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SHORT COMMUNICATION

Ecological Entomology

Reduced size in a montane butterfly at its warm range boundaries

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Abstract

1. Variation in insect size is often related to temperature during development and may affect the persistence of populations under future climate warming if smaller individuals have reduced fitness. Montane species are particularly vulnerable to climate-driven local extinctions due to range retractions at their warm range margins, and so we examined spatial and temporal variation in body size in the butterfly *Erebia epiphron* (Lepidoptera: Nymphalidae) in the United Kingdom, where it is restricted to two montane regions in England and Scotland. We examined spatial and temporal variation in body size in relation to temperature.
2. We sampled 19 populations (6–15 individuals per population) in England and Scotland between 2018 and 2019 spanning elevations from 380 to 720 m and examined museum specimens collected between 1890 and 1980. We examined individual body size (forewing length) and its relationship with the local temperature of sites, as well as temporal variation in body size over the last century in relation to the temperature during larval development.
3. The forewing lengths of field-collected individuals in England were on average 7%–8% smaller than in Scotland (England, mean = 14.9 mm, Scotland, mean = 15.9 mm), and warmer sites also had smaller individuals (0.13 mm reduction in wing length per 1°C increase in local site mean temperature). However, we found no effect of temporal temperature variation on body size changes during larval development.
4. The observed smaller body size in English populations could have impacts on fecundity and dispersal ability. Future work should seek to understand the life-cycle lengths, genetics and phenotypic plasticity of these two populations to evaluate potential explanations for regional differences.

KEYWORDS
body size, climate change, extinction, montane, temperature

INTRODUCTION

Cold-adapted montane insect species are predicted to be at risk from future climate change (Minter et al., 2020), and local extinctions have already been documented at warming lower elevation range margin sites (Franco et al., 2006). These cold-adapted insects often have restricted distributions, experiencing warming in isolated mountain ecosystems and so are potentially extremely vulnerable to local

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extinctions (Elsen & Tingley, 2015). Montane species experience variation in local temperature due to differences in altitude and latitude across their ranges, which may be associated with variation in traits such as body size (Gunter et al., 2019). Because potentially reduced body sizes could affect the persistence of local populations under future warming, it is important to examine body size variation in montane species with spatial and temporal variation in temperature.

Body size in ectothermic species often shows variation along latitudinal and altitudinal thermal gradients which can be the result of phenotypic plasticity or genetic adaptation (Blanckenhorn & Demont, 2004). Higher temperatures during development can result in smaller body size, for example, temperature-size rule (Atkinson, 1994), which can reduce fecundity and dispersal and, potentially, reduced colonisation ability (Gao et al., 2016; Lopez et al., 2014). In contrast, some ectothermic species show the opposite pattern with smaller individuals at cooler temperatures (Gunter et al., 2019), which is thought to often be genetic and related to season length (Blanckenhorn & Demont, 2004).

Here, we examine the Mountain Ringlet butterfly *Erebia epiphron* (Knoch, 1783) which in Britain occurs in two discrete mountain regions: the Lake District in England and the Scottish Highlands (Figure 1). In the United Kingdom, populations in the two regions differ genetically, due to different post-glacial colonisation routes of Britain from continental Europe (Minter et al., 2020). Populations in the two regions also differ in their susceptibility to climate change, with populations in England (warm range edge) projected to be more at risk under future climate change scenarios (Minter et al., 2020), and a lack of opportunities for some populations to shift to cooler sites. Examining the relationships between temperature and body size in these regions will improve our understanding of the species' vulnerability to climate change.

In this study, we compare the forewing lengths of field-caught butterflies in England and Scotland, and how they relate to the local temperature of sites. We also use museum material to examine variation in body size over ~100 years and investigate whether body size varies over time in relation to temporal variation in temperature during butterfly development. Assuming smaller individuals are likely to develop under warmer conditions, we test (1) whether warmer regions (i.e., England) and populations in warm low-elevation range boundaries have smaller individuals; and (2) whether, over the past century, smaller individuals emerge in years with warmer temperatures. Given that there are genetic differences between the English and Scottish populations, we also test (3) whether within-population variation in size (coefficient of variation) differs among regions, indicating potential differences in plasticity within populations.

MATERIALS AND METHODS

Sampling of contemporary and museum material

In 2018 and 2019, we collected 6–15 male *E. epiphron* from each of 9 populations in England and 10 populations in Scotland, representing

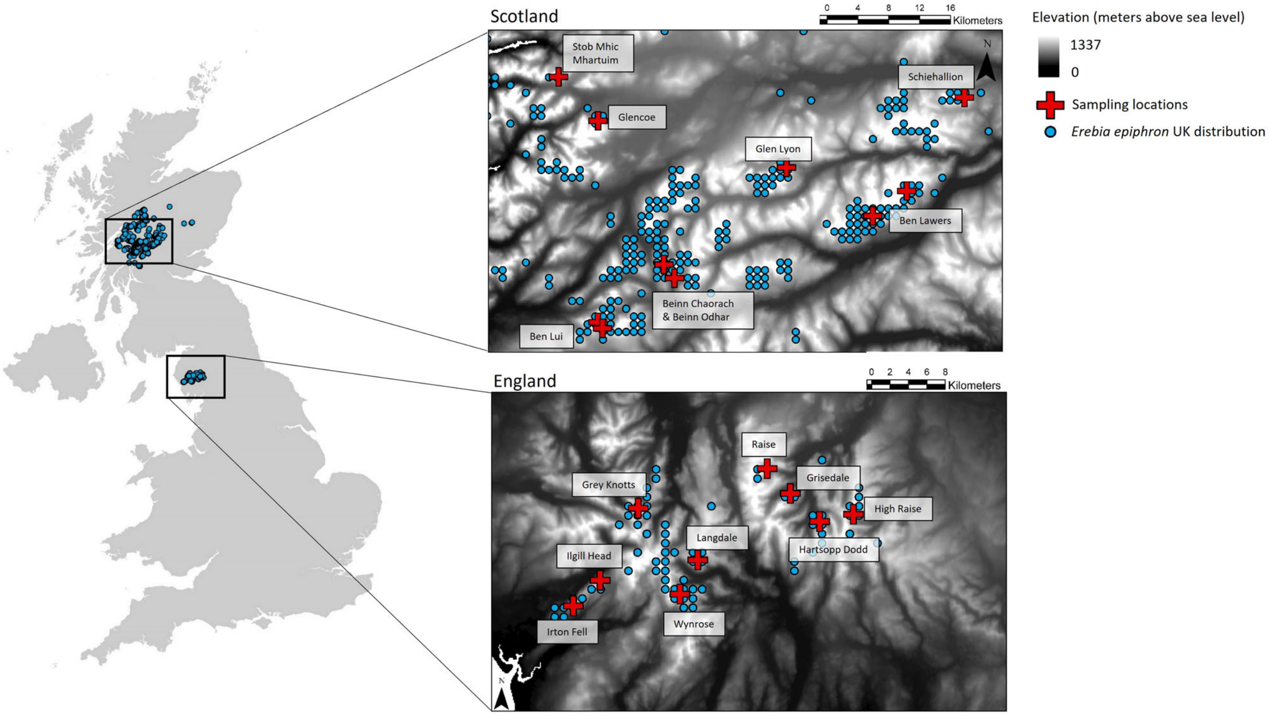

FIGURE 1 *Erebia epiphron* sample populations (red crosses) for contemporary material, and current distribution (1 km × 1 km resolution; blue circles) in England and Scotland. Butterfly distribution data were acquired by the Butterflies for the New Millennium recording scheme courtesy of Butterfly Conservation (Fox et al., 2015). Elevation data were acquired from https://dAta.globalchange.gov/dataset/nasa-srtm-90m-digital-elevation-data.

a wide range of local elevation (380–780 m above sea level) and temperature gradients (5–8°C mean annual temperature) (Figure 1). Wings were removed from individuals and electronically scanned.

Photographs of specimens held at the Natural History Museum, London (2014) were downloaded (https://data.nhm.ac.uk/), and up to five males collected per year between 1890 and 1987 were measured (England $n = 127$ individuals, Scotland $n = 100$).

Measuring size

We measured forewing length (distance between cell base and v10 wing margin veins; see Supporting Information S1: SM1), a widely accepted proxy for body size (Brehm et al., 2019; Graca et al., 2016), using the 'draw line' tool in Image J (https://imagej.nih.gov/ij/index.html) and converted into millimetres using the scale bar. Only wings where all veins and cell bases were visible were used for measurements. For each individual, both left and right forewings were measured and averaged. A measurement accuracy of ±0.3 mm was estimated based on three replicate measurements of 10 random individuals.

Climate data

We calculated the mean annual temperature at each of the contemporary material collection sites using gridded temperature data (2017–2020) (°C) at a resolution of 1 km (Met Office et al., 2018). For the museum material, temporal variation in temperature during the 5 month larval development period (August–September in the previous year and March–May in the year of collection) was estimated from the Met Office UK climate data series (Met Office et al., 2018) as average monthly temperatures at regional resolution (region data: North England and Scotland) from 1880 to 1987. We used regional resolution temperature data for analyses of museum material due to lack of more fine-scale specific locality information.

Statistical analysis

We used two-sample *t*-tests to examine differences in forewing length between England and Scotland in both the contemporary and museum data. We examined effects of annual temperature on forewing length in the contemporary data using a GLM with region (England or Scotland) and annual mean temperature of sample sites as predictors. We created a GLM for the museum data, with forewing length as the response variable and larval development temperature and region as the predictor variable. We calculated the coefficient of variation for forewing length in contemporary data as a measure of within-population wing size variation and tested for differences in wing size variation between England and Scotland populations by analysing the coefficient of variation in wing size using a two-sample *t*-test.

RESULTS

The forewing lengths of field-collected individuals from populations in England (mean = 14.9 mm, SE = 0.05 mm) averaged ~7% smaller than individuals from Scotland (mean = 15.9 mm, SE = 0.05 mm; Figure 2a) (*T*-test: $T_{(247.7)} = -15$, $p < 0.001$). Museum material confirmed that specimens from English populations (mean = 14.8 mm, SE = 0.08 mm) are ~8% smaller than individuals from Scottish populations (mean = 16.2 mm, SE = 0.09 mm) (*T*-test: $T_{(212.4)} = -11.4$, $p < 0.001$) (Figure 2b). Smaller individuals occur in warm range edge populations ($F = 115.8$, $R^2 = 0.48$, $p < 0.001$), with wing size decreasing by 0.13 mm per 1°C increase in annual mean temperature in field-collected specimens (Supporting Information S1: SM2, Figure 2c). Separate analyses of the two regions revealed that smaller butterflies are found in warmer sites within Scotland ($p = 0.04$) but not within England ($p = 0.4$) (Supporting Information S1: SM3).

We found no change in body size over time, either (a) comparing contemporary samples with museum material or (b) in terms of the effect of annual temperature during larval development on body size. In models, only region (i.e., England or Scotland) was a significant predictor of body size in museum material ($F = 66.6$, $R^2 = 0.36$, $p < 0.001$, Figure 2d; Supporting Information S1: SM2), confirming our previous finding that individuals in England are smaller than in Scotland. We found no differences in the coefficient of variation in forewing length between England and Scotland (*T*-test: $T_{(12.6)} = 0.2$, $p = 0.84$).

DISCUSSION

English *E. epiphron* are smaller than Scottish individuals, and the smallest individuals are found at sites with the highest temperatures. Our findings are consistent with some other studies of Lepidoptera, which are also smaller at lower altitudes/latitudes (Brehm et al., 2019; Taylor-Cox et al., 2020). However, other studies have shown the opposite pattern, with smaller body size at higher altitudes/latitudes (Gunter et al., 2019; Nygren et al., 2008). Within the two populations, this relationship between body size and temperature was only present in Scotland, suggesting that the overall patterns observed could be related to regional environmental and genetic factors. There was no relationship between annual development temperature and size, whereas some insect species have smaller wings under warmer seasonal temperatures (Wonglersak et al., 2020). This could be due to the coarse resolution of yearly climate and location information on museum specimens, and individuals may have some capacity to moderate the temperatures experienced at the microscales. We did not find any differences in within-population variation, suggesting similar levels of plasticity across Britain, even at the warm range edge.

Our results are in line with the 'temperature-size' rule, but the mechanism of this remain poorly understood (Verberk et al., 2020), although environmental (phenotypic plasticity) and genetic factors are likely to play a role. For example, these regional differences in body size may reflect plastic responses to environmental variation in local

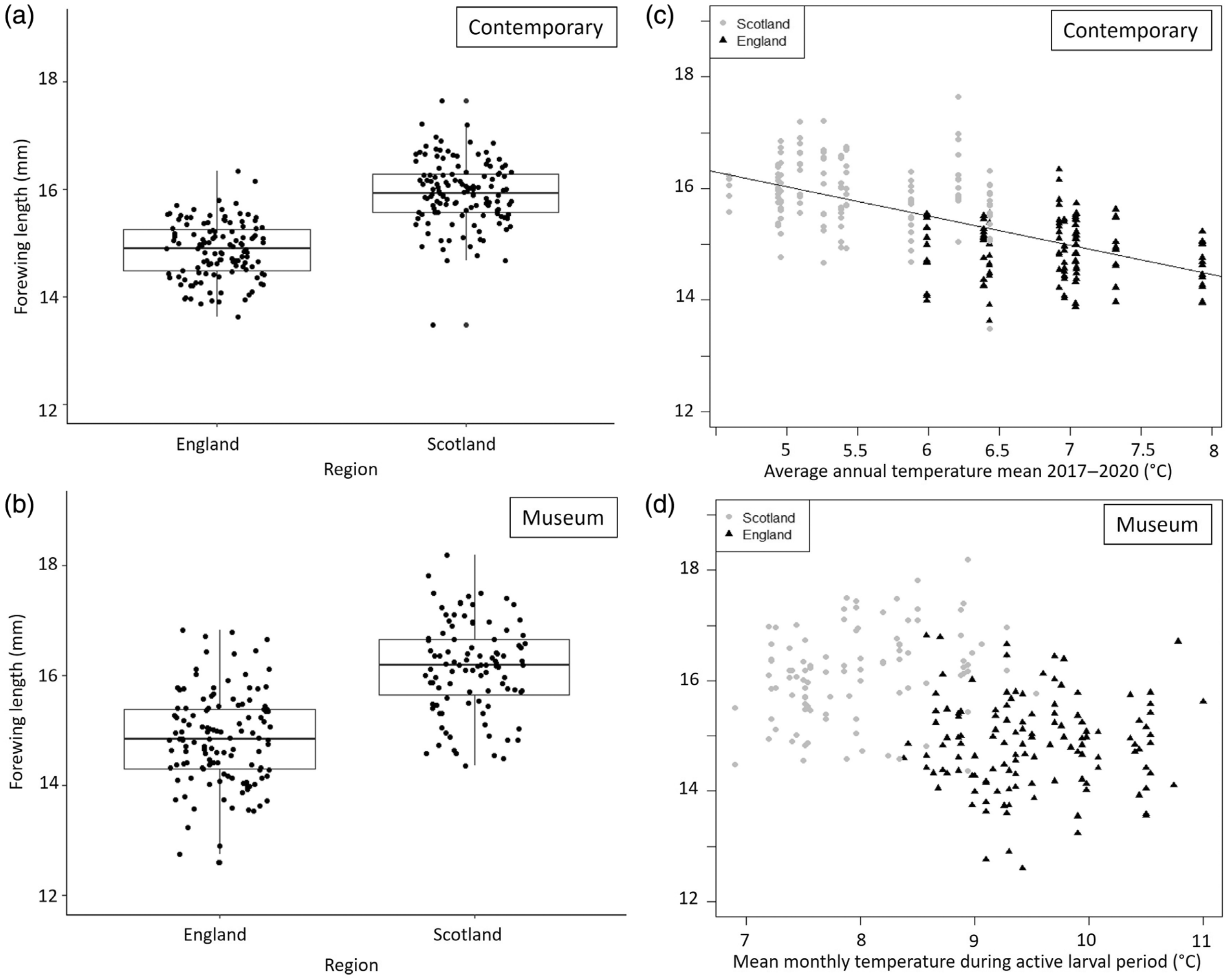

FIGURE 2 Variation in forewing length between regions and in relation to temperature, in contemporary and museum material. (a) Boxplots showing that populations in England are smaller than in Scotland in contemporary specimens ($p < 0.001$) and (b) in museum specimens ($p < 0.001$). (c) Forewing length shows a negative relationship with annual mean temperature (°C) in modern specimens ($p = 0.01$). (d) Forewing mean length shows a nonsignificant relationship with mean temperature during active larval period (°C) in museum specimens ($p = 0.11$).

resource quality (Pineda-Munoz et al., 2016; e.g., smaller individuals from areas which contained low-quality food plants; Dempster et al., 1976), as well as regional variation in direct and indirect impacts of seasonal temperature variation. Our results did not find any effect of temperature during development on body size; however, because of the coarse spatial resolution of the museum material, it is not possible to rule out plasticity as a potential mechanism. Genetic factors may also have influenced the observed size differences. The English and Scottish populations are genetically distinct, with separate post-glacial colonisation histories of Britain (Minter et al., 2020), potentially from historic (glacial) populations that already differed in size. In addition, following colonisation of Britain, it is possible that populations in these two regions evolved and adapted to local conditions in their respective regions. There may also be reduced predation at higher elevations/latitudes, allowing for larger body size to evolve in these areas (Brehm et al., 2019). Of course, body size variation may be due to a combination of environmental (phenotypic plasticity) and genetic factors (Nygren et al., 2008).

Body size may also be affected by voltinism. Some insect species have variable life cycles, which depend on temperature (Macgregor et al., 2019). For example, some species in Britain have annual life cycles in the south, but 2-year life cycles in cooler northern areas (Kempe et al., 2006). These 2-year life cycles may allow longer feeding and development times during cooler conditions, which result in larger body size compared with annual life cycles (Everall et al., 2015). It has been suggested that *E. epiphron* may have a two-year life cycle in Scotland, based on breeding information in captivity (Wheeler, 1982), which is observed in other *Erebia* butterflies in Europe (Kleckova et al., 2015), but there is no evidence of this in English populations. Exploring whether differences in the life-cycle length affect body size differences between regions, and disentangling the relative importance of genetic and environmental factors, require further study, for example, through rearing individuals from different populations under controlled conditions.

The implications of this size variation is complex under environmental and climate change. The body sizes of other species have ‘shrunk’ in response to recent climate change (Gardner et al., 2011; Wu et al., 2019), with annual life cycle changes (Everall et al., 2015). In contrast, our results show that sizes have not declined over time, despite regional warming. However, the level of warming may be insufficient to be detectable in samples (through time) yet, given that the size reduction is only 0.2 mm per 1°C increase in local site mean temperature (in space). In addition, a lack of evidence for any changes in size through time (as the climate has warmed) may be due to populations tracking recent warming by moving to higher elevations or otherwise cooler microclimates. As many of the lowest-elevation historical populations have died out (Franco et al., 2006), if there was any underlying shrinkage through time in body size within individual population, it may have been counteracted within our data by the disproportionate disappearance of (small bodied) populations from the warmest sites. If the spatial pattern of reduced size with warmer temperatures converts into reduced size with future warming, it could affect voltinism (Macgregor et al., 2019), development rates (Atkinson, 1994; Beerli et al., 2019; Pineda-Munoz et al., 2016) and reduce fecundity (Gao et al., 2016). Flight ability may also decline (Lopez et al., 2014), resulting in reduced colonisation rates and thereby lower metapopulation capacity (Hill et al., 1999; Taylor-Cox et al., 2020). Larger sized individuals, in contrast, may be better buffered against harsh environments and more resilient to starvation and desiccation (Ashton, 2002; Cushman et al., 1993).

To conclude, we find that English *E. epiphron* are smaller than Scottish individuals, which is associated with temperature differences between regions and different post-glacial histories of colonisation. We also find smaller individuals at warmer sites but no shrinkage over time. How populations containing smaller individuals might respond to future climate change requires future research.

AUTHOR CONTRIBUTIONS

Melissa Minter: Conceptualization; methodology; formal analysis; project administration; writing – original draft; writing – review and editing; investigation; funding acquisition; data curation; visualization. **Kanchon K. Dasamahapatra:** Conceptualization; writing – review and editing; funding acquisition; methodology; supervision. **Mike D. Morecroft:** Conceptualization; funding acquisition; writing – review and editing; supervision. **Chris D. Thomas:** Conceptualization; funding acquisition; writing – review and editing; methodology; supervision. **Jane K. Hill:** Conceptualization; methodology; funding acquisition; writing – review and editing; supervision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All *Erebia epiphron* morphological measures can be found in the Dryad repository https://doi.org/10.5061/dryad.ttdz08m61.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Data S1. SM1. Morphological measurements taken using Image J. (A) Forewing length was measured in field scanned images as the distance between the cell base and vein 10. (B) Forewing length was measured in Natural History Museum photographs as the distance between the cell base (near to thorax) and vein 10.

SM2. Model outputs of GLMs to explain forewing mean length with regional and temperature affects in modern and museum material. Tables present the estimate (slope), the standard error, t value and p value of the explanatory variables. Adjusted R^2 and F-statistic of the overall models are presented below: (A) Model output of contemporary population forewing mean length with region and annual mean temperature 2017–2020 (1 km) (°C) and (B) Model output of museum material forewing mean length with region and mean temperature during larval development (°C). Asterisk denotes whether the test was significant, $^*p \leq 0.05$, $^{**}p \leq 0.01$, $^{***}p \leq 0.001$.

SM3. (A) Relationship between annual mean temperature 2017–2020 (1 km) and forewing length within both regions, the grey line represents the linear model within Scotland ($p = 0.04^*$), the black line for within England ($p = 0.4$) and the red line across both regions ($p = 0.03^*$). (B) Relationship between mean temperature during larval development (°C) and forewing length within both regions, the grey line represents the linear model within Scotland ($p = 0.03^*$), the black line for within England ($p = 0.8$) and the red line across both regions ($p = 0.1$).

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