ORIGINAL ARTICLE

Physiological effects of climate on distributions of endothermic species

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ABSTRACT

Aim Determining the mechanisms underlying climatic limitation of species distributions is essential for understanding responses to current climatic change. Disentangling direct (e.g. physiological) and indirect (e.g. trophic) effects of climate on distributions through occurrence-based modelling is problematic because most species use the same area for both shelter and food acquisition. By focusing on marine birds that breed on land but feed at sea, we exploit a rare opportunity to dissociate direct from indirect climatic effects on endothermic species.

Location Coastal Europe.

Methods We developed climate-response surfaces (CRS) for 13 seabird species in coastal Europe, linking terrestrial climatic variables considered important for heat transfer with presence/absence data across each species' entire European breeding range. Agreement between modelled and actual distribution was assessed for jackknifed samples using area under the curve (AUC) of receiver operating characteristic plots. Higher AUC values indicated closer correspondence between observed breeding distribution and terrestrial climate. We assessed the influence of several ecological factors on model performance across species.

Results Species maximum foraging range and breeding latitude explained the greatest proportion of variation in AUC across species. AUC was positively related to both latitude and foraging range.

Main conclusions The positive relationship between foraging range and AUC suggests that species foraging further are more likely to be constrained by environmental heat stress conditions at the breeding site. One plausible explanation is that long foraging trips result in one parent spending long periods in continuous nest attendance, exposed to such conditions. These may include negative impacts through predation and parasitism in addition to physiological responses to the thermal environment, which probably explains why our models performed better for species breeding at higher latitudes, where such species interactions are considered less important. These data highlight the importance of considering physiological impacts of climate for endothermic species, and suggest that widespread oceanographic changes that reduce prey quality and quantity for seabirds at sea may be exacerbated by additional impacts of climate at the breeding site.

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INTRODUCTION

Recent climatic change has made investigation of species distributional limits a high priority (Harrington *et al.*, 1999), particularly because of the sensitivity of conservation planning to predicted species distributions (Wilson *et al.*, 2005). Large-scale, biogeographical studies are useful tools for assessing the potential impact of climatic change on species distributions at regional and global scales (Pearson & Dawson, 2003; Wiens *et al.*, 2009; Kearney *et al.*, 2010). Although mechanisms behind observed and predicted responses to climatic change have been identified in some cases (e.g. Pounds *et al.*, 2006), for many species the mechanisms behind climatic limitation of distributions remain elusive (Parmesan *et al.*, 2005), restricting confidence in modelling approaches (Pearson & Dawson, 2003).

One debate among ecologists concerns the extent to which climate acts to limit species distributions (and therefore diversity patterns) directly, for example through thermoregulatory or physiological constraints, or indirectly, by limiting available food or habitat resources and biotic interactions (Lennon *et al.*, 2000). It is difficult to distinguish between direct and indirect climatic limitations on species distributions, however, because individuals are usually exposed to both concurrently. The extent to which range shifts resulting from climatic change may depend on changing direct or indirect factors is therefore unclear for the majority of species.

Here, we exploit an opportunity to dissociate the direct physiological effects of climate on distributions of endothermic species from the indirect effects, by modelling the influence of terrestrial climate on the coastal breeding distributions of seabirds. Individuals in these coastal breeding colonies nest on land but feed mainly at sea. Thus they are directly exposed to climatic conditions in the colony that differ from those driving prey quality and abundance offshore. Previous studies investigating the effect of terrestrial climates on species distributions (e.g. Lennon *et al.*, 2000) have excluded marine birds because the literature emphasizes the significance of food and habitat for these species (see recent reviews by Durant *et al.*, 2004; Gremillet & Boulinier, 2009). Even so, direct effects of weather have been recorded (Schreiber, 2002; Frederiksen *et al.*, 2008) and some recent studies have emphasized the potential importance of heat stress at seabird breeding colonies (Gaston *et al.*, 2002; Oswald *et al.*, 2008). Assuming appropriate food and habitat resources are present within the breeding range, physiological limits may therefore act to shape distributions directly, as in the case of intertidal organisms (Helmuth *et al.*, 2005).

In view of recent work suggesting that thermoregulation may be a strong factor determining the climatic niches of endotherms (Porter & Kearney, 2009), we aimed to test whether or not thermal environments at breeding sites could explain the breeding distributions of endothermic species. We developed predictive climate response surfaces (CRS; Huntley *et al.*, 1995) relating the coastal breeding distributions of ground-nesting seabirds in Europe to terrestrial climatic variables associated with heat transfer (temperature, solar radiation and wind speed). These variables have been found to play a major role in thermoregulation (McNab, 2002) and have been used in biophysical models to estimate thermal stress under field conditions (Cartar & Morrison, 1997). We focused on coastal populations of ground-nesting gulls, terns and skuas because they are less likely to be limited by habitat availability than those with specialist habitat requirements (e.g. cliff nesters). Although many gulls, terns and skuas also maintain inland breeding colonies, individuals that nest inland are likely also to feed inland. Coastal populations, however, rely more heavily on marine prey (Strang, 1982; Becker *et al.*, 1997), which enables indirect trophic impacts of marine climate and direct effects of terrestrial climate at breeding colonies to be dissociated. Inland populations may also differ physiologically, for example in the functioning of the nasal salt gland, for the duration of breeding or perhaps as a result of microevolutionary change (Sabat, 2000). Thus we restricted our analysis to coastal populations.

To separate effects of terrestrial climate on distributions from those of marine climate (i.e. those mediated by prey quality or availability), we compared how the accuracy of breeding distributions simulated from CRS fitted using terrestrial climatic variables varied across species with different latitudinal distributions and foraging ranges. Parents typically do not leave their chicks unattended except in rare circumstances (Hamer *et al.*, 2002), and a long foraging trip by one parent forces the partner to be continuously present at the nest (Catry & Furness, 1999), directly exposed to extremes of terrestrial climate. Therefore a strong positive relationship between species foraging ranges and the accuracy of distributions generated using terrestrial climate variables associated with heat transfer would support the hypothesis that distributions are constrained by physiological effects of terrestrial climate at the colony. Prolonged nest attendance could also increase parents' exposure to adverse biological interactions such as predation and parasitism, but these are considered less important at higher latitudes, where there are fewer biotic interactions obscuring direct climatic effects (Suttle *et al.*, 2007; Beale *et al.*, 2008). Thus a combination of a close fit between observed and simulated distributions and a positive relationship between goodness-of-fit and both latitudinal distribution and foraging range would be more compatible with the above hypothesis than with alternative mechanisms. This effect would be separate from impacts of terrestrial climate on foraging conditions that would cause a negative relationship between model goodness-of-fit and foraging range. Our analysis therefore provides a rare opportunity to decouple the effects of marine and terrestrial climates on these marine predators and to investigate whether climatic niches of endothermic species suggest a physiological constraint on their distributions.

MATERIALS AND METHODS

Bioclimatic modelling

Climate response surfaces were constructed that separately related the presence/absence of breeding gull, tern and skua

species (Hagemeijer & Blair, 1997) in *c.* 50 × 50 km coastal Universal Transverse Mercator (UTM) grid cells throughout Europe (1073 cells) to three climatic variables, following the methods of Huntley *et al.* (1995) with modifications outlined below. Coastal cells were defined as cells intersected by the coastline of European land masses and islands. Species with insufficient range within Europe (assessed as ≤ 5% of grid cells) or specialized nesting habitat requirements were excluded from this analysis (details in Table S1.1 of Appendix S1 in Supporting Information). Mean (± 1 SD) prevalence (proportion of testing cells in which breeding was observed) of the 13 species selected was 0.32 ± 0.17; range 0.08–0.55.

Each CRS incorporated three climatic variables that reflected terrestrial conditions important for heat transfer during the breeding season (May–July): the sum of daily air temperature above a thermal threshold (13 °C), and two variables important in heat transfer, namely mean solar radiation and mean wind speed. Temperature sum > 13 °C was chosen because this threshold was suggested as a distributional thermal limit for great skuas *Catharacta skua* (Furness, 1988), and adults begin to desert their breeding territories to engage in thermoregulatory behaviour such as bathing at around this temperature (Oswald *et al.*, 2008). Although other species have different thermal limits, predictions from CRS models were robust across different thresholds and a known, lower threshold was therefore chosen (S.A.O., unpublished data).

To ensure there were no indirect mechanisms associated with any of our three predictor variables, we determined correlations between these variables and indices of nesting habitat availability and marine climate (winter/spring sea surface temperature) using Pearson's correlation coefficient corrected for spatial autocorrelation (Dutilleul, 1993), implemented in program Mod_t_test (Legendre, 2000). For each species, available nesting habitat within each 50 × 50 km cell of the simulated distribution was calculated as the number of 0.0089 decimal degree grid cells (*c.* 1 km^2) from the 2000 Global Landcover Classification (GLC2000; Bartholomé & Belward, 2005) that were suitable for nesting (i.e. vegetation height < 1 m: GLC2000 classes 10, 13, 16, 19 and 22). Marine climate was assessed in terms of winter/spring sea surface temperature (SST) (mean of February and March SST) because localized biological productivity is most strongly related to SST during this period of the year (Durant *et al.*, 2004).

Climatic data were extracted from the 0.5 × 0.5° resolution Climate Research Unit (CRU) 1960–91 30-year mean climatology (New *et al.*, 1999) and interpolated to generate a mean value at the centre of each grid cell (final grid extent was 30.0° N to 81.7° N, 31.2° W to 66.9° E). Temperature sums were calculated from 'quasi-daily' values estimated by linear interpolation between monthly means (Prentice *et al.*, 1992). Response surfaces were fitted by locally weighted regression (Cleveland & Devlin, 1988), which requires no assumptions regarding the form of the

relationship between climate and distribution (Beerling *et al.*, 1995).

Model performance

For each species, the probability of breeding in each grid cell was simulated by the response surface using observed climatic data and then compared with observed distributions. To avoid statistical over-fitting by testing surfaces with data used in their construction, we randomly jackknifed data into training (444 cells) and testing (629 cells) sets 100 times, allowing 100 separate evaluations for 'novel regions' of the same data (Fielding & Bell, 1997). This 41:59% split was determined following the protocol described by Fielding & Bell (1997, p. 40).

Simulated probabilities of occurrence from each of the 100 test datasets were compared with observed presence/absence to produce 100 receiver operating characteristic (ROC) plots of sensitivity against 1 – specificity (Manel *et al.*, 2001). Mean area under the curve (AUC) of ROC plots across all 100 simulations was calculated for each species: this reflected the ability of surfaces to define a species' climatic requirements, that is, the association of species distribution with terrestrial climate. AUC values of 0.5 indicated predictive performance identical to chance; 0.5–0.7 indicated poor predictive accuracy; 0.7–0.9 indicated potentially useful predictive accuracy; and > 0.9 indicated highly accurate predictive models (Manel *et al.*, 2001).

The indiscriminate use of AUC to assess the performance of species distribution models has been criticized, mainly because it cannot account for errors of omission or commission in the data used to generate the models, and because AUC can be sensitive to a species' prevalence within the modelled landscape (Lobo *et al.*, 2008). However, breeding colonies of our study species are very conspicuous and well reported, making errors of omission or commission unlikely. Moreover, AUC is affected mainly by extreme values of prevalence (close to 0 or 1), and an independent analysis of 306 species indicated that, for the range of values encompassed by our study species (0.08–0.55), the effect of prevalence on AUC was negligible (Huntley *et al.*, 2004). In keeping with this expectation, there was no relationship between prevalence and AUC in our data (Pearson correlation: $r = 0.29$, $n = 13$, $P = 0.3$). Other studies have also found AUC to be the most appropriate metric for assessing the performance of predictive models of distribution (Manel *et al.*, 2001; Wisz *et al.*, 2008) and we are confident that it is a robust metric for our analyses.

To check that our CRS results were not method-dependent, we separately fitted all models using generalized additive models (GAMs) (Yee & Mitchell, 1991). To permit maximum comparability with the CRS models, we fitted the GAMs with binomial error distributions and logistic link functions to all three variables, smoothed across two nodes with a spline smoother. The results of the two methods were similar and led to the same conclusions, so only the CRS results are reported here (see Tables S2.1–2.4 in Appendix S2).

Table 1 Discriminatory performance of climate response surface models for breeding seabirds in coastal Europe (assessed using area under the curve of receiver operating characteristic plots, AUC) and variables used in generalized linear models to explore interspecific ecological associations with AUC.

ID	Species	AUC (± 1 SE)	Latitude of northern range margin (°N)	Latitude of southern range margin (°N)	Mean available nesting habitat (no. of cells)	Extent of breeding range (km)	Body mass (g)	Percentage of pelagic items in diet	Maximum foraging range (km)
1	*Larus argentatus*	0.899 (± 0.02)	71.0	36.7	30.2	3815	1085	40.0	50
2	*Larus michahellis*	0.741 (± 0.03)	53.9	22.3	28.2	3505	1154	35.0	120
3	*Larus canus*	0.874 (± 0.02)	71.9	44.1	28.5	3083	404	3.5	40
4	*Larus fuscus*	0.834 (± 0.02)	71.0	37.8	29.4	3690	766	40.0	80
5	*Larus hyperboreus*	0.840 (± 0.04)	80.0	54.1	18.9	2878	1413	20.0	70
6	*Larus marinus*	0.875 (± 0.02)	79.5	33.9	28.5	5071	1659	15.0	60
7	*Stercorarius parasiticus*	0.882 (± 0.02)	80.0	50.9	17.4	3238	446	86.0	50
8	*Stercorarius skua*	0.832 (± 0.04)	80.0	54.4	22.8	2845	1340	62.0	50
9	*Sternula albifrons*	0.654 (± 0.03)	65.7	3.5	33.2	6909	57	100.0	7
10	*Hydroprogne caspia*	0.804 (± 0.04)	65.7	3.5	19.4	6909	623	100.0	70
11	*Sterna hirundo*	0.743 (± 0.02)	71.2	6.5	29.5	7186	120	83.0	15
12	*Sterna paradisaea*	0.903 (± 0.01)	80.0	41.0	26.8	4334	110	87.0	20
13	*Sterna sandvicensis*	0.654 (± 0.03)	58.4	36.5	39.1	2434	208	100.0	17

Range margins were estimated from Furness (1996), Burger & Gochfeld (1996) and Gochfeld & Burger (1996); body masses from Dunning (2007). Sources for maximum foraging range and diet are listed in Table S1.2 in Appendix S1. Mean available nesting habitat is the mean number of *c.* 1 km² GLC2000 (Bartholomé & Belward, 2005) grid cells in each 50 × 50 km grid cell with simulated presence.

Estimating the strength and direction of association between species foraging range and model performance

Generalized linear models (GLM) were fitted that related species' AUC values (the association between species distribution and terrestrial climate) to species foraging ranges and a number of potentially confounding variables (Table 1). Body mass and breeding latitude (northern and southern range margins) were included because both may affect how strongly species are affected by climate (Stevenson & Bryant, 2000; Nudds & Oswald, 2007). Diet was included, in terms of relative dependence on pelagic prey, to check that any relationship with foraging range was independent of the extent to which species fed close to shore. Family (Sternidae, Laridae or

Stercorariidae) was included to control for possible confounding effects of phylogeny.

Maximum foraging ranges were the highest values reported in the literature for breeding adults within coastal Europe; diets (the proportion of pelagic species in the diet) were averages across reported European breeding locations (where European dietary data were not available, averages from other temperate or Arctic populations were substituted). Sources are given in Table S1.2 in Appendix S1. Both maximum foraging range and body mass were normalized by log transformation prior to all analyses.

As many of these ecological factors covary (see Table S2.4 in Appendix S2), GLM model selection was performed in two ways using the MuMIn package (Barton, 2009) in R (R

Table 2 Correlation between the three variables used in climate response surface models for breeding seabirds in coastal Europe, and habitat availability and marine productivity indices (see text for variable descriptions).

Variable 1	Variable 2	*n*	Corrected Pearson's correlation coefficient	d.f.	*F*	*P*
Habitat availability	Temperature sum	593	−0.16	28	0.73	0.40
Habitat availability	Mean solar radiation	712	−0.16	17	3.19	0.08
Habitat availability	Mean wind speed	712	0.01	43	0.01	0.94
Mean sea surface temperature (FM)	Temperature sum	820	−0.48	6	1.78	0.23
Mean sea surface temperature (FM)	Mean solar radiation	1058	−0.34	13	1.68	0.22
Mean sea surface temperature (FM)	Mean wind speed	1058	0.27	15	1.17	0.30

Pearson's correlation coefficient and degrees of freedom are corrected for spatial autocorrelation using the method of Dutilleul (1993); the *F* statistic corresponds to a two-tailed *t* of the Pearson correlation coefficient between the two variables (Legendre, 2000). Probability (*P*) of obtaining the coefficient value by chance is given. All variables are calculated across May, June and July, except sea surface temperature, which was a winter/spring index calculated across February and March (FM).

Development Core Team, 2009). To address the relative strength of the relationship between AUC and foraging range, we ranked candidate models using Akaike's information criterion for small sample sizes (AIC$_c$) (Burnham & Anderson, 2002). To address the direction of the relationship between AUC and foraging range, we used model averaging to provide robust parameter estimation independent of the combination of parameters within any particular model (Burnham & Anderson, 2002).

RESULTS

The mean ($\pm$ SD) AUC value across all species was 0.81 ($\pm$ 0.09), and AUC values ranged from 0.65 to 0.90 (Table 1), indicating that CRS models based on heat-transfer variables produced simulated distributions that usefully described the distributions of most of the study species. None of the three climatic predictor variables used in the development of our response surfaces was significantly correlated with either marine productivity or habitat availability indices (Table 2).

The AUC was positively related to both maximum foraging range (Fig. 1a) and latitude of northern range margin, independently of one another (Fig. 1b; GLM: $F_{1,11} = 33.4$, $P < 0.001$; adjusted $R^2 = 0.73$). These two variables together explained 73% of the variation among species in AUC, and they were the only components of the most parsimonious GLM, identified by the lowest AIC$_c$ value (see Table S2.1 in Appendix S2). This model was preferred over the next best competing GLM that incorporated an extra parameter but did not explain significant extra variation in AUC among species (AIC$_c$ weights: 0.51 vs. 0.07; likelihood ratio: $G = 1.6$, $P = 0.2$).

Maximum foraging range and northern range margin also had the highest relative importance of all the variables explored in model averaging (Table 3). Although many of the predictors exhibited strong simple correlations (Pearson) with AUC, only foraging range exhibited a significant (partial) correlation once the influence of northern range margin was removed (Table S2.4 in Appendix S2). This indicates that only foraging range had a strong, additional effect on AUC, independent from the influence of latitude of the northern range margin (the most important single predictor). No consistent relationship was found between AUC and the latitude of the southern range margin (Table 3). Substituting body mass for foraging range explained less of the overall variance in AUC ($R^2 = 0.63$; Table S2.1 in Appendix S2), indicating that the effect of foraging range on AUC was not simply a result of differences in body size. Family was absent from the best models (Table S2.1 in Appendix S2) and had low relative importance (Table 3), indicating that these results are unlikely to have been confounded by phylogeny.

DISCUSSION

For endothermic organisms, climatic exposure comprises both direct mechanisms (e.g. physiological) and indirect mechanisms (e.g. through changes in food availability or quality).
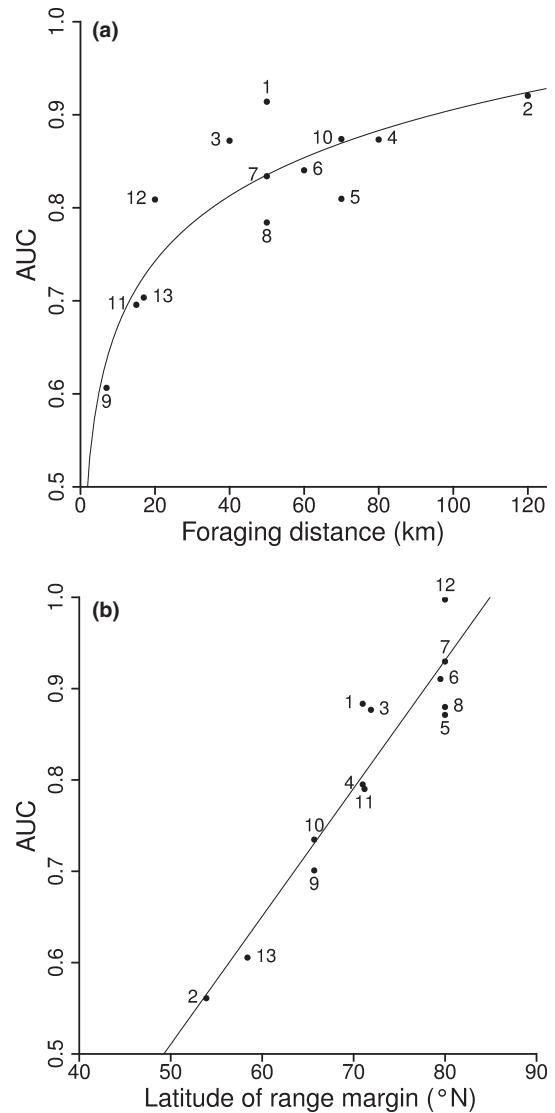

Figure 1 Relationship between the association of species breeding distributions with terrestrial climate [assessed using area under the curve of receiver operating characteristic plots (AUC) of climate response surface (CRS) models] and (a) maximum foraging range and (b) latitude of northern range margin for 13 species of gull, tern and skua in coastal Europe. Data shown are partial residuals from a generalized linear model in each case. For each plot, the *y*-axis is represented in the original units by adding to all data the product of the coefficient and mean of the variable not shown. Thus AUC values shown are for when one variable is held constant, and differ from original AUC values (Table 1). Numbers identify species (see Table 1).

Although there is much evidence for the latter, there is far less evidence for direct effects of climate on distributions of endothermic species (but see Jiguet *et al.*, 2006). For coastal populations of seabirds that breed on land but feed at sea, we find that the agreement between distribution and terrestrial climate (i.e. AUC) has a strong positive relationship with both species maximum foraging ranges (Fig. 1a) and the latitude of species northern range margins (Fig. 1b). Model averaging

Table 3 Model averaged components, standard errors, confidence intervals and relative importance across all possible candidate generalized linear models employing ecological variables to predict the discriminatory performance of climate response surface (CRS) models.

Ecological predictor variable	Model averaged component	Component SE	Lower confidence interval	Upper confidence interval	Relative importance
Northern range margin	0.00662	0.00210	0.0021	0.0112	0.95
Foraging range	0.09070	0.07010	−0.0543	0.2360	0.71
Body mass	−0.00075	0.01540	−0.0326	0.0311	0.17
Mean available nesting habitat	−0.00012	0.00064	−0.0015	0.0012	0.10
Diet	−0.00066	0.00148	−0.0037	0.0023	0.13
Southern range margin	0.00008	0.00020	−0.0003	0.0005	0.08
Family (skuas)	−0.00008	0.00018	−0.0004	0.0003	0.01
Family (terns)	−0.00044	0.00117	−0.0029	0.0020	–

CRS models were of breeding seabird distributions in coastal Europe; discriminatory performance was assessed using area under the curve of receiver operating characteristic plots (AUC). Relative importance is the sum of all Akaike weights for each of the models in which the predictor was included (Burnham & Anderson, 2002). Levels of family are relative to a 0.0 component for gulls; relative importance given is for all levels of family combined. See Table S2.3 in Appendix S2 for model averaged results for generalized additive models.

demonstrated that these positive relationships held across models, accounting for potential confounding effects such as body size, breeding habitat availability and phylogeny.

The positive relationship between AUC and foraging range supports the notion that species that forage further from breeding colonies are more directly constrained by terrestrial climatic conditions at the colony. This pattern is the opposite of that expected were breeding distributions of these species related to climate indirectly through impacts on marine food resources, because concordance between marine climate (affecting prey availability) and our terrestrial climate indices should decrease with increasing distance from the colony. Additionally, the positive relationship between AUC and foraging distance does not conform to the notion that species that forage more widely may be less sensitive to climate fluctuations (Sandvik & Erikstad, 2008).

Latitude of the northern range margin was the most important single predictor of the strength of association between species distributions and terrestrial climate. This probably reflected increasing climatic extremes placing a stronger constraint on breeding ranges of species at higher latitudes. The positive relationship between the accuracy of simulated distributions derived from terrestrial climate (AUC) and species foraging range was separate from these effects of latitude. As the impacts of habitat availability and diet on distribution were also allowed for by our modelling approach, our analysis suggests that species that forage further from the nesting site are more constrained by direct effects of climate at breeding colonies, over and above any of these indirect effects. As the three climatic variables we used to predict distributions are strongly associated with heat transfer and thermoregulation (McNab, 2002), our results support the notion that distributions of these species are influenced by the physiological constraints of climate.

Although our correlative approach is unable directly to elucidate the precise mechanisms of constraint, one possibility supported by the relationship we find with foraging range is that one member of each breeding pair normally remains at the colony to guard the offspring whilst its partner is at sea. Under adverse climatic conditions, long periods of continuous nest attendance for long-range foragers may increase the necessity for thermoregulation in response to heat stress, or to replenish water lost through panting, and may lead to temporary nest desertion (Oswald et al., 2008). Unattended offspring are vulnerable to being killed by both predators and conspecifics (e.g. Ashbrook et al., 2008) and so even temporary desertion of offspring can lead to breeding failure. Additionally, species with distributions that are more dependent on terrestrial climate may have been forced to nest further from foraging zones in the first instance, whereas species less constrained by terrestrial climate can nest closer to such zones. An alternative or complementary mechanism is that as our surfaces incorporated mean wind speed during the breeding season, they also encompassed the effect of wind on foraging ability. Wind strength can directly influence the foraging ability of seabirds (Dunn, 1973) and long-range foragers may be more constrained to breed in areas of consistently high wind speed (Furness & Bryant, 1996). Whatever the precise mechanism, our analyses indicate the likely importance of direct physiological effects of climate on the breeding distributions of endothermic species. These data add to the accumulating evidence (Helmuth et al., 2010; Kearney et al., 2010) that incorporating physiology into models of species distributions and directly testing thermal or other physiological constraints at range margins through experimentation and biophysical modelling will provide more robust predictions of the impacts of climatic change on species distributions.

Direct impacts have previously been considered important for ectothermic species (Beebee, 1995) and for the survival of endotherms in winter (Frederiksen et al., 2008), but rarely in summer (Jiguet et al., 2006; Oswald et al., 2008) or across species' geographical ranges. As energetic costs of maintaining a stable core temperature may be altered by climatic change, we can expect many endothermic species to respond directly (Porter & Kearney, 2009). Until now, direct climatic impacts on marine birds have been considered rare or short-lived

(Schreiber, 2002; Durant *et al.*, 2004), but our study indicates that breeding distributions may be influenced directly by climate in addition to any indirect effects of climate. Long-term, colony-based studies have shown that climate influences populations of marine birds and mammals indirectly through changes in prey and/or habitat availability (e.g. Forcada *et al.*, 2008). Many of these associations have been linked to large-scale climatic cycles that may have both direct and indirect effects (e.g. Irons *et al.*, 2008). The positive relationship we report for foraging range and AUC suggests that species spending more time foraging are vulnerable to direct climatic constraint (such as overheating) at breeding sites. The link we find between foraging range and sensitivity to terrestrial climate also suggests that widespread oceanographic changes that reduce prey quality or quantity and therefore extend adult foraging trips (Wanless *et al.*, 2005) will also increase species' susceptibility to direct climatic effects. Thus for marine birds, climate-induced changes in food supply may increase the severity of direct climatic constraints.

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SUPPORTING INFORMATION

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

Appendix S1 Species selection criteria (Table S1.1) and sources for diet and foraging range (Table S1.2).
Appendix S2 Further analytical results and results from generalized additive model analyses (Tables S2.1–2.4).

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BIOSKETCH

Stephen Oswald is investigating the implications of climate and climatic change for endothermic organisms. In particular, he seeks to quantify the physiological and behavioural constraints on heat loss for seabirds and waterbirds, and to understand how these shape spatial, demographic and evolutionary responses to environmental change.

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