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Global change biology

High-Arctic butterflies become smaller with rising temperatures

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The response of body size to increasing temperature constitutes a universal response to climate change that could strongly affect terrestrial ectotherms, but the magnitude and direction of such responses remain unknown in most species. The metabolic cost of increased temperature could reduce body size but long growing seasons could also increase body size as was recently shown in an Arctic spider species. Here, we present the longest known time series on body size variation in two High-Arctic butterfly species: *Boloria chariclea* and *Colias hecla*. We measured wing length of nearly 4500 individuals collected annually between 1996 and 2013 from Zackenberg, Greenland and found that wing length significantly decreased at a similar rate in both species in response to warmer summers. Body size is strongly related to dispersal capacity and fecundity and our results suggest that these Arctic species could face severe challenges in response to ongoing rapid climate change.

1. Introduction

Body size change is regarded as a third universal species response to climate change along with shifts in phenology and range [1,2]. Body size is a key trait related to the life history of individuals with implications for reproductive success [3,4] and dispersal capacity [5,6]. In ectothermic species, like arthropods, body size is especially influenced by the abiotic environment. Two patterns in ecology summarize the general pattern of ectothermic body size variation in response to temperature change. The adaptation of Bergmann's rule to ectotherms describes latitudinal or thermal variation in size, such that larger individuals occur at higher latitudes and in colder environments [7]. Similarly, the specific pattern of higher temperatures resulting in smaller adult size of ectotherms, deemed the temperature–size rule, has been commonly found via experiments on numerous taxa [8–10]. While there are several proposed ways that temperature may influence final adult body size (including effects on food limitation and predation rates), the role of metabolism is central [1,9].

Although both Bergmann's rule and the temperature–size rule predict larger individuals in colder environments, the opposite pattern also occurs [7,9]. Hence, two hypotheses detail how external temperatures may drive size responses to climate change in arthropods in seasonal environments. First, the metabolic rates of arthropods increase with warmer temperatures [1,11]. Therefore, in warmer environments, organisms become smaller if they cannot offset energy losses related to increased metabolic costs during growth. Conversely, rising temperatures in seasonal environments associated with longer growing seasons may allow arthropods to obtain more resources and grow larger [2,12]. These two mechanisms may act in concert, moderating the outcomes of each or the effect of a longer growing season could depend upon trophic level [2]. Although feeding rates of herbivores may

increase to some peak [13], extended seasons could also mean lower plant-food quality, especially during late season [14].

Temperature and timing of snowmelt define the activity and growing season for numerous Arctic taxa and influence life histories (e.g. [15,16]). Here, we present the longest time series of body size variation within arthropod (i.e. butterflies) species at high latitude. We tested which of the hypotheses was better supported by our data using snowmelt as a proxy for season length and temperature as a proxy for the metabolism hypothesis and predicted that previous year's temperature would best explain variation in body size as it covers the majority of the larval growing period.

2. Material and methods

(a) Study area and data

Butterfly specimens and climate (snowmelt and temperature) data were collected in northeast Greenland (74°28' N, 20°34' W) from 1996 to 2013 as part of the Zackenberg Basic Monitoring Programme [17]. See the electronic supplementary material (detailed Material and methods) and references therein for more details on climate data collection and plant community characteristics.

Arthropods were collected weekly during the activity season each year in one window trap plot and six pitfall trap plots in an area less than 1 km², but the peak flight period for adult butterflies occurs mid-late July depending upon snowmelt and temperature [18]. The butterfly community at Zackenberg has four species but is dominated by the Arctic fritillary, *Boloria chariclea* Schneider and the northern clouded yellow, *Colias hecla* Lefèbvre. We measured all 3629 (1934 males and 1695 females) *B. chariclea* and 847 (531 males and 316 females) *C. hecla* collected. Both of these species most probably have a 2 year generation time at our site [19] with adult size depending on resources accrued during their larval stages. We determined sex, and measured the length of one forewing from thoracic attachment to apex of the wing to the nearest 0.01 mm⁻¹ using a Diesella® 150 mm digital caliper.

(b) Data analysis

We used current year's May–June ($temp_t$) and previous year's May–August ($temp_{t-1}$) temperatures to encompass the larval growing season. Current and previous years' snowmelt date ($snow_t$ and $snow_{t-1}$) were used as proxies for season length. We used linear mixed-models with a Gaussian error distribution to determine which predictor(s) best explained variation in wing length using annual averages (years as replicates) for each sex in each species. We composed an *a priori* list of candidate models based upon what we currently know about the development of these species (electronic supplementary material, table S1) and the best model was determined by model selection using the Akaike information criterion corrected for small sample size (AICc). We repeated the analyses using individuals as replicates to test for random effects of day of year (DOY) and plot using log-likelihood ratio tests. We tested for plot variation using Tukey's honestly significant difference (HSD). Differences in body size between plots were tested in subsequent models using individuals as replicates when there was a significant plot effect. Normality was assessed using *q-q*-plots. Statistical tests were conducted using the R environment for statistical computing [20].

3. Results

Timing of snowmelt is occurring significantly earlier (figure 1a) and average temperatures over the activity period of caterpillars have increased significantly (figure 1b,c) during the study period. While some of the variables were significantly

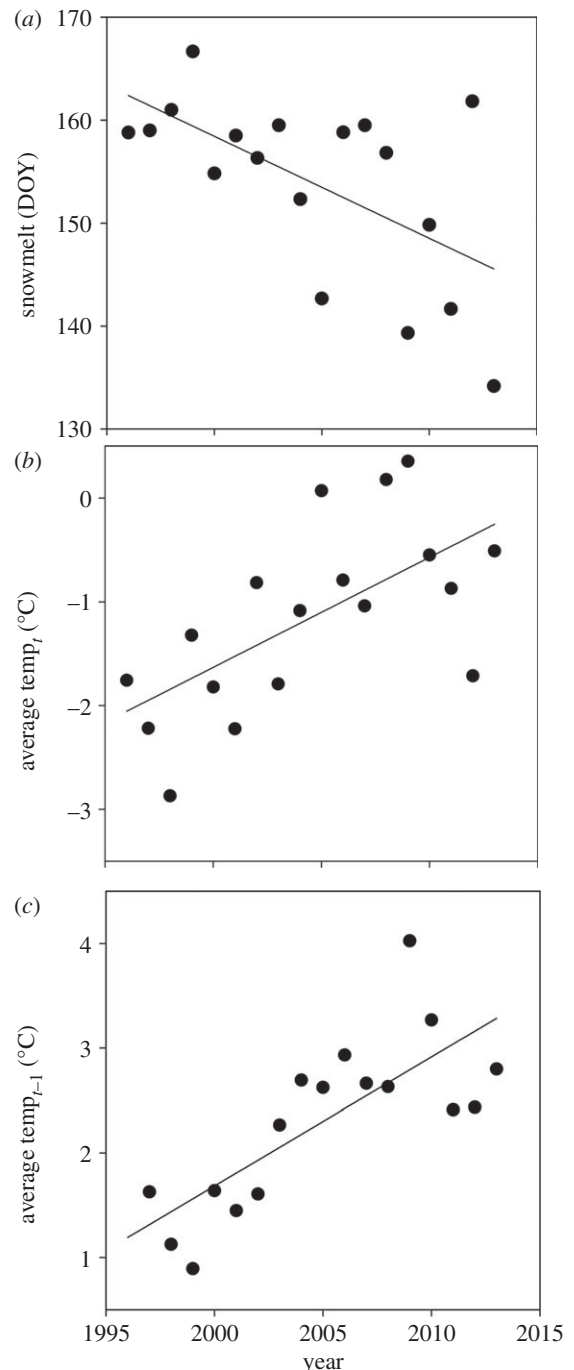


Figure 1. (a) Timing of snowmelt ($F_{1,16} = 8.92$, estimate = -1.05 , $R_{Adj}^2 = 0.32$, $p = 0.008$), (b) May–June_t temperature ($F_{1,16} = 10.87$, estimate = 0.11 , $R_{Adj}^2 = 0.37$, $p < 0.005$) and (c) May–August_{t-1} temperature ($F_{1,16} = 22.52$, estimate = 0.11 , $R_{Adj}^2 = 0.56$, $p = 0.001$) from 1996–2013 at Zackenberg, Greenland.

correlated, there was no indication of multicollinearity (electronic supplementary material, table S2).

Average wing length \pm s.e. in male (17.96 ± 0.02 mm) and female (18.87 ± 0.02 mm) *B. chariclea* differed significantly ($F_{1,3626} = 1145$, $p < 0.001$, analysis of variance (ANOVA)). The wing lengths of male (22.45 ± 0.04 mm) and female (23.19 ± 0.06 mm) *C. hecla* also differed ($F_{1,845} = 108.8$, $p < 0.001$, ANOVA). Wing lengths varied greatly in both species over time (figure 2a,b), yet were strongly correlated between the sexes in *B. chariclea* ($r = 0.88$, $p < 0.001$) and *C. hecla* ($r = 0.80$, $p < 0.001$), and between species (all $r > 0.6$, $p < 0.01$).

Average annual body size decreased significantly in response to previous year's temperature ($temp_{t-1}$) for both

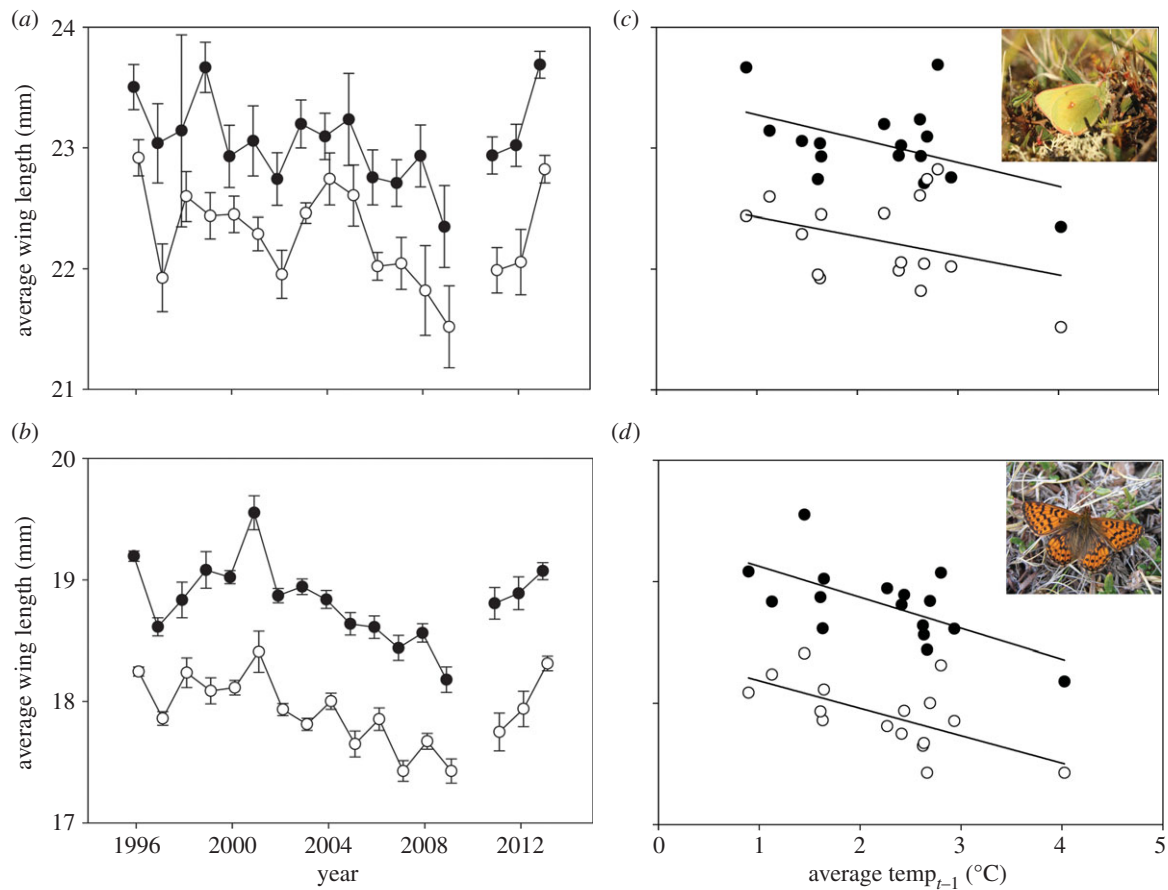


Figure 2. Inter-annual variation in average male (open circles) and female (filled circles) wing length over the sampling period for (a) *Colias hecla* and (b) *Boloria chariclea* and their responses (c,d, respectively) to average May–August $_{t-1}$ temperature. Error bars represent s.e. Data for 2010 are not available. (Online version in colour.)

Table 1. Summary statistics showing the best-fit models as selected by AICc on wing length for each sex of *Boloria chariclea* and *Colias hecla* collected between 1996 and 2013 at Zackenberg, Greenland using annual averages. Significance of individual parameters is indicated by asterisks.

species	sex	intercept	snow $_t$	snow $_{t-1}$	temp $_t$	temp $_{t-1}$	p-value	R^2_{Adj}	F (d.f.)
<i>Boloria chariclea</i>	♂	20.41**	−0.01	n.a.	n.a.	−0.31**	0.01	0.42	6.46 (13)
	♀	19.38**	n.a.	n.a.	n.a.	−0.25**	0.007	0.38	10.16 (14)
<i>Colias hecla</i>	♂	25.68**	−0.02	n.a.	n.a.	−0.29*	0.19	0.06	1.88 (13)
	♀	26.25**	−0.02	n.a.	n.a.	−0.32*	0.05	0.27	3.72 (13)

* $p < 0.05$; ** $p < 0.01$. n.a., not applicable.

species (table 1 and figure 2c,d) and was consistently selected in the top models for all tests (electronic supplementary material, table S3). The models using individuals as replicates also revealed significant effects of current year's snowmelt on wing length (electronic supplementary material, table S4). DOY and plot significantly improved model fit for *B. chariclea*, but not for *C. hecla* (electronic supplementary material, table S5) and some sites differed significantly from one another (electronic supplementary material, table S6). We re-analysed the dataset excluding the plots that showed significant differences from others, but as temperature remained included in the top models with very similar estimates (electronic supplementary material, table S5) data from all plots were retained in the final models (table 1). We tested for inter-annual variation in size for *B. chariclea*, controlling for collection date by re-analysing the data with individuals collected from the same peak abundance day of each season; in this way, we

effectively controlled for seasonal variation. These models similarly included the negative effects of temperature on body size in the top models (electronic supplementary material, table S7).

4. Discussion

We show that body size of males and females in two High-Arctic butterfly species fluctuated in synchrony from year to year, strongly supporting the influence of external factors on inter-annual size variation in these species. We further show that increasing summer temperatures lead to smaller adult body size, thus corroborating earlier short-term experiments suggesting that higher temperatures result in smaller adult size [3,10]. Even though longer, warmer seasons may mean a longer period of time to obtain resources, the seasonal quality of resources, combined with the higher cost of obtaining them,

suggests that the larvae cannot compensate for energy losses. While some species could be capable of increasing their feeding rate to offset increased metabolic costs with warming, this ability appears to be relatively uncommon and species likely possess some locally adapted optimal feeding temperature [21]. Indeed, Barrio *et al.* [22] recently showed that respiration rates in the Arctic moth (*Gynaephora groenlandica*) were significantly higher and growth rates significantly lower at lower elevation, adding support to the metabolism hypothesis. While we believe our study presents the longest time series available on body size variation in butterflies, the mechanistic basis for the observed variation remains to be demonstrated. We also cannot rule out that generation time is extended in particularly short growing seasons.

We have demonstrated that two butterfly species in the High-Arctic responded similarly and negatively to warming temperatures over 18 years. Smaller body size in these Arctic species could have significant consequences for their population dynamics by leading to decreased dispersal capacity or lower fecundity and fitness. *B. chariclea* has already demonstrated a significant shift towards earlier and shorter flight seasons at Zackenberg [18] and both *B. chariclea* and *C. hecla* are considered under extremely high climate change risk by the Climatic risk atlas of European Butterflies given future

bioclimatic models [23]. While these models include dispersal capacity, *in situ* adaptation to climate change or plasticity may enable some populations of a species to persist. Indeed, the degree to which phenotypic plasticity and adaptation ultimately play a role in this system remains to be thoroughly investigated. A recent review by Seebacher *et al.* [24] suggests that terrestrial ectotherms in less stable environments are less capable of physiological plasticity in response to climate change, particularly at high latitudes. Hence, species such as these found at high latitudes, adapted to cold climates, could suffer from further warming.

Data accessibility. Supporting data can be accessed via the Dryad data repository (<http://dx.doi.org/10.5061/dryad.43gt3>).

Authors' contributions. A.E. and T.T.H. conceived the idea and J.J.B. measured specimens, generated data, performed analyses and prepared the first draft. A.E., T.T.H., C.M.K., R.R.H. and K.O. contributed to data interpretation, article revisions and final approval.

Competing interests. We have no competing interests.

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