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Elevational differences in developmental plasticity determine phenological responses of grasshoppers to recent climate warming

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Annual species may increase reproduction by increasing adult body size through extended development, but risk being unable to complete development in seasonally limited environments. Synthetic reviews indicate that most, but not all, species have responded to recent climate warming by advancing the seasonal timing of adult emergence or reproduction. Here, we show that 50 years of climate change have delayed development in high-elevation, season-limited grasshopper populations, but advanced development in populations at lower elevations. Developmental delays are most pronounced for early-season species, which might benefit most from delaying development when released from seasonal time constraints. Rearing experiments confirm that population, elevation and temperature interact to determine development time. Population differences in developmental plasticity may account for variability in phenological shifts among adults. An integrated consideration of the full life cycle that considers local adaptation and plasticity may be essential for understanding and predicting responses to climate change.

1. Introduction

Phenological shifts are among the most ubiquitous responses to recent climate change: 80% of species show advances in the seasonal timing of reproduction or adult emergence [1]. Most studies of animal phenology have exclusively examined adults, obscuring differences in exposure and sensitivity to climate across life cycles [2]. Laboratory studies examining growth and development have revealed the complex trade-offs shaping thermal responses [3], but these trade-offs have seldom been invoked to explain field observations [4]. Can such trade-offs help explain why 20% of species show seasonal delays rather than advances in response to climate change [5]?

In most insects and other ectotherms, higher temperatures typically reduce development time and decrease adult body size [6]. However, many insect populations with short growing seasons at high latitudes or high elevation show a reversal of this temperature-size rule, in which higher rearing temperatures produce larger adult size [7]. Grasshoppers at high elevations often hatch early and develop rapidly to ensure adequate time to complete their life cycle [8]. Studies of annual grasshopper populations along an elevational gradient in the Alps show that development time, adult size and fecundity are all positively correlated, suggesting that longer development times may be selectively favoured when life cycle duration is not seasonally constrained [9]. Adaptations by high-elevation and -latitude populations to development at low temperatures can decrease climate sensitivity [10], but the populations tend to exhibit more pronounced responses as they are released from seasonal constraints [7]. Here, we ask whether the relaxation of seasonal constraints owing to

recent warming can cause plastic responses that extend development in high-elevation populations. This may generate different phenological responses to climate change in populations at low versus high elevations. We focus on grasshoppers that have shifted the timing of reaching adulthood differentially across species and populations in response to recent warming [11].

2. Material and methods

We integrate historic and current field observations and laboratory rearing to investigate how development rates have influenced responses by Colorado grasshoppers to recent climate change along an elevation gradient. Weekly survey data from 1959 to 1960 were assembled from field notebooks as part of the Gordon Alexander Project (ghopclimate.colorado.edu). Weekly resurveys have been conducted since 2006 [11] following the original protocol, consisting of 1.5 person-hours of sweep netting (divided among one to three surveyors) and 0.75 person-hours of searching for adults and juveniles that may have been missed by sweep netting [12]. We focus on four univoltine (annual) grasshopper species that are abundant across the elevation gradient and study period: *Camnula pellucida*, *Melanoplus boulderensis*, *Melanoplus dawsoni* and *Melanoplus sanguinipes*. Each species overwinters in an egg diapause, but they differ in their seasonal timing and dispersal ability: in particular, *C. pellucida* and *M. boulderensis* are 'early' species that complete post-diapause development earlier in the season, whereas *M. dawsoni* and *M. sanguinipes* are 'late' species [11]. *Melanoplus dawsoni* and *M. boulderensis* have short wings and thus a limited capacity for dispersal. We examine development rates and phenology among populations and species across four prairie, montane or subalpine sites along the 40th N parallel in Boulder County, CO, USA: Chautauqua Mesa (1752 m, 40.00 N, 105.28 W), A1 (2195 m, 40.01 N, 105.37 W), B1 (2591 m, 40.02 N, 105.43 W), C1 (3048 m, 40.03 N, 105.55 W) (descriptions: niwot.colorado.edu/site_info/site_info.html). The sites are all grassy meadows, with somewhat denser vegetation at the lower elevation sites. Grasshopper eggs are deposited as pods just below the surface in areas with exposed soil. We combine our field data with laboratory experiments for *M. sanguinipes* to assess how the effects of rearing temperature on development time and adult size may vary among populations at different altitudes.

(a) Field studies

We calculated degree days as the accumulated product of time and temperature between the lower and upper developmental temperatures (LDT and UDT, respectively). The calculation employed a single-sine approximation [13] based on daily minimum and maximum temperatures and a fixed spacing of 12 h between temperature minima and maxima. We used daily maximum and minimum temperature data from weather stations at our study sites [14]. Recent survey data were analysed for 2006–2008 and 2011 due to limitations on weather station data.

We estimated the degree days available for development during the two time periods (1959–1960 versus 2006–2011) for *M. sanguinipes* based on biophysical model estimates of field body temperature and estimates of LDT from rearing data (see below). We incorporated weather data in a biophysical model to estimate a grasshopper's maximum daily body temperature [15] (electronic supplementary material, appendix S1). We confirmed that increasing or decreasing the body size, body absorptivity or ground albedo estimates by 10% in the biophysical model had little effect on our estimates of the ratio of growing degree days available at the 3048 m site between the initial and recent survey periods (mean \pm s.e. = $0.68 \pm 0.24\%$, maximum

1.5% change in the ratio across all parameter combinations). We estimated available degree days between the maximum daily body temperature and minimum daily air temperature. We assumed mean windspeed and median radiation values for July observed at our study sites, which should reasonably approximate available development time given that wind gusts and radiation spikes are relatively rare [15]. We estimated the LDT from rearing data using the relationship $D(t - \text{LDT}) = \text{degree days}$, where D is the development time (days) from hatching to adulthood and t is the rearing temperature [16]. This approach yielded an estimate of 16.4°C for the LDT across populations. We assumed a UDT of 40°C , which approximates the upper thermal limits for performance among the study populations [17] and calculated degree days from the mean snowmelt date at the 3048 m site (21 May) through to August.

For the field analysis, we calculated degree days based on air temperature to avoid assumptions regarding thermoregulatory behaviour, radiation, windspeed and soil temperatures. This is also in response to our only having an LDT estimate from rearing for *M. sanguinipes*. We used a LDT of 12.0°C [11] to account for differences between air and body temperatures. We additionally estimated degree days as above for *M. sanguinipes* to confirm that the results were robust to the degree days calculation methods. Our estimation of degree days for field populations are intended as an approximate translation of environmental temperature into physiological time, but are not specific to populations or species.

We used a development index, which represents the average development stage of the population and ranges from 1 (all first instars) to 6 (all adults), to describe the developmental stage of communities sampled through field surveys. We used linear mixed-effects (LME) models and ANOVAs in R to examine the determinants of the development index. We included degree days as a third-degree polynomial and controlled for survey year as a random variable.

(b) Rearing experiments

Melanoplus sanguinipes were reared at constant 24, 27 or 30°C and a long day 14 L:10 D cycle in Percival I-36VL incubators with 32 W fluorescent bulbs (Phillips F32T8/TL741). There was no indication that the grasshoppers were able to use the lights to thermoregulate. The final analysis included grasshoppers that survived to maturity from populations at 2195 m ($n = 118$), 2591 m ($n = 127$) and 3048 m ($n = 68$). We additionally reared the other species as well as *M. sanguinipes* at 18°C , but low hatching or survival rates prevented analysis.

Eggs were collected by allowing females to oviposit in damp sand and then sieving the sand. Eggs were stored in damp vermiculite within 2oz polyurethane containers. The surface was periodically coated with 0.25% methyl-p-hydroxy benzoate to inhibit fungal or microbial growth. The eggs developed for three weeks at $25\text{--}30^\circ\text{C}$ and were then stored at 2°C for approximately 110 days to enable diapause. The egg containers were subsequently placed in a 24, 27 or 30°C incubator. Upon hatching, the egg containers were enclosed within rectangular 2.25 l polyurethane containers with lettuce and wheat bran provided. The grasshoppers were reared together until they reached third instar. Subsequently, grasshoppers were reared individually in 0.47 l polyurethane containers, which were changed every other day and supplied with romaine lettuce and wheat bran. We checked for eclosion when containers were changed. Our rearing data suggest that 430 ± 5 (mean \pm s.e.) degree days are required for *M. sanguinipes* to complete development irrespective of source population.

We used LME models and ANOVAs in R to estimate the significance of rearing temperature and population elevation as predictor variables. We included egg pod identification (ID) as a random variable. We lack the power to include the interaction

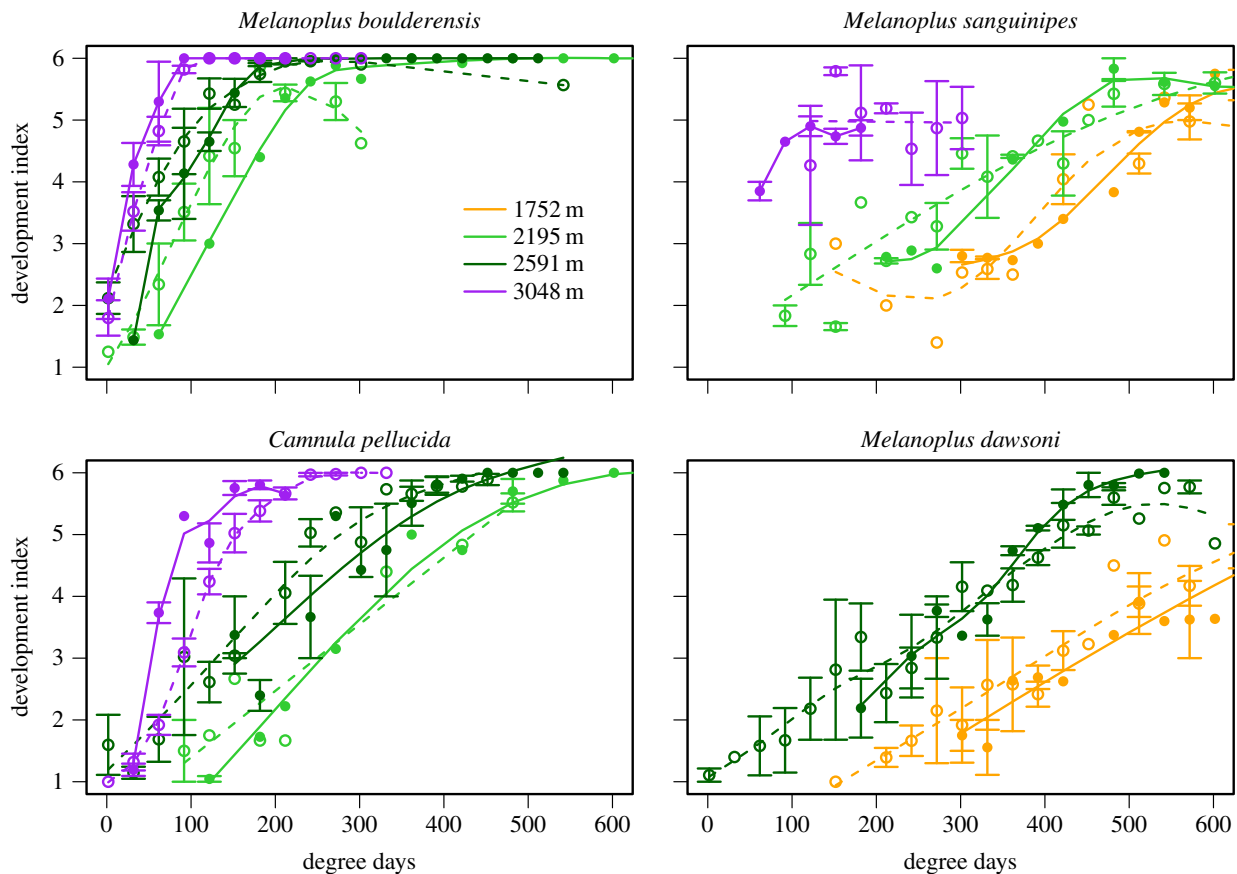


Figure 1. The development index (means \pm s.e.), which represents the average development stage of the population and ranges from 1 (all first instars) to 6 (all adults), increases as degree days accumulate through the season. Sites are depicted by colour. Development has generally accelerated or remained constant with respect to degree days between the initial surveys (1959–1960: solid lines) and resurveys (2006–2011: dashed lines), but some high-elevation populations of early-season species (left column) have relaxed development. (Online version in colour.)

between temperature and elevation in the LME models; we thus also ran linear fixed-effects models examining rearing temperature, elevation and their interaction without accounting for egg pod ID as a random variable. We find that sex is a significant determinant of mass, but not development time. We thus only account for sex in models examining mass.

3. Results and discussion

Development rates have shifted in response to 50 years of warming. Degree days accumulate more rapidly now than 50 years ago, particularly at high-elevation sites (electronic supplementary material, figure S1). Developmental phenology has generally advanced as a function of ordinal date (electronic supplementary material, figure S2), but we focus on physiological time (degree days) to better capture developmental responses. Development stage (as captured in the development index) advances significantly as degree days accumulate through the season ($F_{3,657} = 525.4$, $p < 0.0001$; figure 1). The rate of development differs significantly between species ($F_{3,657} = 124.5$, $p < 0.0001$) and elevations ($F_{1,657} = 316.9$, $p < 0.0001$). Development has advanced in response to climate change since 1960 (time period: $F_{1,5} = 8.7$, $p = 0.03$), but a significant interaction between time period and elevation indicates that high-elevation populations are delaying development relative to low-elevation populations ($F_{1,657} = 10.0$, $p = 0.002$). When accounting for the species' seasonal timing rather than species *per se* in the ANOVA, we find that the developmental rate of early-season species

shows a more pronounced response to recent climate change (time period \times seasonal timing: $F_{1,656} = 8.3$, $p = 0.004$), particularly at high elevation (time period \times seasonal timing \times elevation: $F_{1,656} = 5.3$, $p = 0.02$). The shifts in seasonal timing at high elevations are apparent when examining the composition of development stages through the season: early instars of the early-season species now persist longer at high elevation (figure 2 and the electronic supplementary material, figure S3).

We estimate that *M. sanguinipes* at the high (3048 m) elevation site required 71.7% of the available degree days during the initial survey (1959–1960) to complete development, but that recent warming (2006–2011) has relaxed the seasonal constraint and decreased this value to 64.4%. Development was estimated to correspond to less than 50% of the available degree days at the other sites initially and the subsequent decrease was observed to be less than that at the 3048 m site.

Laboratory rearing of *M. sanguinipes* confirms that population elevation and temperature interact to determine development rate. Warmer temperatures accelerate development, but do not alter mass (figure 3). A significant interaction between temperature and instar indicates that the acceleration of development at warmer temperatures becomes more pronounced through development (table 1, repeated measures ANOVA). Populations from different elevations do not differ overall in development rate, but the populations differ in their response to temperature and this response varies among instars. High-elevation populations tend to develop slower than low-elevation populations in

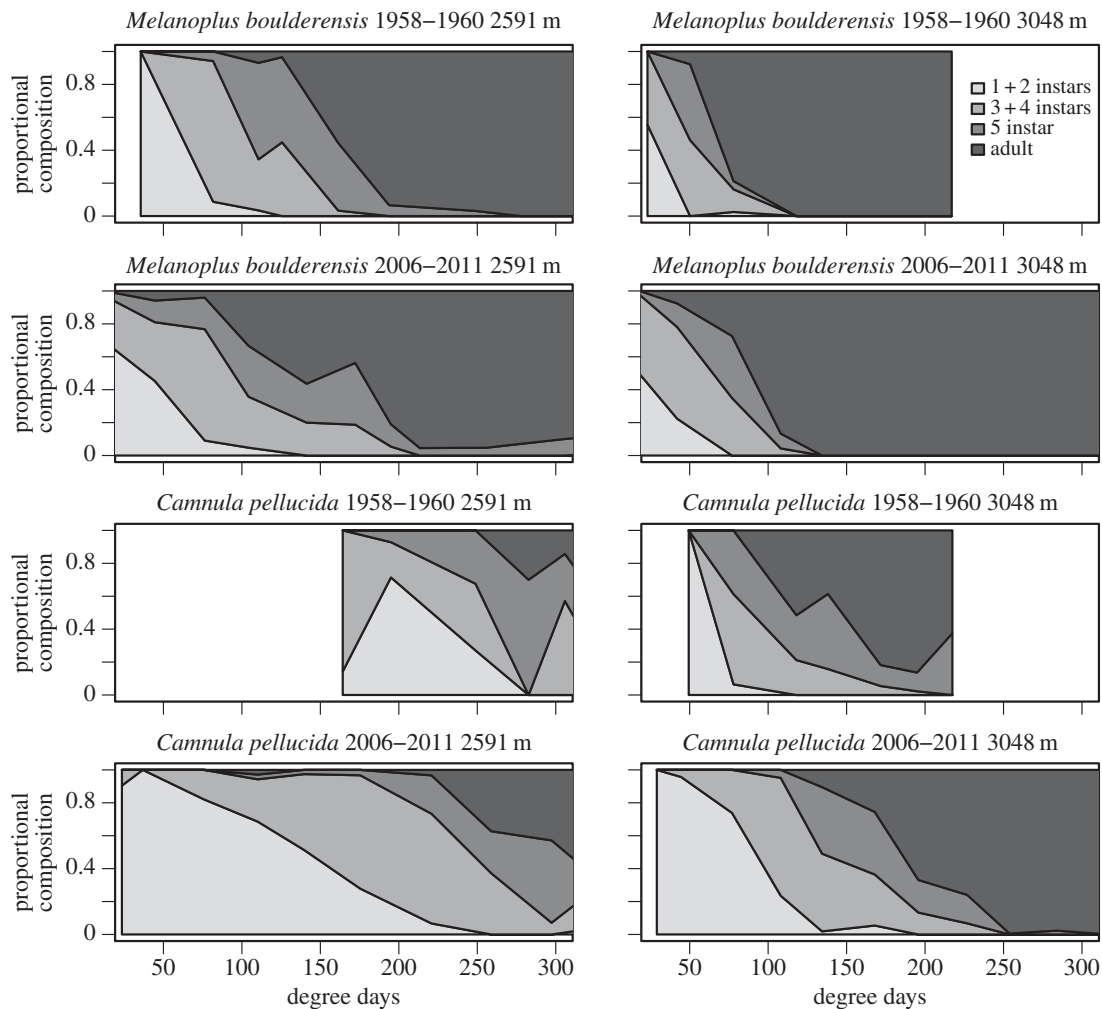


Figure 2. The proportion of individuals accounted for by each development stage (early to late: light to dark grey) as degree days accumulate through the season. Early instars tend to persist later in the season in resurveys (2006–2011) compared with the initial surveys (1959–1960), particularly at the high-elevation site (3048 m).

cool temperatures but faster in warm temperatures (table 1). Increases in mass through development are not sensitive to rearing temperature. However, sex exhibits a significant main effect and significant interaction with temperature, elevation and instar (table 1).

The interaction between rearing temperature and elevation of the source population is consistent with higher elevation populations of the late season *M. sanguinipes* accelerating development to capitalize on warmer temperatures and increasing time available for reproduction. The field observations suggest that this developmental plasticity may be reversed for early-season species (*C. pellucida* and *M. boulderensis*), such that season-limited, high-elevation populations are able to relax development when released from seasonal constraints [17]. Our rearing results contrast those for California populations of *M. sanguinipes*, where high-elevation populations develop faster across temperatures [8]. This discrepancy may stem from the more severe seasonal constraints in Colorado. Observations that low-elevation California populations do accelerate development in cool, short-day conditions suggest the importance of seasonal constraints [8]. A field warming experiment found that acceleration of embryonic development with warming depended on the grasshopper species' seasonal timing [18].

We find little evidence that accelerated development reduces *M. sanguinipes* body size in either the laboratory or field in

contrast to other studies along elevational gradients [7,16]. Mean body size in the field does decline with elevation along the gradient for the short-winged species (*M. boulderensis*), but not for the long-winged species (*M. sanguinipes* and *C. pellucida*) [19,20]. Laboratory rearing of *M. boulderensis* could help assess whether delaying development allows the high-elevation populations to reach larger body sizes. Body size changes for *M. boulderensis* and *C. pellucida* between the initial and recent surveys provide limited support that delaying development at the high-elevation site enables achievement of larger body sizes: *M. boulderensis* males have become smaller at the mid-elevation (2591 m) site and size increases for *C. pellucida* are significant for females and suggestive for males at the high-elevation (3048 m) site (C. Nufio 2014, unpublished data). Further research will be required to confirm the mechanism favouring slower development when seasonal length allows.

Our field data suggest that seasonal timing is a better predictor of whether warming will delay development at high elevations than thermal adaptation. All populations of the species we consider here excepting *M. dawsoni* increase consumption and digestion rates with temperature up to high temperatures (40°C) [17]. This suggests that warming should increase the amount of assimilated resources available to species across the gradient. The delay in development with warming appears to be independent of the thermal adaptation

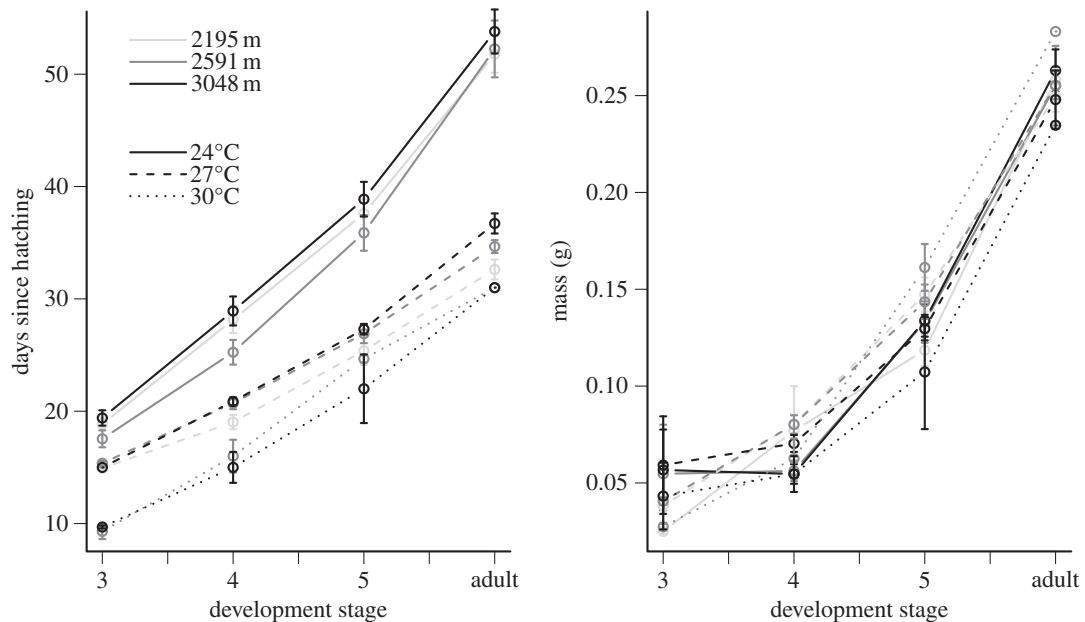


Figure 3. The (a) days since hatching and (b) mass corresponding to instars 3 through to 5 and adults (6) for *M. sanguinipes* collected from three elevations and reared at three temperatures. Data are means \pm s.e. Development rates, but not mass, respond to rearing temperature differentially between populations. Data for the 2195 m population at 30°C were omitted owing to high levels of mortality.

Table 1. Results of ANOVAs examining the extent to which rearing temperature (temp, °C), source elevation of the population (elevation, m), sex and their interactions influence development time (days) and mass (g) in *M. sanguinipes*. (Measurements repeated across instars. Significance levels are depicted as asterisks. * $p < 0.05$, *** $p < 0.001$.)

	development time (days) F_{292}	mass (g) F_{292}
temp (°C)	108.7***	0
elevation (m)	0.1	0
instar	2533.3***	757.4***
sex		9.9***
temp : elevation	0.1	0
temp : instar	163.8***	0
elevation : instar	4.9*	0.9
temp : elevation : instar	5.5*	0.2
temp : sex		3.9*
elevation : sex		4.6*
instar : sex		12.2***

of performance for the species: performance data suggest that *M. boulderensis* is cool-adapted, but *C. pellucida* is warm-adapted [17]. We note that development of *M. sanguinipes* is highly thermally dependent over a narrow range of constant temperatures as we observed very slow development at 18°C and high levels of mortality at 30°C. Our experiment thus spanned nearly the full range of temperatures suitable for development and should provide a robust estimate of developmental limits.

Phenological responses are often observed to vary with the seasonal timing of species owing to differences in the

timing of and exposure to warming [21–23]. Geographical heterogeneity in phenological responses are widespread and usually attributed to differences in environmental conditions [24,25]. Our analyses point to the importance of additionally considering how local adaptation in developmental plasticity can influence phenological responses to climate change. Ubiquitous increases in the number of insect generations per year in response to climate warming highlight the importance of developmental responses [26]. Phenological delays have been attributed to shifts in voltinism and developmental timing [27]. The magnitude of phenological shifts for butterflies varies with respect to overwintering stage and host plant specificity, indicating a role of developmental plasticity [22,23,28].

Differences in developmental timing between populations and species may alter interactions and community structure. Mismatches between resource requirements and availability frequently occur [29]. The nature of interactions among species often changes across ontogeny owing to changes in relative body size [30]. A mechanistic understanding of how climate change alters trade-offs between growth and development for multiple species should enhance our ability to predict how phenological shifts will impact communities.

How plasticity and adaptation will interact to adjust development rates in response to climate change remains uncertain [31]. Critical photoperiod for insect species is closely adapted to geographical gradients and evidence is beginning to emerge for evolutionary shifts in response to climate change [32]. Similarly, evolutionary shifts in thermal performance curves for larval feeding rate in response to recent climate change has been detected in *Colias* butterflies [33]. Plastic responses may be adequate for generalist herbivores such as our focal grasshopper species. However, adaptation may be more important when synchrony with other trophic levels has a strong effect on fitness. Evolutionary shifts in development timing in response to climate change have been observed in tightly coupled trophic systems such

as the oak–moth–great tits [34,35]. Our study highlights that considering multiple development stages and plastic responses may be crucial for understanding phenological and fitness responses to climate change.

Data accessibility. Data are available at <http://dx.doi.org/10.5061/dryad.mp238>.

Authors' contributions. L.B., C.N. and J.K. conceived and designed the study; C.N. performed the field observations and collections; L.B.

and E.K. performed the laboratory experiments; L.B. analysed the data and led the writing; C.N., E.K. and J.K. contributed to writing.

Competing interests. We declare we have no competing interests.

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