potential lags in the response of other ecosystem components, this result indicates that range-restricted species are likely to suffer a more severe negative impact.

Our simulations have not considered the potential impacts of climatic change on stopover areas, some of which are vital refuelling sites without which migration across extensive unfavourable areas, such as the Sahara, would be impossible. No account has been taken either of the likely impacts of seasonal climatic changes on the timing of migration, nor of the potential changes in habitat availability resulting from changes in human land-use in response to climatic change. It is likely, however, that all of these factors will act to increase the pressures upon migratory species as a result of climatic change. Increased migration distances amongst trans-Saharan migrants may further exacerbate recently observed mismatches between the timing of arrival of long-distance migrants and the seasonal peak in food availability in their breeding areas (Both & Visser, 2001; Both *et al.*, 2006). Furthermore, maximum potential migration distances are simulated to increase substantially for trans-Saharan migrants. Although knowledge of migration patterns amongst populations of trans-Saharan migrant *Sylvia* species is extremely limited, there is evidence of 'leap-frog' migration in other European breeding trans-Saharan migrants (Bell, 2007) and in New World warblers (Kelly *et al.*, 2002; Clegg *et al.*, 2003). It is likely that at least some *Sylvia* species exhibit this behaviour, in which case the potential impacts upon their most northerly breeding populations are considerable. As much as 900 km may be added to their migration distances. Such an additional distance would either require an additional fuel load of about 20% of lean body mass (using the formulae given in Erni *et al.*, 2005), or would necessitate additional stopovers, extending the time spent migrating. The physiology of migration is complex, however, and remains understudied; we thus cannot confidently predict the likelihood of the simulated potential changes in migration distances being attainable.

These results emphasize the complexity of responses that migratory species may be expected to show to climatic change. They also serve to highlight that considering only the response of the breeding ranges of migratory species to climatic changes is likely seriously to underestimate the potential negative impacts of climatic change on these species. Although the phenomenon of seasonal migration may have evolved in response to past climatic changes (e.g. Mila *et al.*, 2006), and it is clear that species' migrations adapted to the changing climatic conditions of the Pleistocene ice age, the challenge now faced by many species is unprecedented. The future for many migratory species will depend not only upon their ability to adapt, but also critically upon our success in meeting the challenge of ensuring that conservation strategies are designed to facilitate changes in breeding and non-breeding ranges, changes in stopover requirements and adaptation of migration routes, all of which are likely to form part of the response of these species to future climatic changes.

ACKNOWLEDGEMENTS

We are grateful to Stuart Butchart and his colleagues at Birdlife International, Cambridge, for making available distribution maps from the 'World Bird database', to the EBCC and Ward Hagemeijer for access to breeding range data for Europe. N. D. is supported by a studentship from NERC (NER/S/A/2005/13276) complemented by a CASE partnership with the RSPB. We thank Bruno Bruderer and an anonymous referee for their constructive comments on an earlier version of this paper.

REFERENCES

Alerstam, T. & Lindström, A. (1990) Optimal bird migration: the relative importance of time, energy and safety. *Bird migration: physiology and ecophysiology* (ed. by E. Gwinner), pp. 331–351. Springer, Berlin.

Alerstam, T., Hedenstrom, A. & Akesson, S. (2003) Long-distance migration: evolution and determinants. *Oikos*, **103,** 247–260.

Araújo, M.B., Thuiller, W. & Pearson, R.G. (2006) Climate warming and the decline of amphibians and reptiles in Europe. *Journal of Biogeography*, **33,** 1712–1728.

Austin, G.E. & Rehfisch, M.M. (2005) Shifting nonbreeding distributions of migratory fauna in relation to climatic change. *Global Change Biology*, **11,** 31–38.

Baillie, S. & Peach, W. (1992) Population limitation in Palaearctic-African migrant passerines. *Ibis*, **134,** 120–121.

Bearhop, S., Fiedler, W., Furness, R.W., Votier, S.C., Waldron, S., Newton, J., Bowen, G.J., Berthold, P. & Farnsworth, K. (2005) Assortative mating as a mechanism for rapid evolution of a migratory divide. *Science*, **310,** 502–504.

Bell, C.P. (2007) Climate change and spring migration in the yellow wagtail *Motacilla flava*: an Afrotropical perspective. *Journal of Ornithology*, **148,** S495–S499.

Bensch, S. (1999) Is the range size of migratory birds constrained by their migratory program? *Journal of Biogeography*, **26,** 1225–1235.

Berthold, P. (1988) Evolutionary aspects of migratory behaviour in European warblers. *Journal of Evolutionary Biology*, **1,** 195–209.

Berthold, P. (2001) *Bird migration: a general survey*, 2nd edn. Oxford University Press, Oxford.

Berthold, P. & Helbig, A.J. (1992) The genetics of bird migration – stimulus, timing, and direction. *Ibis*, **134,** 35–40.

Böhning-Gaese, K. & Lemoine, N. (2004) Importance of climate change for the ranges, communities and conservation of birds. *Birds and climate change, Advances in Ecological Research Vol. 35* (ed. by A.P. Møller, H. Caswell, W. Fiedler and P. Berthold), pp. 211–236. Academic Press, London.

Böhning-Gaese, K., Schuda, M.D. & Helbig, A.J. (2003) Weak phylogenetic effects on ecological niches of *Sylvia* warblers. *Journal of Evolutionary Biology*, **16,** 956–965.

Böhning-Gaese, K., Caprano, T., van Ewijk, K. & Veith, M. (2006) Range size: disentangling current traits and phylogenetic and biogeographic factors. *The American Naturalist*, **167,** 555–567.

Both, C. & Visser, M.E. (2001) Adjustment to climate change is constrained by arrival date in a long-distance migrant bird. *Nature*, **411,** 296–298.

Both, C., Bouwhuis, S., Lessells, C.M. & Visser, M.E. (2006) Climate change and population declines in a long-distance migratory bird. *Nature*, **441,** 81–83.

Christensen, J.H., Hewitson, B., Busuioc, A., Chen, A., Gao, X., Held, I., Jones, R., Kolli, R.K., Kwon, W.-T., Laprise, R., Magaña Rueda, V., Mearns, L., Menéndez, C.G., Räisänen, J., Rinke, A., Sarr, A. & Whetton, P. (2007) Regional climate projections. *Climate Change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), pp. 847–940. Cambridge University Press, Cambridge.

Clegg, S.M., Kelly, J.F., Kimura, M. & Smith, T.B. (2003) Combining genetic markers and stable isotopes to reveal population connectivity and migration patterns in a Neotropical migrant, Wilson's warbler (*Wilsonia pusilla*). *Molecular Ecology*, **12,** 819–830.

Cleveland, W.S. & Devlin, S.J. (1988) Locally weighted regression: an approach to regression analysis by local fitting. *Journal of the American Statistical Association*, **83,** 596–610.

Cohen, J. (1960) A coefficient of agreement for nominal scales. *Educational and Psychological Measurements*, **20,** 37–46.

Cotton, P.A. (2003) Avian migration phenology and global climate change. *Proceedings of the National Academy of Sciences USA*, **100,** 12219–12222.

Crick, H.Q.P. (2004) The impact of climate change on birds. *Ibis*, **146,** 48–56.

Crick, H.Q.P., Dudley, C., Glue, D.E. & Thompson, D.L. (1997) UK birds are laying eggs earlier. *Nature*, **388,** 526.

Erasmus, B.F.N., Van Jaarsveld, A.S., Chown, S.L., Kshatriya, M. & Wessels, K.J. (2002) Vulnerability of South African animal taxa to climate change. *Global Change Biology*, **8,** 679–693.

Erni, B., Liechti, F. & Bruderer, B. (2005) The role of wind in passerine autumn migration between Europe and Africa. *Behavioural Ecology*, **16,** 732–740.

Fielding, A.H. (2002) What are the appropriate characteristics of an accuracy measure? *Predicting species occurrences: issues* *of accuracy and scale* (ed. by J.M. Scott, P.J. Heglund, F. Samson, J. Haufler, M. Morrison, M. Raphael and B. Wall), pp. 271–280. Island Press, Covelo, CA.

Fielding, A.H. & Bell, J.F. (1997) A review of methods for the assessment of prediction errors in conservation presence/ absence models. *Environmental Conservation*, **24,** 38–49.

Gordo, O., Brotons, L., Ferrer, X. & Comas, P. (2005) Do changes in climate patterns in wintering areas affect the timing of the spring arrival of trans-Saharan migrant birds? *Global Change Biology*, **11,** 12–21.

Gordon, C., Cooper, C., Senior, C.A., Banks, H., Gregory, J.M., Johns, T.C., Mitchell, J.F.B. & Wood, R.A. (2000) The simulation of SST, sea ice extents and ocean heat transports in a version of the Hadley Centre coupled model without flux adjustments. *Climate Dynamics*, **16,** 147–168.

Green, R.E., Collingham, Y.C., Willis, S.G., Gregory, R.D., Smith, K.W. & Huntley, B. (2008) Performance of climate envelope models in retrodicting recent changes in bird population size from observed climatic change. *Biology Letters*, **4,** 599–602.

Hagemeijer, E.J.M. & Blair, M.J. (1997) *The EBCC atlas of European breeding birds: their distribution and abundance*. T & AD Poyser, London.

Hastie, T. (2006) *GAM: generalized additive models. R Package Version 0.97*. Available at http://cran.r-project.org/web/packages/gam/index.html(last accessed 28/01/2009).

Herrmann, S.M., Anyamba, A. & Tucker, C.J. (2005) Recent trends in vegetation dynamics in the African Sahel and their relationship to climate. *Global Environmental Change: Human and Policy Dimensions*, **15,** 394–404.

Hirst, A.C., Gordon, H.B. & Ofarrell, S.P. (1996) Global warming in a coupled climate model including oceanic eddy-induced advection. *Geophysical Research Letters*, **23,** 3361–3364.

Huntley, B., Berry, P.M., Cramer, W.P. & McDonald, A.P. (1995) Modelling present and potential future ranges of some European higher plants using climate response surfaces. *Journal of Biogeography*, **22,** 967–1001.

Huntley, B., Green, R.E., Collingham, Y.C., Hill, J.K., Willis, S.G., Bartlein, P.J., Cramer, W., Hagemeijer, W.J.M. & Thomas, C.J. (2004) The performance of models relating species' geographical distributions to climate is independent of trophic level. *Ecology Letters*, **7,** 417–426.

Huntley, B., Collingham, Y.C., Green, R.E., Hilton, G.M., Rahbek, C. & Willis, S.G. (2006) Potential impacts of climatic change upon geographical distributions of birds. *Ibis*, **148,** 8–28.

Huntley, B., Green, R.E., Collingham, Y.C. & Willis, S.G. (2007) *A climatic atlas of European breeding birds*. Lynx Editions, Barcelona.

Huntley, B., Collingham, Y.C., Willis, S.G. & Green, R.E. (2008) Potential impacts of climatic change on European breeding birds. *PLoS ONE*, **3,** e1439.

Jansen, E., Overpeck, J., Briffa, K.R., Duplessy, J.-C., Joos, F., Masson-Delmotte, V., Olago, D., Otto-Bliesner, B., Peltier, W.R., Rahmstorf, S., Ramesh, R., Raynaud, D., Rind, D., Solomina, O., Villalba, R. & Zhang, D.E. (2007) Palaeoclimate. *Climate Change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), pp. 433–497. Cambridge University Press, Cambridge, UK.

Jenni, L. & Kéry, M. (2003) Timing of autumn bird migration under climate change: advances in long-distance migrants, delays in short-distance migrants. *Proceedings of the Royal Society B: Biological Sciences*, **270,** 1467–1471.

Jetz, W., Wilcove, D.S. & Dobson, A.P. (2007) Projected impacts of climate and land-use change on the global diversity of birds. *PLoS Biology*, **5,** 1211–1219.

Jones, P., Vickery, J., Holt, S. & Cresswell, W. (1996) A preliminary assessment of some factors influencing the density and distribution of Palaearctic passerine migrants wintering in the Sahel zone of West Africa. *Bird Study*, **43,** 73–84.

Jonzén, N., Hedenström, A., Hjort, C., Lindström, Å., Lundberg, P. & Andersson, A. (2002) Climate patterns and the stochastic dynamics of migratory birds. *Oikos*, **97,** 329–336.

Kelly, J.F., Atudorei, V., Sharp, Z.D. & Finch, D.M. (2002) Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios. *Oecologia*, **130,** 216–221.

Lack, P. (1986) *The atlas of wintering birds in Britain and Ireland*. T & A.D Poyser, Calton.

Lemoine, N. & Böhning-Gaese, K. (2003) Potential impact of global climate change on species richness of long-distance migrants. *Conservation Biology*, **17,** 577–586.

Markovets, M. & Yosef, R. (2005) Phenology, duration, and site fidelity of wintering bluethroat (*Luscinia svecica*) at Eilat, Israel. *Journal of Arid Environments*, **61,** 93–100.

Marra, P.P., Francis, C.M., Mulvihill, R.S. & Moore, F.R. (2005) The influence of climate on the timing and rate of spring bird migration. *Oecologia*, **142,** 307–315.

Martínez-Meyer, E., Peterson, A.T. & Navarro-Siguenza, A.G. (2004) Evolution of seasonal ecological niches in the *Passerina* buntings (Aves: Cardinalidae). *Proceedings of the Royal Society B: Biological Sciences*, **271,** 1151–1157.

Meehl, G.A., Stocker, T.F., Collins, W.D., Friedlingstein, P., Gaye, A.T., Gregory, J.M., Kitoh, A., Knutti, R., Murphy, J.M., Noda, A., Raper, S.C.B., Watterson, I.G., Weaver, A.J. & Zhao, Z.-C. (2007) Global climate projections. *Climate Change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (ed. by S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K.B. Averyt, M. Tignor and H.L. Miller), pp. 747–845. Cambridge University Press, Cambridge.

Mila, B., Smith, T.B. & Wayne, R.K. (2006) Postglacial population expansion drives the evolution of long-distance migration in a songbird. *Evolution*, **60,** 2403–2409.

Mitchell, T.D., Carter, T.R., Jones, P.D., Hulme, M. & New, M. (2004) *A comprehensive set of high-resolution grids of monthly climate for Europe and the globe: the observed* *record (1901–2000) and 16 scenarios (2001–2100)*. Working Paper 55. Tyndall Centre for Climate Change Research, Norwich.

Nakicenovic, N. & Swart, R. (2000) *Emissions scenarios. Special Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge.

New, M., Hulme, M. & Jones, P. (1999) Representing twentieth-century space–time climate variability. Part l: Development of a 1961–90 mean monthly terrestrial climatology. *Journal of Climate*, **12,** 829–856.

Olsson, L., Eklundh, L. & Ardö, J. (2005) A recent greening of the Sahel – trends, patterns and potential causes. *Journal of Arid Environments*, **63,** 556–566.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421,** 37–42.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A. & Solomon, A.M. (1992) A global biome model based on plant physiology and dominance, soil properties and climate. *Journal of Biogeography*, **19,** 117–134.

R Development Core Team (2006) *R: a language and environment for statistical computing, 2.4.1*. R Foundation for Statistical Computing, Vienna, Austria.

Robinson, R.A., Learmonth, J.A., Hutson, A.M., Macleod, C.D., Sparks, T.H., Leech, D.I., Pierce, G.J., Rehfisch, M.M. & Crick, H.Q.P. (2005) *Climate change and migratory species. Report 414*. British Trust for Ornithology, Thetford.

Robinson, R.A., Crick, H.Q.P., Learmonth, J.A., Maclean, I.M.D., Thomas, C.D., Bairlein, F., Forchhammer, M.C., Francis, C.M., Gill, J.A., Godley, B.J., Harwood, J., Hays, G.C., Huntley, B., Hutson, A.M., Pierce, G.J., Rehfisch, M.M., Sims, D.W., Santos, M.B., Sparks, T.H., Stroud, D.A. & Visser, M.E. (2008) Travelling through a warming world – climate change and migratory species. *Endangered Species Research*, doi: 10:3354/esr.00095.

Roeckner, E., Oberhuber, J.M., Bacher, A., Christoph, M. & Kirchner, I. (1996) ENSO variability and atmospheric response in a global coupled atmosphere–ocean GCM. *Climate Dynamics*, **12,** 737–754.

Ruegg, K.C. & Smith, T.B. (2002) Not as the crow flies: a historical explanation for circuitous migration in Swainson's thrush (*Catharus ustulatus*). *Proceedings of the Royal Society B: Biological Sciences*, **269,** 1375–1381.

Ruegg, K.C., Hijmans, R.J. & Moritz, C. (2006) Climate change and the origin of migratory pathways in the Swainson's thrush, *Catharus ustulatus*. *Journal of Biogeography*, **33,** 1172–1182.

Saino, N., Szép, T., Ambrosini, R., Romano, M. & Møller, A.P. (2004a) Ecological conditions during winter affect sexual selection and breeding in a migratory bird. *Proceedings of the Royal Society B: Biological Sciences*, **271,** 681–686.

Saino, N., Szép, T., Romano, M., Rubolini, D., Spina, F. & Møller, A.P. (2004b) Ecological conditions during winter predict arrival date at the breeding quarters in a trans-Saharan migratory bird. *Ecology Letters*, **7,** 21–25.

Sanderson, F.J., Donald, P.F., Pain, D.J., Burfield, I.J. & van Bommel, F.P.J. (2006) Long-term population declines in Afro-Palaearctic migrant birds. *Biological Conservation*, **131,** 93–105.

Schwartz, M.W., Iverson, L.R., Prasad, A.M., Matthews, S.N. & O'Connor, R.J. (2006) Predicting extinctions as a result of climate change. *Ecology*, **87,** 1611–1615.

Shirihai, H., Gargallo, G. & Helbig, A.J. (2001) *Sylvia warblers: identification, taxonomy and phylogeny of the genus* Sylvia. Christopher Helm Publishers Ltd, London.

Snow, D.W. & Perrins, C.M. (1998) *The birds of the Western Palaearctic*, concise edn. Oxford University Press, Oxford.

Sutherland, W.J. (1998) Evidence for flexibility and constraint in migration systems. *Journal of Avian Biology*, **29,** 441–446.

Swets, J.A. (1988) Measuring the accuracy of diagnostic systems. *Science*, **240,** 1285–1293.

Sykes, M.T. (1997) The biogeographic consequences of forecast changes in the global environment: individual species' potential range changes. *Past and future rapid environmental changes: the spatial and evolutionary responses of terrestrial biota, NATO ASI Series I: Global Environmental Change*, Vol. 47 (ed. by B. Huntley, W. Cramer, A.V. Morgan, H.C. Prentice and J.R.M. Allen), pp. 427–440. Springer-Verlag, Berlin.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J., Collingham, Y.C., Erasmus, B.F.N., de Siqeira, M.F., Grainger, A., Hannah, L., Hughes, L., Huntley, B., van Jaarsveld, A.S., Midgley, G.F., Miles, L., Ortega-Huerta, M.A., Peterson, A.T., Phillips, O.L. & Williams, S.E. (2004) Extinction risk from climate change. *Nature*, **427,** 145–148.

Thuiller, W. (2003) BIOMOD – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, **9,** 1353–1362.

Thuiller, W., Broennimann, O., Hughes, G., Alkemade, J.R.M., Midgley, G.F. & Corsi, F. (2006) Vulnerability of African mammals to anthropogenic climate change under conservative land transformation assumptions. *Global Change Biology*, **12,** 424–440.

Walther, G.R., Post, E., Convey, P., Menzel, A., Parmesan, C., Beebee, T.J.C., Fromentin, J.M., Hoegh-Guldberg, O. & Bairlein, F. (2002) Ecological responses to recent climate change. *Nature*, **416,** 389–395.

Walther, B.A., Schaffer, N., Van Niekerk, A., Thuiller, W., Rahbek, C. & Chown, S.L. (2007) Modelling the winter distribution of a rare and endangered migrant, the aquatic warbler *Acrocephalus paludicola*. *Ibis*, **149,** 701–714.

Williams, P.H., Hannah, L., Andelman, S., Midgley, G.F., Araújo, M.B., Hughes, G., Manne, L., Martínez-Meyer, E. & Pearson, R.G. (2005) Planning for climate change: identifying minimum-dispersal corridors for the Cape Proteaceae. *Conservation Biology*, **19,** 1063–1074.

Zalakevicius, M., Bartkeviciene, G., Raudonikis, L. & Janulaitis, J. (2006) Spring arrival response to climate change in birds: a case study from eastern Europe. *Journal of Ornithology*, **147,** 326–343.

SUPPORTING INFORMATION

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

Table S1 Model performance for *Sylvia* warblers in Europe and Africa as assessed by the area under the curve (AUC) for a receiver operating characteristic plot.

BIOSKETCHES

The research team are largely based at the Centre for Ecosystem Science in Biological and Biomedical Sciences at Durham University (Nathalie Doswald, Stephen Willis, Yvonne Collingham and Brian Huntley), and collaborate with the RSPB (Deborah Pain and Rhys Green) and others to integrate climate change impacts into conservation planning.

Nathalie Doswald is a PhD student funded by an RSPB CASE-supported NERC studentship and is studying the potential impacts of climatic change on European breeding migratory birds.

Stephen Willis and **Brain Huntley** conceived the idea. **Stephen Willis**, **Brian Huntley** and **Rhys Green** (and formerly Deborah Pain) supervised **Nathalie Doswald**, who undertook the modelling and writing with assistance from her supervisors.

Yvonne Collingham assisted with data extraction, manipulation and modelling.

Editor: Jon Sadler