THE ROYAL SOCIETY

Received 26 April 2002
Accepted 10 July 2002
Published online 20 September 2002

Responses of butterflies to twentieth century climate warming: implications for future ranges

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We analyse distribution records for 51 British butterfly species to investigate altitudinal and latitudinal responses to twentieth century climate warming. Species with northern and/or montane distributions have disappeared from low elevation sites and colonized sites at higher elevations during the twentieth century, consistent with a climate explanation. We found no evidence for a systematic shift northwards across all species, even though 11 out of 46 southerly distributed species have expanded in the northern part of their distributions. For a subset of 35 species, we model the role of climate in limiting current European distributions and predict potential future distributions for the period 2070–2099. Most northerly distributed species will have little opportunity to expand northwards and will disappear from areas in the south, resulting in reduced range sizes. Southerly distributed species will have the potential to shift northwards, resulting in similar or increased range sizes. However, 30 out of 35 study species have failed to track recent climate changes because of lack of suitable habitat, so we revised our estimates accordingly for these species and predicted 65% and 24% declines in range sizes for northern and southern species, respectively. These revised estimates are likely to be more realistic predictions of future butterfly range sizes.

Keywords: climate change; range expansion; habitat fragmentation; colonization

1. INTRODUCTION

Global climates are warming (IPCC 2001) and are affecting species in a variety of ecosystems (Hughes 2000; McCarty 2001; Walther *et al.* 2002). Quaternary responses of species indicate that most species would be expected to shift their distributions to keep track of current climate change, rather than adapt *in situ* (Huntley 1991; Coope 1995), and some species have expanded their distributions polewards (Hill *et al.* 1999*b*; Parmesan *et al.* 1999; Thomas & Lennon 1999; Warren *et al.* 2001) or to higher altitudes (Grabherr *et al.* 1994; Parmesan 1996) during recent twentieth century climate warming. Quaternary studies also indicate that species are likely to respond individualistically to climate change (Huntley & Birks 1983) and responses to recent climate change have been related to species' ecology; highly mobile species whose breeding habitat is widespread are more likely to track climate changes than are sedentary species (Warren *et al.* 2001). Responses to climate change are also likely to differ in relation to species' range; low-latitude species may benefit and have the potential to expand their ranges, although high-altitude and/or high-latitude species may have little opportunity to shift their ranges and may decline or become extinct (Huntley *et al.* 1995; Saetersdal *et al.* 1998; Pounds *et al.* 1999). Predictions are for continued climate warming by 1.4–5.8 °C during the twenty-first century (IPCC 2001) and the consequences that this will have for the conservation of biodiversity are of current concern (Peterson *et al.* 2002).

In this study, we use a combination of modelling and the analysis of existing distribution records to investigate the role of climate in limiting the distributions of 51 non-migratory British butterflies. This group includes butterflies with contrasting habitat specializations, as well as species that reach either a northern or southern range margin in Britain (Asher *et al.* 2001). We investigate changes in butterfly distributions in Britain during the twentieth century (Asher *et al.* 2001; Warren *et al.* 2001), when the climate warmed by 0.6 °C (IPCC 2001). Our previous analysis focused on changes in distribution size (Warren *et al.* 2001); here, we investigate the extent to which species have shifted their latitudinal and elevational range margins in Britain. Based on climate alone, we predict that during the twentieth century all species should have shifted their range margins northwards. Northern species should contract northwards and to higher elevations as areas in the southern part of their ranges become climatically unsuitable, and southern species should expand northwards into areas that become climatically suitable. Some studies have indicated that northern but not southern range margins have shifted in response to recent climate warming (Parmesan *et al.* 1999; Thomas & Lennon 1999), suggesting that climate may be less important in

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limiting southern range margins. However, in continental Europe, many species reach their southern range limits in mountainous regions and the perceived lack of response of species to climate change at southern margins may be due to species moving to higher altitudes, rather than latitudes, in these regions. We investigate altitudinal changes in species' distributions in Britain and test the hypothesis that, based on climate alone, species that reach their southern range margin in Britain will have been more likely to disappear from low elevation sites, compared with southerly distributed species.

We also investigate the role of climate in limiting species' continental distributions by modelling the relationship between each species' geographical distribution and present climate. The models generate climate surfaces that represent the probability of encountering species under a given combination of climate conditions. We use these models to determine the importance of climate in limiting butterfly distributions at a continental scale in Europe. We investigate whether climate is equally important in determining southern and northern continental range margins by measuring differences in the reliability of the models in simulating butterfly distributions in these two regions. We then incorporate output from a future climate-change scenario into the models to determine the extent of suitable climate for each species and their potential European distributions at the end of the twenty-first century. We produce two estimates, assuming that (i) species keep perfect track of future climate changes; or (ii) species show similar responses in the future to those observed during twentieth century climate changes.

2. METHODS

(a) *Study species and data sources*

We included all 51 species of non-migratory British butterfly in our study (with the exception of *Papilio machaon* (swallowtail), *Pieris brassicae* (large white) and *Pieris rapae* (small white); Warren *et al.* 2001). Four of the 51 study species have northern distributions (*Erebia aethiops* (scotch argus), *Coenonympha tullia* (large heath), *Aricia artaxerxes* (northern brown argus)) or montane distributions (*Erebia epiphron* (mountain ringlet)) in Britain and reach warm, southern and/or low elevation limits to their distributions in Britain. One additional species, *Carterocephalus palaemon* (chequered skipper), is currently restricted to northern Britain, but occurs at low elevations in northern and central Europe, south of Britain (Tolman 1997), so the southern/low elevation boundary of this species in Britain is unlikely to be dictated by climate. The remaining 46 species have southern distributions and reach the cool, northern limits of their ranges in Britain.

Butterfly distribution data for Britain were obtained from datasets compiled by the Biological Records Centre (CEH, Monks Wood) and Butterfly Conservation. Most records are from two time-periods (1970–1982 and 1995–1999), coinciding with periods of intensive recording effort prior to the publication of two national distribution atlases (Heath *et al.* 1984; Asher *et al.* 2001). All analyses are based on records of species' presence/absence at a 10 km-grid resolution. Determining changes in distribution from these records may be confounded by changes in recorder effort over time (65 826 record cards contributed to the first atlas and 437 690 record cards contributed to the second atlas), and also by differences in recorder effort between species as well as among regions. We accounted for these differences in recording effort in two ways, depending on the analyses being carried out (see § 2b). Disappearance of one of the northern species, *C. palaemon,* from England during the 1970s led to intensive surveys in Scotland during the 1980s and 1990s, which resulted in many more colonies being discovered in a small region that had previously been under-recorded (Asher *et al.* 2001). This may bias analyses of range margin shifts and elevation changes (see § 2b,c), so we carried out analyses both including and excluding *C. palaemon*; unless otherwise stated, the inclusion or exclusion of *C. palaemon* did not alter the significance of results, or our conclusions.

Multi-species analyses may be confounded by phylogeny, so we investigated responses of species to climate by using independent contrasts (CAIC) (Purvis & Rambaut 1995). In some analyses this was not possible. For example, CAIC cannot be used to test for significant differences in intercepts of regressions, and in some other analyses sample sizes were too small (too few contrasts). For these analyses, we present only results for non-phylogenetically controlled analyses. In no case did controlling for phylogeny affect our conclusions from non-phylogenetic analyses.

(b) *Analyses of range margin shifts*

We investigated shifts in species' British range margins between two time-periods, 1970–1982 and 1995–1999 (Heath *et al.* 1984; Asher *et al.* 2001). To equalize effort between these two time-periods, we sub-sampled the 1995–1999 dataset by randomly selecting the same number of record cards to those available for 1970–1982 from the 1995–1999 data. In order to retain the broad geographical distribution of 1970–1982 records, we carried out the sub-sampling separately for each 100 km Ordnance Survey grid square. For each time-period, we calculated the location of each species' range margin as the distance north of the 10 most northerly occupied 10 km grid squares (on the UK National Grid) for southerly distributed species, and the 10 most southerly occupied grid squares for northern species. Populations arising from introductions of species into areas beyond their range margin were ignored (Asher *et al.* 2001). We determined the size of the area occupied by each species in the two time-periods as the number of 10 km grid squares with one or more butterfly record. In order to investigate range changes in relation to species' ecology, we coded each species according to its habitat requirements (either widespread throughout the countryside, or a habitat specialist; Pollard & Yates 1993) and according to mobility (either mobile (following Dennis & Shreeve (1997), combining ranks 3–6) or sedentary (combining ranks 0–2)). However, these two characteristics are highly correlated in butterflies, as 32 out of 34 specialist species are sedentary and 18 out of 19 widespread species are mobile.

(c) *Altitudinal changes in distribution*

We studied altitudinal changes in the distribution of species during three time-periods (pre-1970, 1970–1982 and 1995–1999) by determining changes in the presence or absence of species in relation to the mean elevation of 10 km grid squares. The most comprehensive butterfly records are post-1970, but nonetheless we included all historical records in analyses because a 30-year period may not be sufficiently long to record the disappearance of species from entire 10 km grid squares. Because recording effort has greatly increased over time, we included all distribution records from before 1970 into a single historical time-period. Even though it covered a longer time-

period, the number of butterfly records during this historical period was *ca.* 50% of those for 1970–1982 (most records in this historical period are from the 1950s and 1960s).

As before, these analyses are likely to be sensitive to changes in recorder effort over time, particularly because many northern species occur in remote areas that may have been better recorded more recently. Our previous method of sub-sampling will not be sensitive enough for altitudinal analyses because information on butterfly presence/absence in particular 10 km grid squares is crucial. As an alternative, we compared altitudinal changes in distributions of the five northern species with those of 11 'control' species. Control species were selected if they were southern species (i.e. reach a northern limit to their distributions in Britain) but nonetheless have substantial distributions in Scotland. To account for phylogenetic effects, control species included all species in the same families or sub-families as the five study species (Lycaenidae, Hesperidae and Satyrinae). Two species (*Lasiommata megera* and *Hipparchia semele*) that are confined to coastal areas in Scotland were excluded. For control species, we restricted our analyses to distributions in northern Britain, north of the Ordnance Survey 500 km northing line. Thus, control species occur in similar regions to northern species and are likely to have experienced similar changes in recorder effort in these areas over time. Control species were *Ochlodes venata* (large skipper), *Erynnis tages* (dingy skipper), *Callophrys rubi* (green hairstreak), *Quercusia quercus* (purple hairstreak), *Lycaena phlaeas* (small copper), *Cupido minimus* (small blue), *Polyommatus icarus* (common blue), *Pararge aegeria* (speckled wood), *Maniola jurtina* (meadow brown), *Aphantopus hyperantus* (ringlet) and *Coenonympha pamphilus* (small heath).

(d) *Generating the climate models*

Climate-response surface models use locally weighted regression techniques to fit species' distributions at a 50 km grid resolution to three bioclimate variables. The methods that we used are explained in detail elsewhere (Beerling *et al.* 1995; Huntley *et al.* 1995; Hill *et al.* 1999*b*, 2001*a*, 2002). We generated climate-response surface models only for those British species ($n = 35$ species; table 1) that reach both a northern and southern range margin within the European study area (Tolman 1997; nine of these species have small, isolated populations in north Africa). All species that were excluded have substantial distributions in north Africa; for these species, southern range margins could not be included in the response surface models, making it impossible to predict future distributions in those parts of their ranges. We computed three bioclimatic variables chosen to reflect principal limitations on butterfly growth and survival (Hill *et al.* 1999*b*: (i) annual temperature sum above 5 °C; (ii) coldest-month mean temperature; and (iii) moisture availability) and fitted climate-response surfaces describing current European distributions of each butterfly species in terms of these three variables. The goodness-of-fit between species' observed distributions and those simulated from models was measured using the kappa statistic, which ranges from approximately zero when the fit is no better than random, to one when there is an exact fit (Monserud & Leemans 1992).

(e) *Importance of climate at northern and southern range margins*

In order to test if climate is more important in limiting northern than southern range margins, we divided the study area (Mediterranean to northern Scandinavia) into seven bands of 5° latitude width (latitudinal range 35–70° N). We used the kappa statistic to determine the proportion of 50 km grid squares correctly or incorrectly assigned by the model in the most northern and southern bands of each species' distribution. Bands with fewer than 30 grid squares with butterfly records were excluded and the adjacent band was used for analysis.

(f) *Predicting future distributions*

We obtained output from a climate-change scenario for the period 2070–2099 (UK Hadley Centre; HADCM2) using methods described in Hill *et al.* (1999*b*). We used output from HADCM2 to compute values for the three bioclimate variables for 2070–2099. These predicted future values were then used with the climate-response surfaces to generate simulated potential distributions for each of the 35 species that reaches both a northern and southern range-margin within the study area. The sizes of current and future ranges were calculated as the number of 50 km grid squares predicted to have suitable climate (i.e. above the threshold probability of butterfly occurrence). We also estimated future range sizes assuming that species will be unable to track climate precisely, i.e. species will disappear from southern parts of their ranges that become climatically unsuitable, but be unable to colonize any newly available, climatically suitable areas in the north.

3. RESULTS

(a) *Recent changes in butterfly distributions in Britain*

Between 1970–1982 and 1995–1999, the location of species' range margins moved very little (mean = 8.2 km movement southwards, s.d. = 54.7, $n = 51$ species). Over the same period, there was a mean decrease in distribution size of 15% (s.d. = 27.4, $n = 51$ species; maximum decline of 71% by *Argynnis adippe* (high brown fritillary); maximum increase of 76% by *Thymelicus lineola* (Essex skipper)). There was a significant, positive relationship between the change in range margin location and the change in range area (figure 1; regression of change in location of range margin against change in area$^{0.5}$ of 10 km grid squares with butterfly records, $F_{1,49} = 5.44$, $p = 0.024$). However, the intercept was not significantly different from zero ($t = 0.75$, $p = 0.5$) and thus range margin changes were consistent with overall changes in range area. This analysis was fairly insensitive to the method of determining location of range margin; there was also no significant intercept in this analysis if margin location was measured as the distance north of the single most northerly (or southerly for northern species) occupied 10 km grid square ($p > 0.1$). Thus, there was no evidence for margins shifting systematically north or south (for a given distribution size) in this cross-species comparison, although this does not preclude the possibility that expanding species are responding to climate warming. There was no significant difference in either slopes or elevations of regression lines in relation to species dispersal ability or habitat specificity ($p > 0.3$ in both cases), or between northern and southern species ($p > 0.1$). Nonetheless, the data presented in figure 1 show that 9 out of 11 species that have increased their distribution sizes (i.e. change in area of more than zero) are southerly distributed, widespread, mobile species; i.e. the species most capable of responding to climate warming (Warren *et al.* 2001).

Table 1. Range changes in a subset of 35 British butterfly species that reach a southern limit to their ranges in Europe. (kappa, goodness-of-fit of climate models; recs, number of 50 km Universal Transverse Mercator grid squares with records; sim, number of grid cells where the butterfly is simulated present for the 1931–1960 climate normal period (sim 1) and for a future (2070–2099) climate scenario (sim 2); match, number of grid cells where the butterfly currently occurs and that are predicted to be climatically suitable in the future; percentage change, predicted changes in range for the period 2070–2099 assuming instantaneous shifts in species' distributions; percentage change (revised), revised predictions for those species that have failed to track recent UK climate changes, and assuming that species only persist in squares that they currently occupy that continue to be climatically suitable in the future with no range shifts (* indicates southern species that have recently expanded their distributions in the UK and for which these revised estimates may not be appropriate). Species in bold type have northern and/or mountainous distributions.)

		current		future			
species	kappa	recs	sim 1	sim 2	percentage change	match	percentage change (revised)
Carterocephalus palaemon	0.76	1337	1397	926	−34	679	−51
Hesperia comma[a]	0.79	1610	1670	1851	+11	1375	−18
Ochlodes venata	0.80	1927	1934	2083	+8	1686	−13
Erynnis tages	0.77	1848	1861	2095	+13	1589	−15
Pyrgus malvae	0.83	1930	1952	2091	+7	1710	−12
Leptidea sinapis	0.75	2082	2078	2375	+14	1979	−5
Pieris napi[a]	0.73	2461	2449	2263	−8	2204	−10
Anthocharis cardamines	0.75	2137	2137	2132	0	1860	*
Thecla betulae	0.82	1481	1455	1453	0	1040	−29
Satyrium w-album	0.84	1631	1623	1782	+10	1310	−19
Satyrium pruni	0.82	1090	1025	834	−19	500	−51
Cupido minimus	0.76	1782	1776	1895	+7	1392	−22
Plebeius argus	0.79	1955	1911	2072	+8	1722	−10
Aricia artaxerxes[a]	0.70	1051	1123	818	−27	361	−68
Lysandra coridon	0.78	1270	1246	1456	+17	879	−30
Lysandra bellargus	0.79	1480	1419	1707	+20	1154	−19
Hamearis lucina	0.77	1227	1168	1431	+23	827	−29
Limenitis camilla	0.79	1098	1116	789	−29	335	−70
Apatura iris	0.83	1168	1175	893	−24	491	−58
Aglais urticae	0.73	2833	2818	2612	−7	2553	−9
Inachis io	0.83	2214	2254	2459	+9	1985	*
Boloria selene	0.79	1653	1716	1126	−34	942	−45
Boloria euphrosyne	0.78	2025	2014	1832	−9	1557	−23
Argynnis aglaja[a]	0.67	2420	2445	2268	−7	2170	−11
Argynnis paphia[a]	0.78	1884	1791	1961	+10	1582	−12
Euphydras aurinia[a]	0.75	1653	1627	1583	−3	1122	−31
Melitaea cinxia[a]	0.85	1633	1586	1796	+13	1305	−18
Melitaea athalia	0.82	2092	2063	2016	−2	1782	−14
Erebia epiphron	0.40	189	157	338	+115	49	−69
Erebia aethiops	0.80	862	790	566	−28	309	−61
Melanargia galathea[a]	0.77	1289	1275	1475	+16	866	*
Hipparchia semele	0.75	1764	1743	1698	−3	1286	−26
Pyronia tithonus[a]	0.75	1403	1310	1715	+31	1054	*
Aphantopus hyperantus	0.79	1674	1601	1331	−17	1048	*
Coenonympha tullia	0.81	1212	1229	331	−73	282	−77

[a] Species with small, additional isolated populations in north Africa (see § 2d).

(b) *Changes in elevation*

We compared elevation changes in species distributions over two time-periods; 1970–1982 to 1995–1999, and pre-1970 to 1995–1999. For both time-periods, and for each species, we investigated extinction patterns by calculating the difference in the mean elevation of grid squares that were occupied in the first time-period but for which there were no records in the second time-period, with those that were occupied in both time-periods. We also investigated patterns of colonization, and calculated the difference in the mean elevation of grid squares that were occupied in both time-periods, with those for which there were no records in the first time-period but records in the second time-period. Over the longer time-period (pre-1970 to 1995–1999), distributions of both northern and southern species moved to higher elevations (northern species excluding *C. palaemon*, mean increase in elevation of distributions = 40.7 m, s.d. = 24.5, $n = 4$ species; southern species, mean = 22.3, s.d. = 32.2, $n = 11$; one-sample t-test testing for a significant difference from zero, $p < 0.05$ in both cases). Northern species were more likely to have become extinct from lower-elevation sites, compared with southern species (phylogenetic analysis, t-test comparing mean difference in elevation of extinct versus

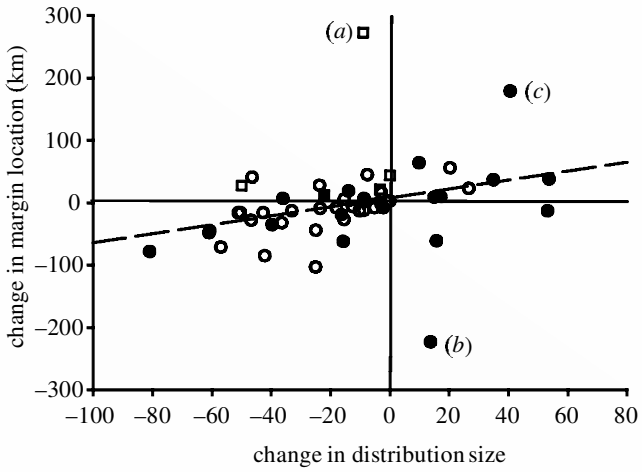

Figure 1. Regression of change in location of the range margin (km northwards) plotted against change in the size of area (area$^{0.5}$ km^2 of 10 km grids with butterfly records) between 1970–1982 and 1995–1999 for 51 non-migratory British butterflies. Circles show southerly distributed species ($n = 46$), squares show northerly distributed species ($n = 5$), open symbols show habitat specialists ($n = 32$), filled symbols show habitat generalists ($n = 19$; see § 2b for details). Outliers are (*a*) *Carterocephalus palaemon* (chequered skipper), which has disappeared from England during the past 30 years and is now restricted to Scotland; and (*b*) *Inachis io* (peacock), which has expanded its distribution within the core of its range but is less abundant at its range margin in northern Scotland. The range margin of *Polygonia c-album* (comma; (*c*)) has moved more than 170 km northwards in the past 30 years.

continuously occupied sites, $t = 4.29$, 2 d.f., $p < 0.05$; northern species, extinct sites = 42.7 m lower mean elevation than occupied sites (s.d. = 18.1; $n = 4$ species); southern species, extinct sites = 24.2 m higher mean elevation than occupied sites (s.d. = 41.8; $n = 11$)). Colonized sites were at a higher elevation than continuously occupied sites (mean = 35.6 m higher, s.d. = 34.3, $n = 15$ species; one-sample *t*-test testing for a significant difference from zero, $p = 0.001$), but there was no difference between northern and southern species (phylogenetic analysis, $p = 0.4$). Thus, northern species had shifted their distributions to higher elevations (one-sample *t*-test testing whether the difference in elevation of extinct versus colonized sites was significantly different from zero, $t = -3.72$, 3 d.f., $p = 0.034$; extinct sites = 78.7 m lower mean elevation (s.d. = 42.4, $n = 4$) than colonized sites), whereas southern species were more likely both to colonize and become extinct at higher elevations (one-sample *t*-test, $p > 0.4$).

Similar overall patterns were evident over the shorter time-period (1970–1982 to 1995–1999), but the effects were weaker and less likely to achieve statistical significance over this period; there was no difference between northern and southern species in the elevations of extinct versus continuously occupied sites (phylogenetic analysis, $t = 0.90$, 2 d.f., $p = 0.5$). As before, colonized sites were at higher elevations than continuously occupied sites (mean difference = 20.6 m, s.d. = 30.6, $n = 15$ species; one-sample *t*-test, $p = 0.021$), due mainly to southern species colonizing higher elevation sites. Overall, this resulted in little change in mean elevation of distributions over this shorter time-period (northern species, mean increase in elevation of distributions = 15.9 m, s.d. = 21.9, $n = 4$ species; southern species, mean increase = 0.6 m, s.d. = 18.2, $n = 11$).

However, a problem with these analyses is that species distributions are confounded by their ecology; for example, all northern species are sedentary, and eight out of 11 of the southern species that were included in this analysis are mobile. We therefore repeated our analyses to include only those species that are habitat specialists ($n = 7$ species; three northern and four southern species) and to include only sedentary species ($n = 7$ species; four northern and three southern species). Sample sizes were too small for phylogenetic analysis, but non-phylogenetic analyses confirmed our previous findings; over the longer time-period (pre-1970 to 1995–1999), northern species were more likely to have disappeared from low elevation sites compared with southern species (*t*-test, comparing mean difference in elevation of extinct versus continuously occupied grid squares, $p < 0.045$ both for habitat specialists and sedentary species), but this effect was not evident over the shorter period ($p > 0.4$). Since 1982, northern species were more likely to colonize high-elevation sites than southern species ($p < 0.04$ both for habitat specialists and for sedentary species; e.g. northern sedentary species, colonized sites = 12.6 m higher mean elevation than continuously occupied sites (s.d. = 20.4, $n = 4$ species); southern sedentary species, colonized sites = 12.7 m lower mean elevation than occupied sites (s.d. = 4.0, $n = 3$ species)). This different result for southern species compared with the full dataset indicates that colonization of higher elevation sites apparent across all southern species was predominantly by widespread and/or mobile species.

(c) *Importance of climate in limiting continental distributions in Europe*

The goodness-of-fit of the models was generally very good across all species (kappa, mean = 0.77, s.d. = 0.08, $n = 35$; number of 50 km grid squares predicted to have suitable climate, mean = 1626.7, s.d. = 519.5, $n = 35$ species; number of grid squares with records, mean = 1639.0, s.d. = 515.4, $n = 35$ species). The exception was *Erebia epiphron* (kappa = 0.40), where the three bioclimate variables did not describe well the current distribution. Based on the current distribution of *E. epiphron*, the climate models predicted this species to occur not only in mountainous regions of continental Europe and Britain where it does occur, but also in mountainous areas of Scandinavia where it has not been recorded (Tolman 1997). Excluding *E. epiphron*, kappa values for goodness-of-fit between observed and simulated distributions ranged from 0.67 to 0.87 ($n = 34$ species; table 1) and there was no difference between northern and southern species in the goodness-of-fit of models (phylogenetic *t*-test, $t = -0.86$, 3 d.f., $p = 0.5$), or in relation to either species mobility or habitat specificity ($p > 0.2$ in both cases).

(d) *Importance of climate in determining northern and southern range margins*

The climate models were equally good at simulating distributions at southern and northern range margins in Europe (southern margin, kappa mean = 0.65, s.d. = 0.10,

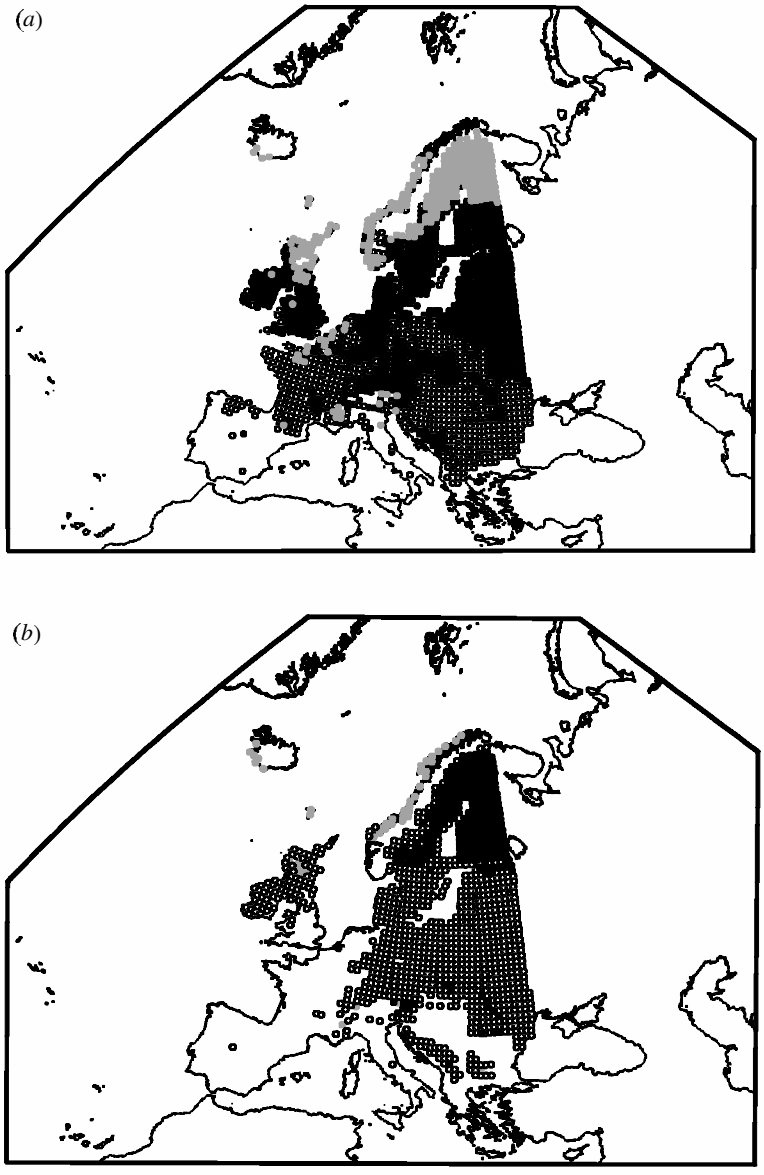

Figure 2. We illustrate two examples of climate-response surface models for (*a*) a southerly distributed species *Aphantopus hyperantus* (ringlet), and (*b*) a northern species *Coenonympha tullia* (large heath). The kappa goodness-of-fit values between the observed and simulated distributions for both species were typically high, showing that climate is important in limiting butterfly distribution at a continental scale (*A. hyperantus*, kappa = 0.79 at a threshold probability of butterfly occurrence of 0.61, 1674 grid cells with records versus 1601 grid cells simulated occupied; *C. tullia*, kappa = 0.81, threshold probability = 0.55, 1212 grid cells with records versus 1229 grid cells simulated occupied). Maps also show potential future distributions if species were to track predicted future climate changes (HADCM2) completely. Black filled and open circles show current simulated distributions, black and grey show predicted future (2070–2099) distributions. Open circles show areas where species currently occur but that are not predicted to be occupied in the future. *Aphantopus hyperantus* is predicted to decrease its range area in the future (17% decrease), but a worst-case scenario (see § 2f) indicates a decline of 35%; *C. tullia* is predicted to decline by 73% in the future (worst-case scenario indicates a decline of 77%).

northern margin, mean = 0.70, s.d. = 0.14, $n = 35$ species; paired t-test, $t = 1.35$, 34 d.f., $p = 0.19$). Thus, the models indicate that climate is an equally strong correlate of both northern and southern range margins.

(e) *Predicting potential future distributions in Europe*

We incorporated output from a climate-change scenario for the period 2070–2099 into the climate models that predicted that species' distributions would generally shift northwards in Europe as species disappeared from southern regions of their current ranges, but expanded at their northern range margins (figure 2). Overall, this resulted in little change in the sizes of species' current and future distributions, assuming that all species keep perfect track of changing climates (mean number of 50 km squares currently simulated occupied = 1626.7, s.d. = 519.5, $n = 35$ species; in the future, mean = 1601.5 squares, s.d. = 607.6; paired t-test, $t = 0.52$, 34 d.f., $p = 0.61$; figure 3). This was because losses in southern regions were balanced by increases at northern margins. There was no significant difference in the predicted change in range size between northerly or southerly distributed species (phylogenetic t-test, $t = 1.11$, 3 d.f., $p = 0.35$). However,

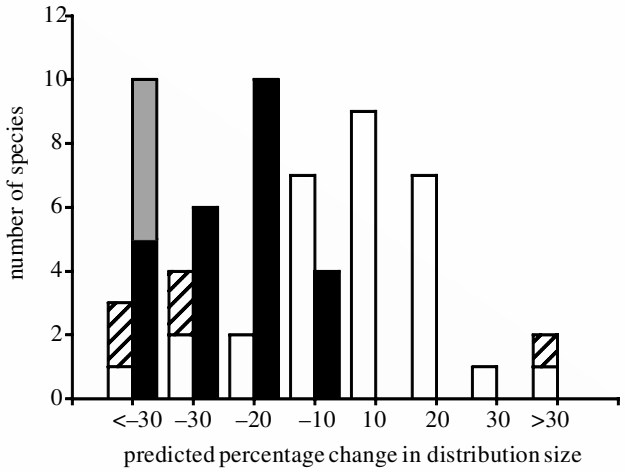

Figure 3. Predicted changes in size of European distributions for a subset of species (see text) for the period 2070–2099. The histogram illustrates two sets of predictions assuming that (i) all species ($n = 35$) perfectly track climate changes (open bars (hatched bars, northern species)), and (ii) those species that have failed to respond to recent climate change ($n = 30$ species) fail to colonize newly available northern areas (black-filled bars (grey bars, northern species).)

the largest increase in range size was predicted for *Erebia epiphron* (115% increase; table 1) because it is predicted to occur in mountainous areas of Scandinavia in the future, where it has never previously, to our knowledge, been recorded. Currently, the closest populations of *E. epiphron* to Scandinavia are either in the Carpathian Mountains in southern Poland, or in Scotland, and natural expansion from these sites into Scandinavia would be extremely unlikely. Excluding *E. epiphron* from the analysis resulted in northerly distributed species that was predicted to have significantly reduced range sizes in the future (mean = 40.6% decrease in range size, s.d. = 21.9, $n = 4$ species) compared with southerly distributed species (mean = 1.8% increase in range size, s.d. = 15.5, $n = 30$ species; phylogenetic t-test, $t = 6.76$, 3 d.f., $p < 0.01$; figure 3). This is because northern species were predicted to disappear from the southern parts of their range, but had little potential to shift their ranges northwards as most northern areas were already occupied (e.g. *Coenonympha tullia*, figure 2).

Our data on observed changes in range size in the subset of 35 study species included in the climate modelling show that only 5 out of 30 (17%) southerly distributed species (table 1) have expanded in the northern parts of their ranges since 1982. This is in broad agreement with the values observed across all southerly distributed British species (24% of species have expanded their ranges; Warren *et al.* 2001). For our subset of 35 species, we produced revised estimates of future distribution sizes for those species (25 southern, plus five northern) that have failed to track recent climate changes, assuming that these species will disappear from southern areas of their range that become climatically unsuitable but will not be able to expand into northern areas that become climatically suitable (table 1). We have no data for changes at northern range margins for northerly distributed species, but given that all five northern species are habitat specialists, we assumed no expansion in response to climate warming as observed in southern habitat specialists. This produces greatly reduced estimates of distribution sizes in the future (mean number of 50 km squares simulated occupied = 1205.7, s.d. = 644.2, $n = 30$ species), corresponding to a mean decrease of 30.8% in distribution size across species (range, 5–77% decline; northern species, mean = 65.2% decline; southern species, mean = 23.9% decline; figure 3).

4. DISCUSSION

(a) *Responses to recent climate change*

During the twentieth century, temperatures in Europe increased by 0.8 °C, corresponding to a 120 km shift northwards in temperature isotherms (Watson *et al.* 1998). Based on climate alone, we predict that species ranges should have shifted northwards in Britain during this period; southerly distributed species should expand northwards and northern species contract northwards. Few studies have considered species' entire ranges, and range shifts have been inferred from expansions at a single (usually northern) range margin. However, studies on butterfly distributions spanning northern and southern range margins fit the predictions and show that ranges of some species have shifted northwards in Europe during the twentieth century (Parmesan *et al.* 1999). Results from our current study, however, provide no evidence for systematic range shifts in butterflies in Britain since 1982, but show that distances moved by species' range margins are consistent with overall changes in distribution sizes. Nonetheless, during this period, 11 out of 46 southerly distributed species expanded their range margins northwards. These expansions were predominantly by relatively mobile habitat generalists and we interpret these expansions as likely to be responses to climate warming. Our results are consistent with Parmesan *et al.* (1999), who excluded those butterfly species most affected by habitat alteration. Differences between the two studies arise because most butterfly species are not mobile generalist species (species disproportionately included by Parmesan *et al.* (1999)); our recent studies have shown that most southern British butterfly species have declined during a period of climate warming because loss of breeding habitats has outweighed the positive impacts of climate warming (Warren *et al.* 2001). Thus, lack of evidence for range shifts in butterflies in this study may be due to most species being unable to track climate changes, resulting from the lack of suitable breeding habitats to colonize.

Results from this study differ from studies of southerly distributed British birds, which showed systematic shifts northwards of 19 km over a similar time-period (Thomas & Lennon 1999). Thomas & Lennon (1999) showed that 22 out of 52 species (42%) of southerly distributed birds increased in area over a 20-year period, whereas only 11 out of 46 species (24%) of southerly distributed butterflies increased their range sizes in this study. In the plot of change in distribution size *versus* change in range-margin location (figure 1; see fig. 1 for birds in Thomas & Lennon (1999)), the intercept is a measure of how far distributions have shifted latitudinally for a given change in distribution size (given that many

factors may affect distribution size). The intercept can be affected by patterns of both colonization (when a species is expanding) and extinction (when declining). A significant intercept was found for southerly distributed birds, indicating a northwards shift for southern birds (Thomas & Lennon 1999) but not in this study of butterflies. We suggest that this difference is more likely to be due to a difference in dispersal capacity between the two taxa than to different patterns of extinctions within their ranges; the widespread loss of natural and semi-natural habitats in the UK during the twentieth century have affected birds (Gibbons *et al.* 1993) and butterflies (Asher *et al.* 2001) in much the same way. The greater dispersal ability of birds compared with most butterflies may have allowed the former to track climate more rapidly, enabling them to colonize isolated but suitable habitat tens of kilometres beyond their previous range margins (habitat specialists that are good colonists exist in the bird fauna, but are very rare among British butterflies). Such colonization distances are difficult or impossible to achieve for most butterfly species. Those butterfly species that are expanding show expansions along broad fronts, sequentially colonizing adjacent grid squares once populations are sufficiently large. Thus, the greater capacity of birds to cross areas of unsuitable habitat may make their northern range margins more responsive to climate change, despite the fact that the opposite might be predicted based on the fact that butterflies, but not birds, are ectothermic.

Range expansions by butterflies in Britain since 1982 have mainly been confined to generalist, mobile species (Warren *et al.* 2001). The absence of a significant intercept in figure 1 and the lack of a difference according to species' habitat specialization, or dispersal ability, is likely to reflect the inability of even the mobile species in this study to colonize over very long distances. Rather than show a systematic shift northwards, mobile species have simply spread by expanding into adjacent grid squares, resulting in an apparently continuous distribution at coarse spatial scales. At a finer resolution, distributions are much more patchy, providing evidence of dispersal and habitat limitation; range expansions of fairly mobile species are slower in areas where less habitat is available (Hill *et al.* 2001*b*). It may only be the most mobile (e.g. *Polygonia c-album*; figure 1) or migratory butterfly species (which were not included in this study) that are capable of keeping track of climate changes along latitudinal gradients.

This study shows that species that reach a southern limit to their ranges in Britain or have montane distributions have become extinct at low elevation sites in the southern parts of their ranges and colonized sites at higher elevations, supporting other studies showing shifts of species to higher elevations during periods of climate warming (Grabherr *et al.* 1994; Parmesan 1996; Pounds *et al.* 1999). Our analyses control for differences in recording effort over time by comparing distribution changes in northern and southern (control) species in northern Britain, but distribution changes may be confounded by changes in land use. For example, many northern butterfly species are restricted to damp, boggy areas (Asher *et al.* 2001) and it is possible that these habitats have been disproportionately lost at lower elevations, compared with the habitats of control species. This requires further study.

(b) *Changes at northern and southern margins*

Several studies have shown that northern range margins have shifted more than southern margins in Europe during the twentieth century (Parmesan *et al.* 1999; Pounds *et al.* 1999; Thomas & Lennon 1999), indicating that climate may be less important at species' warm, low latitude/altitude range margins. However, our climate models are equally good predictors of butterfly distributions at northern and southern margins. Many species reach their southern range limits in mountainous regions in Europe, and the apparent lack of range shifts in these areas may be due to species moving to higher elevations, rather than higher latitudes, which might not be detected on a coarse grid map. These regions are also topographically diverse and contain a broad range of microclimates; at relatively coarse spatial scales, such margins may appear less responsive to climate change than northern margins. Further studies may reveal that southern margins are as sensitive to climate changes as northern margins, but fine-resolution and longer-term data may be required to detect these effects.

(c) *Future distributions*

Quaternary beetle remains indicate that insects normally shift their distributions in response to climate changes, rather than adapt *in situ*, or become extinct. For example, more than 90% of fossil beetle species found in Quaternary sites in Britain are extant and have shown little evidence of evolution over this period (Coope 1995). The relatively high dispersal ability of beetles may explain their ability to track past climate changes; extinctions of other taxa during the Quaternary (Lowe & Walker 1997) suggest that not all species will be equally capable. Our previous studies on butterflies indicate that only mobile, habitat generalists have tracked twentieth century climate changes at all (many show substantial lags; Warren *et al.* 2001); for most butterfly species, the widespread destruction of natural habitats means that newly available, climatically suitable areas are too isolated to be colonized, or do not contain suitable habitat (Warren *et al.* 2001). Thus, the ability of insects to track past climate changes may be a poor predictor of their ability to do so in the future, as natural habitats continue to be lost.

Our predictions for future European distributions of species assume that distribution relationships with climate will remain the same, and that there will be no local adaptation. For some species, evolutionary changes at range margins may result in some unpredictable responses to future climate changes (Thomas *et al.* 2001). For example, evolutionary increases in dispersal ability (Hill *et al.* 1999*a*) and in range of host-plants used at distribution margins (Thomas *et al.* 2001) may increase species' ability to keep track of the climate. However, these changes may not be adequate for species to keep track of climate change, given the predicted rate of climate warming during this century (IPCC 2001). Many climatically suitable areas will be remote from current distributions (figure 2) and results to date indicate that only the most mobile species will track these changes; these species are usually regarded as already having relatively low conservation value. Moreover, our predictions of declines in range sizes in the future assume that species will persist in all areas where they currently occur and which are predicted to

remain climatically suitable. Most habitat specialists are continuing to decline within these regions as a result of land-use changes.

We thank the huge numbers of volunteers whose records have contributed to the butterfly datasets that are held by Butterfly Conservation and the Biological Records Centre, CEH, Monks Wood. We also thank Wolfgang Cramer (PIK Potsdam) for providing the spline surfaces used to interpolate both the present climate and HADCM2 anomalies. The output from the HADCM2 transient simulation was supplied by the Climate Impacts LINK project (Department of the Environment Contract EPG 1/1/16) on behalf of the Hadley Centre and the UK Meteorological Office. David Viner (CRU UEA) kindly facilitated access to these data. This study was funded by NERC grants GR9/3016 and GR3/12542.

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As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.