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Research article

Wing lengths of three Arctic butterfly species decrease as summers warm in Alaska

EDITOR'S CHOICE

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Climate warming can cause arthropods to express plastic and/or evolved changes in morphology. Previous studies have demonstrated that body sizes of Arctic butterflies are influenced by the temperatures experienced as larvae. To investigate whether this was occurring among Alaskan butterflies, we analyzed temporal trends in the wing sizes of three Holarctic species, *Colias hecla*, *Boloria chariclea* and *Boloria freija*, using museum specimens collected in Arctic tundra regions of Alaska between 1971 and 1995. Wing length was compared to accumulated growing degree days (GDD) during both the spring of the year collected and the previous year's summer during the normal period of larval development. We used mixed-effects models to test if spring and summer temperatures affected adult morphology. Results show that for every 1°C increase in average seasonal temperature, wingspans decreased between 0.7 and 5 mm, with *B. freija* the most strongly affected. Our results suggest that the morphological sensitivity of Arctic butterflies to warming is the outcome of interactions between life-history traits and regional climate, with all species sensitive to warming the summer before the flight year as well as warming the spring of the flight year. *Boloria freija*, which overwinters as late instar larvae that do not feed before pupation the following spring, was particularly strongly affected by summer warming.

Keywords: Arctic, butterfly, climate change, Lepidoptera, morphology

Introduction

Insects exhibit complex morphological changes in response to climate warming. For endothermic animals, Bergmann's rule posits that within a broadly distributed taxon, body size tends to be larger in colder environments and smaller in warmer ones (Blackburn et al. 1999). Bergmann initially hypothesized that larger size was selected in colder environments due to favorable surface area to volume ratios that retain heat more easily (Bergmann 1847, Watt et al. 2010). Such an explanation does not extend

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to ectotherms, but an analogous trend has been noted among ectotherms called the temperature-size rule (Atkinson 1994). In cold-blooded species, larger mass is hypothesized to be adaptive because it enhances fasting ability, which aids survival through winter when food is scarce. Lower temperatures also aid in prolonging fasting ability in ectotherms by reducing metabolism through a decrease in respiration relative to the rate of feeding, promoting accumulation of nutrients when temperatures are cooler. Some ectothermic species exhibit striking size variation along regional temperature gradients (Masaki 1978, Heinze et al. 2003, Nygren et al. 2008) though no universal pattern exists either among insects in general or among Lepidoptera, aka moths and butterflies, specifically (Hawkins and Lawton 1995, Heidrich et al. 2021).

Temperature effects on insect body sizes have been widely observed in both laboratory and field studies. In many cases, warming results in decreased adult body size: for example, the cabbage white butterfly, *Pieris rapae*, reared at varying temperatures (17.5–31°C) exhibited reduced pupal weights at the highest temperatures (Jones et al. 1982). Decreasing body size under warming have also been observed in dung beetles (Fleming et al. 2021), bees (CaraDonna et al. 2018), wasps (Polidori et al. 2020) and flies (Blanckenhorn 2015).

However, there is considerable species-specific variation in the effects of warming on insect morphology. Among dragonflies and damselflies of Britain, only the damselflies were found to have temperature-associated decreases in wing length (Wonglersak et al. 2020). Similarly, larger species of ground beetles in British Columbia, Canada, exhibited the strongest warming-related shrinking effects (Tseng et al. 2018). In chironomid flies, some but not all species exhibited body size declines (Wonglersak et al. 2021). In Lepidoptera, a comparative study of three species of lycaenid butterflies found that life history traits and sex modified the effect of temperature on size (Wilson et al. 2019). The findings from these systems suggest that additional factors such as life history traits and environmental context contribute to the effects of warming on morphology and resiliency of taxa to increasing temperatures generally.

In fact, some butterfly species show increases in size as temperatures warm. Forewing length of *Colias meadii meadii* increased as environments warmed in the Rocky Mountains, where longer growing seasons may promote greater larval food availability (MacLean et al. 2016). An analysis of butterfly species in Seoul and Mokpo, South Korea, also found increases in wing length over time (Na et al. 2021). Increasing body sizes have also been reported to accompany climate warming in bumblebees (Gérard et al. 2020). In addition, for some species, one sex is impacted more than the other. For example, in a study of museum specimens of the univoltine butterfly *Hesperia comma*, rising temperatures correlated with increased body size for males, while females showed no significant size changes (Fenberg et al. 2016). This suggests that how climate change impacts some species may be sex-specific and nuanced, potentially impacting particular physiological pathways that are more important in some stages or sexes.

Generally, however, climate warming is associated with reductions (and not increases) in size and wingspan in Lepidoptera, and warming-associated declines in wing lengths appear more common in colder environments. In two univoltine, Holarctic species of butterflies, *Colias hecla* and *Boloria chariclea*, strong warming-associated decreases in wingspan were found in Greenland (Bowden et al. 2015a). In that case, warming may induce increased metabolic costs for univoltine larvae. If the increased cost of basal metabolism relative to the rate of nutrient acquisition is not compensated for prior to pupation, this could result in smaller adult body sizes due to a net decrease of stored nutrients (Bowden et al. 2015a).

Insect populations at their poleward range limits likely experience strong seasonal restrictions on their life-history traits and the timing of life history events (Strathdee and Bale 1998, Ferris and Philip 2016). Local adaptation may substantially complicate these patterns. For example, in a comparative study of Alaskan and Michigan populations of the swallowtail butterfly, *Papilio canadensis*, Alaskan caterpillars grew significantly faster at lower temperatures (12°C) than those in Michigan, indicating that different subpopulations of the same species have their development rates aligned to their local climate (Ayres and Scriber 1994). Brief Arctic summers likely select strongly for rapid development at lower temperature. These time constraints could mean that Arctic insects have especially rapid physiological developmental pathways, which make them particularly susceptible to warming-induced morphological changes. If so, effects could be especially acute in the Arctic, where arthropods have a very limited amount of time to adapt because of the rapid pace of warming occurring there (Serreze and Barry 2011).

In this study, our main objective is to test whether the declines in butterfly wingspans documented by Bowden et al. (2015a) in Greenland during 1996–2013 have also occurred on the other side of the Arctic, in Alaska during 1971–1995. Observing a similar response of wing size to warming temperature in Alaskan butterflies would indicate the effect is present throughout the Arctic. We interpreted our results in the context of the findings of Bowden et al. and also in the context of differences in the life history traits among the three species analyzed. How species with different life histories are affected by warming may offer some insights into which butterfly species – that were not included in this study but with similar life history traits – are likely to be more (or less) strongly affected by ongoing climate warming across the Arctic.

To do this, we tested for changing wing lengths of Alaskan populations of the same two species studied by Bowden et al. (2015a) in Greenland, *C. hecla* and *B. chariclea*, along with a third species, *Boloria freija*, which overwinters in a more advanced larval stage than *B. chariclea*, and has less development after winter diapause, and thus flies almost three weeks earlier in the season than the other two species (James et al. 2011). Our study takes advantage of a unique period of intensive sampling of the Alaskan butterfly fauna that was conducted by the Alaska Lepidoptera Survey between 1966 and 2013 (Sikes et al. 2017), and analyzes specimens collected during its most intense period of sampling.

Material and methods

Specimens

We studied specimens from the Kenelm W. Philip Lepidoptera Collection, collected by K. W. Philip and volunteers of the Alaska Lepidoptera Survey. This collection was made between 1966 and 2013, and the results reported here are based on measurements from 2501 enveloped specimens collected between 1971 and 1995 when collecting was most intense in northern and western Alaska, covering a 24-year time span prior to the start of the Bowden et al. (2015a) Greenland study (sample sizes listed by sex and year in the Supporting information). The specimens are now part of the University of Alaska Museum Insect Collection, in Fairbanks, Alaska, and their records are available at https://arctos.database.museum/project/10002314.

Species data

We measured *C. hecla* and *B. chariclea* in large part because these were the two species measured at the Zackenberg research station in Greenland by Bowden et al. (2015a). We also measured *B. freija* because its life history differs from the other two species; specifically, though closely related to *B. chariclea*, *B. freija* overwinters at a later instar and emerges considerably earlier in the season. Collection records included geographic coordinates and collection dates (Fig. 1).

Collection regions

Unlike the specimens analyzed in Bowden et al. (2015a) that were all collected at a single location, our specimens were collected at many locations across Alaska. Butterflies were collected in tundra regions in northern and western Alaska between 64°30'N (Nome) to 71°17'N (Barrow / Utqiagvik). We divided collections into three geographic regions: the Seward Peninsula, the western North Slope, and the eastern North Slope (Fig. 1). This division accounts for differences in both climate and collecting effort. The majority of the specimens were collected from the eastern North Slope because, unlike the other two regions, it is accessible by road and consequently was sampled more intensely and consistently over time (Table 1).

Temperature data

Minimum and maximum daily temperature data for 1970–1995 were obtained from the global historical climatology network for twelve weather stations in northern Alaska (Fig. 1) (www.ncei.noaa.gov/products/land-based-station/global-historical-climatology-network-daily). To estimate temperature conditions at the time and locations of specimen collection, specimens were associated with the weather station closest to their collection site (Fig. 1). Inconsistencies in the locations and temporal coverages of weather stations in

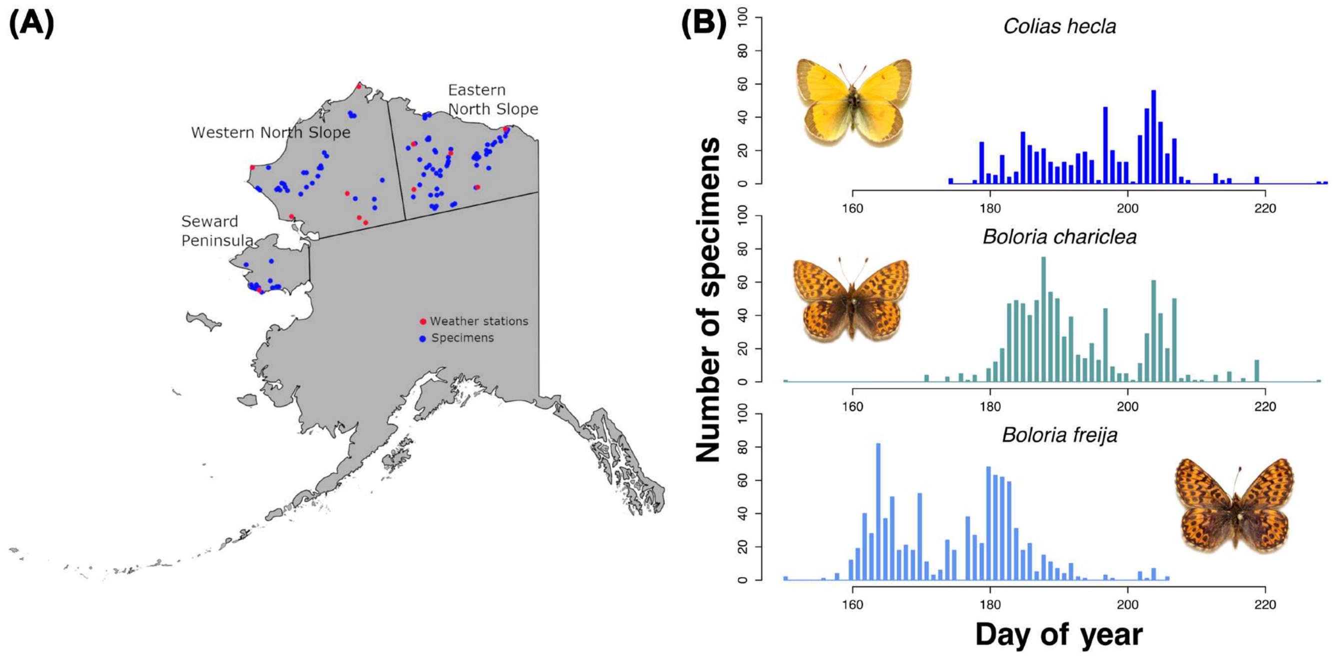

Figure 1. (a) Map of localities where measured butterfly specimens were collected (blue) and weather stations (red) in Alaska, with regions treated as a random effect. (b) Flight periods (number of individuals flying per day of year) for *Colias hecla* (top), *Boloria chariclea* (middle), and *Boloria freija* (bottom) in Alaska from 1970–1995. Note that the apparent bimodality of the flight times, especially for the two *Boloria*, results from the timing of haphazard sampling visits and differences in the flight times across the three regions sampled.

Table 1. Butterfly specimen sample sizes, including total measured individuals ($n = 2501$) by species and region of Alaska.

Species	Seward Peninsula	Western North Slope	Eastern North Slope	Total
Colias hecla	124	157	312	**593**
Boloria chariclea	249	287	433	**969**
Boloria freija	54	189	696	**939**
Total	**427**	**633**	**1441**	**2501**

this remote region of Alaska required interpolation of temperatures experienced by sampled butterflies at collection sites using the nearest available weather data. See the Supporting information for details on how this was performed.

Growing degree days (GDD)

GDD, a cumulative calculation of temperature above a certain threshold (Gordon and Bootsma 1993), was used to quantify the amount of heat experienced during butterfly development during the spring of the year that specimens were collected as well as during the preceding summer when they were larvae. This approach for tracking heat available to heterothermic animals has been widely adopted to model or analyze development rate (Saunders et al. 2016, Kingsolver and Buckley 2020, Zylstra et al. 2022) and Cayton et al. (2015) showed that GDD was a better way to track the effects of warming on butterfly phenology than any other way of quantifying heat. The main drawback using GDD is that it does not account for the retarding effects of very high temperatures on growth rate, but in our study region, such warm temperatures did not occur.

The GDD equation is:

$$\mathrm{GDD} = \sum_{i=1}^{D} T_{\max,i} - T_0$$

where D is the total number of days across which heat is accumulated, $T_{\max,i}$ is the maximum temperature on the ith day, and T_0 is the minimum temperature at which butterfly larvae can develop. We used a T_0 threshold of 5°C for calculating GDD for this analysis of Arctic cold-adapted species, following Morrison et al. (1989), Gordon and Bootsma (1993) and Buckley et al. (2017). Some cold adapted species have been shown to have a T_0 as low as 3°C, but in general Lepidoptera have $T_0 \geq 5$ (Buckley et al. 2017), even at higher latitudes. Moreover, extrapolating the T_0 versus latitude fit by Buckley et al. (2017) to 70°N (the latitude around which most of our specimens were collected) suggests that the mean T_0 for Lepidoptera at 70°N would be slightly above 5°C. As there are no data from this latitude for our species, we chose 5°C as our T_0 to accumulate GDD.

Larval development and temperature

We used flight-period data from the specimen records (Fig. 1) to estimate when larval development occurred in each species. For *B. freija*, the average day of year when species flight began was approximately Julian day 160 (~ 9 June), while for *B. chariclea* and *C. hecla* this is approximately day 180 (~ 29 June). These dates served as cut-offs for accumulated GDD values. We used growing degree day values calculated up to the respective mean first flight date for each species to represent the temperature experienced during larval and pupal development during spring of the flight year, which we termed 'Spring GDD.' We also separately calculated GDD after the mean first flight date for the previous year. This represents the temperature regime experienced by the egg and larvae until winter diapause during the summer prior to the year adults were collected. This meant initiating GDD accumulation on Julian day 161 for *B. freija* and Julian day 181 for *B. chariclea* and *C. hecla*.

Spring GDD (the growing degree days accumulated up until the flight period) and Summer GDD (the growing degree days accumulated during the egg and larval development during the summer prior to an adult's flight) were treated as separate variables. Thus, we separately assessed the effects of temperatures preceding winter diapause (Summer GDD) and its effect after winter diapause (Spring GDD) on adult size. Finally, to translate growing degree day measurements back to the more commonly reported temperatures in degrees Celsius, we calculated the total growing degree days associated with a 1°C increase in average summer (May–August) temperatures from Nome, Alaska between 1975 and 1995. Each 1°C increase corresponded to an additional ~ 133 GDDs.

Specimen measurement

Measurements were performed by a group of 15 undergraduate students at the University of Alaska, Fairbanks. A reference set of 11 specimens was measured by all students to assess among-observer variation in measurements. Measurements taken by each observer were compared to known values for wing length using a one-way ANOVA to detect any significant deviations among students. If differences were found, the students were re-instructed in the measurement protocols. This procedure was repeated until measurements were not appreciably different from the measured standards. Butterfly wings were measured using digital calipers while still in their original glassine collecting envelopes. This minimized damage from handling and afforded more consistent measurements. Each specimen, still inside its collection envelope, was placed on a light box to backlight the wing and thorax. Forewing length from wing apex to thorax segment was measured to the nearest 0.1 mm. Specimens were sexed to account for sexual size dimorphism. *Colias hecla* were sexed by color pattern, whereas *B. chariclea* and *B. freija* were sexed by examination of genitalia under magnification (Winter and Miller 2000).

Statistical analysis

We used R ver. 3.4.3 'Kite-Eating Tree' (www.r-project.org) to analyze the data using mixed effects models implemented

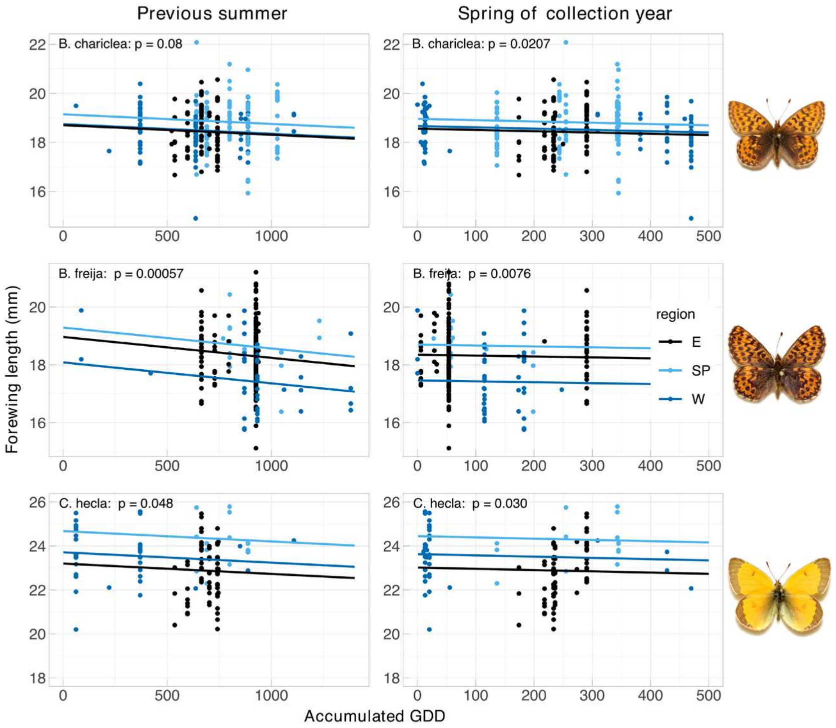

Figure 2. Wing length of female *B. chariclea* (top row), *B. freija* (middle row) and *C. hecla* (bottom row) compared to accumulated growing degree days (GDD) experienced during the previous summer (the summer prior to their year of collection; left column) and GDD the spring of collection year (right column). Regional random effects are represented by the three different regression lines, with Seward Peninsula (SP) having larger individuals in all three species, and eastern (E) and western (W) North Slope having differing random effect on size depending upon species. Males show an identical pattern (not shown). Note that for the model fit to the *B. freija* wing lengths to previous summer's GDD, the three specimens collected during very cold years do not leverage the slope of the regression; the fit does not change meaningfully (in magnitude or significance) if these individuals are excluded.

by the package 'lme4' (Bates et al. 2015), compared models with AIC, and assessed significance levels of model covariates using likelihood ratio tests. We used 'ggplot2' (Wickham 2016) for data visualization.

Models were fit to each species separately. We created mixed-effects models with a random effect on the intercept of the collection region to account for regional variation in wing size and tested wing length as a response variable with the explanatory fixed effects of sex, Spring GDD, and Summer GDD as main effects of candidate models. Spring and Summer GDD were log transformed to improve homoscedasticity of these covariates. Some carefully chosen two-way interactions were also included to test specific biologically motivated hypotheses (i.e. sex × GDD was included to test whether warming affected the sexes differently). The null model excluded GDD data and included sex as the only fixed effect, with collection region as a random effect. These models were created to test specific hypotheses about how temperature influences size, and how demographic and life history traits such as sex and overwintering stage influence temperature effects on adult morphology.

Results

Colias hecla had the largest wings of the three species studied, with mean forewing lengths of 22.90 mm (SE: 0.410) mm for males and 23.86 mm (SE: 0.414) for females. The two *Boloria* had nearly identical wing lengths. Mean forewing lengths for male *B. freija* were 17.88 mm (SE: 0.376), while females were 18.86 mm (SE: 0.381), and forewing lengths for male *B. chariclea* averaged 17.89 mm (SE: 0.187) while females averaged 18.83 mm (SE: 0.188). On average, the *B. freija* we sampled experienced 78 GDD (range: 0–290.5) in the spring of the flight year, while *B. chariclea* experienced 271 GDD (range: 0–507.5) and *C. hecla* experienced 215 GDD (range: 0–507.5). The increased spring heat exposure results from more larval instars in the flight year for *B. chariclea* and *C. hecla*. In the summer prior to the flight year, *B. freija* experienced an average of 894 GDD (range: 87.2–1381.7), *B. chariclea* experienced an average of 705 GDD (range 61.7–1107.7), and *C. hecla* experienced an average of 634.5 GDD (range: 61.7–1107.7).

For all three species, the best-fitting model explaining wing length included sex and either Summer GDD (*B. freija)* or Spring GDD (*B. chariclea* and *C. hecla*) (Table 2, Fig. 2). Interactions between sex and GDD were not supported for any of the three species, indicating that the sexes were similarly impacted by warming (Table 2, Fig. 2). Models that included warming from both the current spring and previous summer were not selected for any species, indicating that warming primarily impacted the season in

Table 2. AIC model ranks. Models ordered in this table by best fit for *B. freija*. Bolded AIC scores indicate the best fitting model. *indicates significant ($p < 0.05$) improvement in fit relative to the null model as assessed by LRT.

	Boloria freija		*Boloria chariclea*		*Colias hecla*	
Model	AIC	Rank	AIC	Rank	AIC	Rank
Sex + $\mathrm{GDD}_{\mathrm{sum}}$	**2537.2***	**1**	2649.1	4	1893.5*	2
Sex + $\mathrm{GDD}_{\mathrm{sum}}$ + $\mathrm{GDD}_{\mathrm{spr}}$	2537.8	2	2648.8	3	1894.1	4
Sex × $\mathrm{GDD}_{\mathrm{sum}}$ + Sex × $\mathrm{GDD}_{\mathrm{spr}}$	2538.4	3	2652.6	7	1897.1	7
Sex × $\mathrm{GDD}_{\mathrm{sum}}$	2538.6	4	2650.6	6	1895.1	5
Sex + $\mathrm{GDD}_{\mathrm{spr}}$	2541.9*	5	**2646.9***	**1**	**1892.7***	**1**
Sex × $\mathrm{GDD}_{\mathrm{spr}}$	2542.5	6	2648.7	2	1893.7	3
Sex (Null model)	2547.1	7	2650.2	5	1895.5	6
$\mathrm{GDD}_{\mathrm{sum}}$ + $\mathrm{GDD}_{\mathrm{spr}}$	2722.4	8	2824.6	8	1952.7	8

which most or all larval development took place. However, when compared to the null model (sex effect on the intercept only), warming in any season was significantly associated with decreased wing size in all cases, except Summer GDD for *B. chariclea*, as assessed by likelihood ratio tests (LRT). This could indicate that some warming in either the year of or the year before adult flight impacts size. However, given that warming from just a single season was the top model in all cases, the more parsimonious explanation for this effect is simply that temperatures in consecutive years are correlated.

Colias hecla and *B. chariclea* appeared to be similarly affected by warming in both degree and pattern. These species were both more impacted by spring warming than warming the previous summer and also generally experienced relatively moderate, warming-related declines in size (Table 3–4, Fig. 2). *Boloria freija*, by contrast, was mostly impacted by warming the previous summer, and the intensity of the warming-related size decreases was much stronger (Table 3–4, Fig. 2).

Discussion

Our results corroborate and add nuance to the patterns of butterfly wing shortening associated with Arctic warming as observed in Greenland (Bowden et al. 2015a). Our findings, in concert with Bowden et al. (2015a), suggest that warming's impacts on butterfly morphology are Arctic wide. The inclusion of *B. freija* showed warming impacted this species differently than *B. chariclea* and *C. hecla*, suggesting life history traits, specifically which instar typically overwinters, may explain their differing responses to warming temperatures. Taken together, our results confirm that warming is causing some Lepidoptera to shrink across the Arctic, but indicate there is considerable regional heterogeneity in how warming is affecting butterfly morphology.

Both *Boloria* species showed considerable shrinkage during warmer years, but our data show that *B. freija* was the most sensitive to warmer temperatures among the three species we studied. This species does most of its development the previous summer, and overwintering as fourth instar larvae it has the earliest flight period (Fig. 1, Layberry et al. 1998, James et al. 2011). When reared in captivity, *B. freija* larvae were not observed to feed in the spring of the year it flies during their fifth and final instar (James et al. 2011). Instead, development during the fifth instar relies completely on fat reserves acquired the year before. Additionally, *B. freija* larvae that were exposed to artificially warmed temperatures in their fourth instar did not break their winter dormancy (an obligate period of 4–7 months of uninterrupted cold) to initiate pupation, suggesting their physiology during that phase of their development is not plastic and is highly sensitive to temperature and warming (James et al. 2011). The observed decreases in wing size, if they are also expressed in overall body size, could impact overall fecundity, as body size is highly correlated with fecundity in butterflies (Boggs 1986). Reduced fecundity could lower a population's potential growth rate and even slow its ability to adapt to new climates by decreasing the pool of individuals on which selection can act.

During winter, temperatures in Arctic Alaska are continuously below freezing, though the length of this frozen period is shrinking. Autumn and winter temperatures are also increasing, especially in northern and western Alaska, which has led to a decrease in seasonal snowpack (Thoman and Walsh 2019). A longer, warmer autumn in the year preceding the adult stage may incur increased metabolic costs prior to winter diapause, resulting in decreased fat reserves for overwintering, and potentially smaller adult sizes. *Boloria freija*'s inflexible diapause requirements and lack of fifth

Table 3. Parameter estimates for the Sex + $\mathrm{GDD}_{\mathrm{sum}}$ + $\mathrm{GDD}_{\mathrm{spr}}$ model. Although this was not the best fitting by AIC rank it was < 2 ΔAIC from the best fit and allows comparison of effect sizes of both spring and summer warming for all three species.

Species	$\mathrm{Sex}_{\mathrm{male}}$	$\log(\mathrm{GDD}_{\mathrm{sum}})$	p	$\log(\mathrm{GDD}_{\mathrm{spr}})$	p
Colias hecla	−0.960	−0.167 [0.083]	0.048	−0.129 [0.059]	0.030
Boloria freija	−0.982	−0.53 [0.150]	< 0.001	−0.098 [0.036]	0.007
Boloria chariclea	−0.952	−0.174 [0.098]	0.08	−0.076 [0.033]	0.02

Table 4. Predicted decreases in total wingspan per 100 GDD of warming and per ~ 1°C average summer temperature increase (equivalent to ~ 133 GDD). Note that predictions were made with parameters fit to log transformed GDD data. Predictions are not valid for temperature ranges outside the range observed in the original regressions.

Species	Summer before flight year		Spring of flight year	
	mm/100 GDD	mm/~ 1°C	mm/100 GDD	mm/~ 1°C
Colias hecla	−1.53	−1.63	−1.19	−1.26
Boloria freija	−4.88	−5.12	−0.82	−0.88
Boloria chariclea	−1.60	−1.70	−0.70	−0.74

instar feeding may contribute to this species' high sensitivity to warming during the previous summer, because increased metabolic costs cannot be compensated for by additional feeding during the spring (Fig. 3). Life history traits such as overwintering stage have previously been linked to decreases in abundance of cold-adapted Lepidopteran species as ranges shift to accommodate climate warming in other parts of North America (Breed et al. 2013).

Our findings for both *B. chariclea* and *C. hecla* align closely with Bowden et al. (2015a) for these two species in both effect size and pattern. However, our findings suggest that warming during the spring of the flight year has a larger impact than warming the previous summer for these species, while Bowden et al. (2015a) found that warming the previous summer was driving decreases in wing size, but not temperature in the current year, which was not significant. In Alaska, for both *B. chariclea* and *C. hecla*, warming the previous summer does appear to have some negative correlation with wing size, but the effect was marginally significant for both species when compared to the null model and did not explain as much variation as spring warming. We interpret this to mean that warming in the current year and warming the previous year is correlated, and the effect of warming on size is occurring during the spring in Alaska, owing to the action of the Pacific Decadal Oscillation on Alaskan climate regimes (Mantua and Hare 2002). We note that Bowden et al. (2015a) did find a weak relationship between size and the timing of snow melt in the current year, with earlier snow melt negatively correlated with size. We didn't test the effect of snow melt timing in our analysis, and thus our findings of a stronger effect of spring warmth on wing size may be via its action on snow melt timing.

Previous Arctic arthropod studies reveal complex changes have already occurred, including declines in Arctic fly abundance and species diversity at Zackenberg, Greenland (Loboda et al. 2018). Earlier snowmelt dates at the Zackenberg Research Station in northeast Greenland have resulted in larger adult wolf spiders (Family Lycosidae) (Høye et al. 2009). Body size in crab spiders (Family Thomisidae) were found to differ between mesic and arid habitats within the tundra at Zackenberg, with significantly larger females in mesic habitats (Bowden et al. 2015b). Additionally, later snowmelt was found to cause a significant decrease in the abundance of female crab spiders within mesic habitats in Greenland (Bowden et al. 2015b).

In Alaska, there is a northward expansion of shrub habitat into the tundra, altering the composition and abundance of different types of arthropods within shrub and open tundra habitats (Boelman et al. 2015, Asmus et al. 2018). Patterns of arthropod abundances, diversity, and body size changes could have important implications for food webs, since arthropods are an essential food source for migrating breeding birds (McDermott et al. 2021). Tundra invertebrates rely on both seasonal and diurnal cues, such as temperature and the resulting snowmelt timing (MacLean 1975). Species-level differences in life history traits may help offset rising temperature effects, with species with more flexible life histories, such as an ability to diapause at different stages or plastic voltinism, better able to persist across a wider range of climates, and thus better able to withstand climate changes in any given region.

Conclusions and implications for Arctic Lepidoptera

Arctic warming has significantly contributed to a global mean surface air temperature increase of 0.12°C per decade (Huang et al. 2017). The Arctic has warmed almost four times faster than the global average (Rantanen et al. 2022), with tremendous spatial and temporal variation. The Arctic Ocean has warmed 1.25°C per decade from 1979–2021 in the region around Novaya Zemlya and Svalbard, while other portions of the Arctic at lower latitudes have experienced minimal warming (Rantanen et al. 2022). In Alaska, temperature trends vary spatially, temporally, and seasonally. The North Slope warmed 1.9°C from 1981–2012 (Bieniek et al. 2014), or about 0.63°C per decade, with significant trends detected in the months of July through November. Alaska experienced a warming trend from the late 1970s through the early 2000s, followed by a cooling pattern for all but the North Slope, which has continued to warm (Bieniek et al. 2014). Alaska's climate variability corresponds to the phase of the Pacific Decadal Oscillation (PDO), a pattern of changing oceanic temperatures between warming and cooling phases, with the positive PDO phase associated with warmer than average temperatures over land in Alaska (Bieniek et al. 2014).

For butterflies, these temperature fluctuations can be detrimental; both extreme warm and cold conditions associated with changing phases of the PDO correlate with population declines in *Parnassius smintheus* in the Rocky Mountains (Roland and Matter 2013). Rising temperatures and earlier seasonal snowmelt have some advantages, such as a lengthening of the tundra growing season (Ernakovich et al. 2014), so butterflies with flexible life histories may be able to adapt to some effects of rising temperature. Butterflies, such as *Euphydryas editha*, may have some resilience to climate warming due to flexibility in their phenology, emerging as smaller adults to lay eggs earlier in the season to match the season advancement in warming years (Bennett et al. 2015). Other life history plasticity, such as overwintering larval stage, as seen in Alaskan North Slope *Colias* sp., including *C. hecla* which can overwinter from first instar larvae up to third instar (Harry 2009), may offer some ability to buffer from climate warming at the population level.

A recent reconstruction of shifts in high latitude North American butterfly communities found that warming has unequally impacted some cold-adapted endemics, including *Boloria* sp., leading to a decline in occupancy while *C. hecla* actually gained in range occupancy (Shirey et al. 2023). In fact, Shirey et al. (2023) found that *B. chariclea* and *B. frejia* were declining faster than any other Arctic butterfly out of nearly 100 populations analyzed, while *C. hecla* was actually increasing. Increasing presence of *C. hecla* across the Arctic suggests the morphological impacts so far experienced have not negatively impacted population dynamics or survival. That pattern may also indicate negative effects of warming are only taking place near this species' northern range limits, while showing resilience to warming in more southern, less isolated, locales.

The differing responses of *B. freija*, *B. chariclea* and *C. hecla* indicate that a species' life history, particularly when and how they diapause, plays a crucial role in determining their morphological, and likely ecological, responses to warming climates. Consequently, how cold-adapted arthropods overwinter and whether or not they are obligately univoltine may be key indicators of their sensitivities to climate warming. Metabolic stress, thought to be the mechanism for the morphological responses observed in *B. chariclea* and *C. hecla* in Greenland (Bowden et al. 2015a) and likely also in Alaska, could lead to higher metabolic costs and lower growth rates among a suite of Arctic Lepidoptera (Barrio et al. 2016), especially those with similar life histories. Warming may favor butterfly species that are able to extend their development across two summers (e.g. *B. chariclea* and *C. hecla*), but negatively affect species with less flexible life histories (e.g. *B. freija*). Species that overwinter as older caterpillars that do not feed after diapause (e.g. *B. freija*) may not have time in their life cycle to compensate for elevated metabolic rates caused by warmer temperatures, resulting in smaller adults (Fig. 3). For arthropods, such life history characteristics, dietary requirements, and metabolic constraints may determine the extent that adult size and morphology is affected by climate warming.

Here we analyzed museum specimens collected over several decades to detect effects of warming on butterflies. Museums will continue to be a crucial resource for understanding how arthropods are impacted by rapidly changing conditions in the

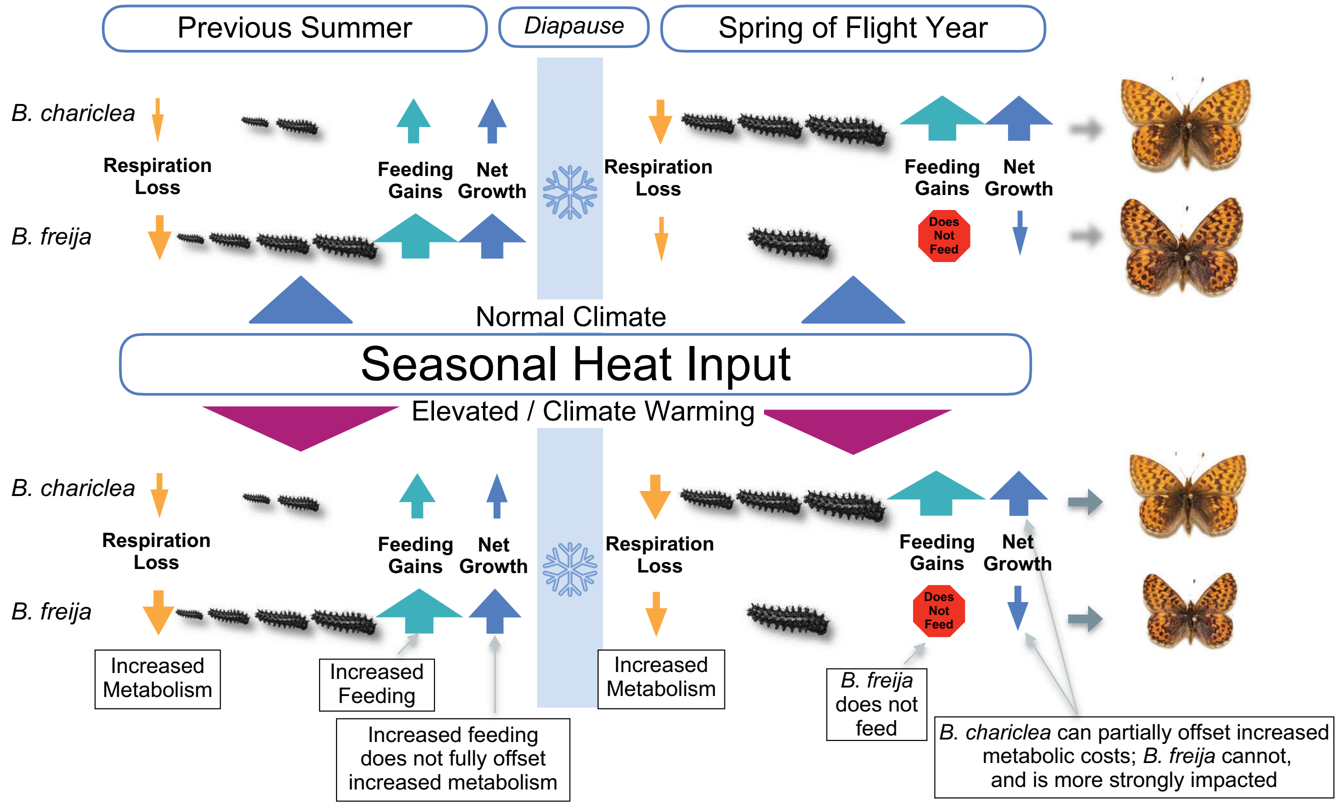

Figure 3. Conceptual figure of the effects of seasonal heat input on *B. chariclea* and *B. freija* experienced in the summer prior to collection (left) and spring (right). Metabolic rates increase with temperature, which, depending on larval overwintering stage, may not be offset by feeding, resulting in a smaller adult body size (right). The inability of *B. freija* to feed in the fifth instar during the spring of the flight year may make it particularly sensitive to warming the previous year. Feeding immediately prior to pupation may be important for mitigating these effects, and why *B. freija* is more sensitive to warming than *B. chariclea*, which is able to feed after diapause during the spring of the flight year.

Arctic (Sikes et al. 2017). Other Lepidoptera, Coleoptera and Hymenoptera, are well-represented in museum collections and often sampled repeatedly over time; allowing for similar analyses of morphological changes over time. Climate effects causing body size reductions could be widespread among other poorly-observed and under-studied taxa; these large and charismatic groups may act as 'climate canaries' for the potential effects of warming on many of these under-studied and even unnamed arthropods that share a warming Arctic ecosystem.

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Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.4qrfj6qh1 (Daly et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

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