Insect development, thermal plasticity and fitness implications in changing, seasonal environments

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Synopsis

Historical data show that recent climate change has caused advances in seasonal timing (phenology) in many animals and plants, particularly in temperate and higher latitude regions. The population and fitness consequences of these phenological shifts for insects and other ectotherms have been heterogeneous: warming can increase development rates and the number of generations per year (increasing fitness), but can also lead to seasonal mismatches between animals and their resources and increase exposure to environmental variability (decreasing fitness). Insect populations exhibit local adaptation in their developmental responses to temperature, including lower developmental thresholds and the thermal requirements to complete development, but climate change can potentially disrupt seasonal timing of juvenile and adult stages and alter population fitness. We investigate these issues using a global dataset describing how insect developmental responds to temperature via two traits: lower temperature thresholds for development (T_0) and the cumulative degree-days required to complete development (G). As suggested by previous analyses, T_0 decreases and G increases with increasing (absolute) latitude; however these traits and the relationship between G and latitude varies significantly among taxonomic orders. The mean number of generations per year (a metric of fitness) increases with both decreasing T_0 and G, but the effects of these traits on fitness varies strongly with latitude, with stronger selection on both traits at higher (absolute) latitudes. We then use the traits to predict developmental timing and temperatures for multiple generations within seasons and across years (1970-2010). Seasonality drives developmental temperatures to peak mid-season and for generation lengths to decline across seasons particularly in temperate regions. We predict that climate warming has advanced phenology and increased the number of generations particularly at high latitudes. The magnitude of increases in developmental temperature vary little across latitude. Increases in the number of seasonal generations has been greatest for populations experiencing the greatest phenological advancements and warming. Shifts in developmental rate and timing due to climate change will have complex implications for selection and fitness in seasonal environments.

Keywords degree days, developmental temperatures, lower developmental threshold, number generations, phenology, voltinism

Introduction

Advances is seasonal timing (phenology) have been widely documented in response to recent climate change (Parmesan 2006), but the fitness implications of these shifts are largely unknown and likely heterogeneous (Miller-Rushing *et al.* 2010). Phenological advancements can increase fitness for multivoltine organisms by enabling the completion of additional generations within a season. Indeed, 190 of 263 species of European moths were able to complete an additional generation in response to recent climate change (Altermatt 2009). Phenological advancements can decrease fitness by leading to seasonal mismatches with resources and interacting species;

phenological mismatches have been widely observed in systems including plants and pollinators as well as birds and insect prey (Visser and Both 2005; Memmott *et al.* 2007). Phenological advancements can also increase exposure to variable early season environmental conditions. For example, earlier migration of Pacific salmon enables avoiding high summer temperatures, but earlier spawning exposes offspring to lethal temperatures (Crozier *et al.* 2008). Plant seedlings can be exposed to frost (Inouye 2008). The balance of fitness detriments and increases due to phenological shifts is likely to vary regionally with cool regions potentially benefitting more from extended active seasons (Levy *et al.* 2016). The fitness consequences will also vary with resource specialization and life history (Singer and Parmesan 2010).

Phenological shifts additionally impact fitness by altering the environmental conditions experienced by developmental stages and generations in seasonal environments. Seasonal environmental variability can drive the magnitude and direction of selection to vary across generations. Temperatures experienced during development may cue plastic responses. Phenological shifts may disrupt the reliability of the cue that selection acted upon and plasticity may become maladaptive (Pau *et al.* 2011). Temperatures experienced by adults may impact performance (e.g., potential activity time and foraging rates) and rates of reproduction. Sensitivity to environmental fluctuations varies across life stages (Kingsolver *et al.* 2011). Phenological shifts may expose sensitive life stages to thermal stress and decrease survival and reproduction.

The complex link between phenology and fitness complicates selection on developmental traits in seasonal environments. We focus on two development traits that have been widely documented in insects: lower temperature thresholds for development (T_0), and the cumulative degree-days required to complete development (G). T_0 declines with increasing latitude and exhibits an inverse relationship with G (Trudgill 1995; Honek 1996, see Results). G thus increases with latitude, suggesting equivalent development rates across latitudes (Trudgill *et al.* 2005). Increases in insect size and dietary specialization correspond to increases in G (Honek 1999). Here we examine the implications of these patterns in development traits for phenology and fitness.

Development traits underlie latitudinal patterns of body size, generation time, and voltinism (number of annual generations). Warmer temperatures speed development, which generally decreases body size. This pattern is known as the temperature-size rule and can result in increases in body size with latitude (Bergmann's or James' rule; Chown, Addo-Bediako and Gaston 2002). Larger body size tends to increase fitness, but growing for longer can reduce the number of generations that can be completed within a year. For example, a field study with *Manduca sexta* indicated strong phenotypic selection on larval development rate to reduce larval mortality and generation time (and increasing fitness), counterbalancing the positive effects of body size on fecundity (Eck *et al.* 2015). This trade-off between developmental rate and adult size can result in variable clines (across gradients in latitude, mean temperature, and seasonality) in body size (Chown, Addo-Bediako and Gaston 2002).

Here we use a global database of insect development traits to document geographic patterns in developmental traits. We then use the developmental traits to predict developmental duration across potential generations and ask: how do changing development rates alter conditions experienced and selection in seasonal environments? More specifically, we investigate three questions:

1. How do developmental temperatures and generation length vary across generations? How do these relationships vary across latitude?

2. How do developmental traits determine the number of generations per year (fitness)? How do these effects vary across latitude?

3. How has developmental timing and temperatures, the number of generations, and their variation shifted over recent decades? How have these shifts varied across latitude?

Methods

Developmental data for 1037 populations of 678 insect species concentrated in 6 orders were extracted from an existing dataset (Jarošík *et al.* 2011)**.** The data for each population includes two parameters that characterize the reaction norm for development rate R across the life cycle: the developmental zero temperature (T_0) below which R=0; and the accumulated degree-days (G) above T_0 needed to complete development from egg to adulthood. Development rate (R) can be approximated as a linear function of temperature (T) below optimal temperatures ($R=aT+b$). The regression enables calculating the lower temperature threshold for development, $T_0= -b/a$, and the degree day accumulation required for development, $G=1/a$ (Trudgill 1995; Honek 1996). This estimation methods was employed for insects reared in different temperatures in most (if not all) the populations in the database used here. Development rate may respond nonlinearly to temperature (Kingsolver, Higgins and Augustine 2015), but we are unable to consider these nonlinearities because the vast majority of data is derived from rearing in constant temperatures.

We refined the source localities in the dataset (Appendix S1**).** Text localities were georeferenced in R using Google's Geocoding API via the geocode function (ggmap library). We confirmed that our findings are robust to the specificity and certainty of georeferencing by assigning a quality score to each record (Appendix S1). The quality score was not a significant predictor in any model. Studies of single populations were often assigned multiple lines in the database due to different rearing conditions. We derived a single value of T_0 and G for each population by taking the mean. Many studies used laboratory colonies, so we confirmed that our findings are robust to whether a population was newly collected or a colony. We omitted several populations from our analysis that were biologically anomalous. We omitted 3 populations with exceptionally cold T_0 ($T_0 < -7$), which likely reflect insects in diapause. We omitted 9 populations with exceptionally high G ($G > 2000$). Some populations were additionally dropped from the initial database (Jarošík *et al.* 2011) because their collection location was unclear. The final dataset is described in Appendix S2 and available as Appendix S3. R code for the analyses are available at https://github.com/lbuckley/ICBseasonality/CodeForICBPaper .

We used linear mixed-effects models to evaluate the fixed effects of latitude, taxonomic order, and their interaction on T_0 and G. Because the overall correlation between T_0 and G was quite low ($r = -0.03$), we analyzed T_0 and G separately. Species was included as a random effect (because there were records for multiple geographic populations for many species).

We estimated developmental time and temperatures using daily minimum and maximum temperatures from the closest weather stations in the Global Historical Climatology Network (GHCN). We accessed the data using the R package rnoaa (Edmund *et al.* 2016). We restricted our analysis to weather stations with data more recent than 2010 and with at least 20 years of nearly (>82%) temporally complete data. We used R's na.approx function (zoo package) to linearly interpolate the few missing values based on previous and subsequent values. Because the insect larvae develop in different microhabitats and microclimates, we make the simplifying assumption that the larvae are experiencing shaded air temperatures at weather station height. Many insects develop in soil, where average temperatures may be warmer, but daily high temperatures are buffered and radiative heating is not experienced. Development models based on air temperature are generally predict development well (Damos and Savopoulou-Soultani 2011).

We used a single sine wave approximation (see http://www.ipm.ucdavis.edu/WEATHER/ddss_tbl.html) to calculate accumulated degree-days (D) based on daily max and minima temperature and T_0. We assume that species do not experience temperatures above their upper thermal limit for development because data is available for only a small subset of species. This assumption should not substantially alter results because selection acts to minimize temperatures greater than upper thermal limits for development.

We use daily degree-day estimates of D to estimate developmental duration (when the accumulated degree-days required to complete development are reached: i.e. when D exceeds G) for each generation. We assume that estimates of developmental duration are indicative of phenology, but note that our analysis requires two simplifying assumptions that are likely to alter phenology systematically for most populations. First, we assume that all populations overwinter as eggs, because the overwintering stage is available for only a subset of species. Second, we assume that the next generation starts as soon as the previous generation reaches adulthood. These assumptions facilitate comparisons across populations. We normalize calendar dates between the northern and southern hemispheres, by assigning a calendar date of 1 to July 1st in southern latitude sites. For each potential generation, we estimated the date that development was completed and the average temperature across development. We additionally examined other temperature metrics (standard deviation and 10% quantiles) and adult temperatures (one week before adulthood to one week after the completion of development), but present developmental temperatures as we found it to be the most informative.

To map geographic patterns (Fig. 1), we used the HadGHCND (Hadley Centre Global Historical Climate Network Database) observed daily minimum and maximum temperatures for 1971 to 1981 (Caesar, Alexander and Vose 2006) to estimate phenology for grid cells (3.75° longitude x 2.5° latitude) globally.

The predicted number of generations per year (N) at a locale represents a useful metric of fitness for a population with given values of the traits T_0 and G. The distribution of N is positively skewed and includes zero values, so a log-transform [log(N+1)] was used to achieve normality. We used mixed-effects models (where species is a random effect) to evaluate how N is influenced by latitude, taxonomic order, and the 1st and 2nd order effects of T_0 and G (and their interaction). We are particularly interested in how the effects of T_0 and G on N vary with latitude, as these indicate how selection on the developmental traits may vary across climatic (latitudinal) gradients.

Results

We first use (approximately) mean developmental traits across our dataset (T_0=10 and G=300) to translate temperature data into thermal opportunity for insect development. Maps of thermal time reveal that the phenology of the first generation delays substantially and the number of potential seasonal generations declines rapidly with movement away from the equator (Fig. 1). We next explore whether geographic gradients in developmental traits alter the phenological patterns.

Data on development traits are widely available across north temperate areas, but more limited in tropical and southern hemisphere regions (Fig. 2). Consistent with previous analyses (Trudgill 1995; Honek 1996), T_0 decreases and G increases with increasing (absolute) latitude (Fig. 3B and 3C). Although the overall correlation between these traits is quite low, the relationship is stronger within orders (Fig. 3A). G varies inversely with T_O ($F_{[1,348]}$=98.7, p<0.001) and varies significantly by order ($F_{[7,656]}$=54.5, p<0.001). The interaction of T_O and order is also significant ($F_{[7,348]}$=10.3, p<0.001).

Both T_0 and G vary significantly among taxonomic orders, and the relationship between G and latitude varies significantly among orders. For each order, T_0 declines with absolute latitude ($F_{[1,348]}$=26.6, p<0.001), suggesting consistent selection to develop at cooler temperatures in colder environments (Fig. 3B). T_0 varies significantly among orders ($F_{[7,656]}$=22.5, p<0.001), but no interaction occurs between absolute latitude and order ($F_{[7,348]}$=0.686, p=0.68). By contrast the association of G to latitude is more heterogeneous, ranging from negative to positive relationships for different taxonomic orders (Fig. 3C). Although G varies significantly among orders ($F_{[7,656]}$=42.2, p<0.001), neither G's relationship with absolute latitude ($F_{[1,348]}$=2.14, p=0.14) nor the interaction of absolute latitude and order ($F_{[7,348]}$=2.04, p=0.05) is significant. We note that the trait G reflects both temperature sensitivity and physiological lifespan (see Discussion).

These patterns in development traits have been well documented elsewhere, but here we leverage the developmental trait data to predict phenology and thermal conditions across generations and years. Developmental temperatures across generations reflect seasonality: early and late season generations experience cool temperatures while midseason species experience warm temperatures (Fig. 4A). The magnitude of seasonal temperature differences increases and the number of annual generations decreases with latitude. The decrease in the duration of generations in the early season is more pronounced than the increase in the late seasonal in most locations (Fig. 4B).

We estimate that warming over recent decades has advanced phenology and increased the number of annual generations and temperatures during development and adulthood (Fig. 5). The slope of the trends varies with latitude. Higher latitude populations complete their first generation earlier in the season (Fig. 5A). The rate of phenological advance and the interannual variability in phenology increases toward the poles. Developmental temperatures experienced by the first generation have largely increased over recent decades. Across sites, phenological shifts have been greater toward the poles ($F_{[1,328]}$=102.3, p<0.0001) (Fig. 5B). The phenological shifts do not vary significantly by order ($F_{[7,626]}$=0.79, p=59), but there is a significant interaction between absolute latitude and order ($F_{[7,328]}$=4.0, $p<0.0004$). In contrast, the increase in developmental temperature experienced by the first generation is relatively flat across absolute latitudes ($F_{[1,328]}$=0.12, p=0.73), in part due to the phenological shifts. Indeed, we predict that at some sites the first generations are experiencing cooler temperatures through time due to the phenological shifts, but few of the cooling examples represent significant shifts. Some sites are predicted to have delayed phenology, which reduces the number of generations, but many of these predicted shifts are likewise not significant. Significant shifts are steeper than non-significant shifts (median slopes non-significant vs significant: phenology= -0.09 vs -0.29, developmental temperature= 0.01 vs 0.03, number generations= 0.00 vs 0.03). We estimate that increases in the number of generations have been greatest toward the poles ($F_{[1,328]}$=30.2, $p<0.0001$) and varies among orders ($F_{[7,626]}$=6.9, $p<0.0001$). There is also a significant interaction between absolute latitude and order ($F_{[7,328]}$=2.64, p=0.01).

As expected the mean number of generations per year (log-transformed N), a metric of population fitness, declines with increasing absolute latitude ($F_{[1,332]}$=925.2, $p<0.0001$) and varies significantly among taxonomic orders ($F_{[7,638]}$=141.5, $p<0.0001$). There are significant 1st order effects of both T_0 ($F_{[1,332]}$=279.0, $p<0.0001$) and G ($F_{[1,332]}$=850.5, $p<0.0001$) (and their interactions, see Table S1 for full results) on N. There is additionally a significant 2nd order effect of G. In general, N declines with increasing T_0 and G, but the fitness surface is strongly curved, becoming flatter at higher values of T_0 and G (Fig. 6). Importantly, the shape of the fitness surface varies consistently with latitude. For example, strength of selection (the steepness of the fitness surface, indicated by the changes in color) is greater at higher latitudes, especially at lower values of T_0 and G (Fig. 6). Selection on T_0 in the tropics is relatively weak, and selection on G becomes relatively more important at higher latitudes (Fig. 6).

We also consider the fitness consequences of shifts in phenology and subsequently developmental temperatures over recent decades (Fig. 7). Populations that have experienced the greatest increase in the number of annual generations are those that experienced the largest phenological advancement ($F_{[1,312]}=170.8$, $p<0.0001$). Among populations experiencing a substantial phenological shift, those that have experienced increases in developmental temperatures experienced the greatest increase in the number of annual generations ($F_{[1,312]}=17.5$, $p<0.0001$). The increase in the number of generations varies across orders ($F_{[7,626]}=8.7$, $p<0.0001$; Fig. S1), but two-way interactions among phenology, temperature, and order are not significant.

Discussion

Rates of insect development and thus phenology and the number of seasonal generations depend on two development traits: the lower temperature threshold for development (T_0) and the degree day accumulation required for development (G). Because enzymes adapted to function at lower temperatures utilize each thermal unit less efficiently (Trudgill *et al.* 2005), one might expect that these two traits would be inversely related (Trudgill 1995; Honek 1996). However, the overall correlation of T_0 with G in our dataset is quite weak, suggesting that these traits can evolve independently among populations and species. As expected, mean T_0 declines with increasing (absolute) latitude, allowing development during cooler seasonal conditions. In contrast the relationship (slope) between mean G and latitude varies among taxonomic orders, ranging from positive, zero, or negative slopes in different orders (Fig. 3). A stronger relationship between T_0 and G within orders suggests that evolutionary constraints may be taxonomically unique. Because adult size, thermal sensitivity of development, physiological lifespan and adult size may all influence G, this geographic pattern in G may reflect taxonomic differences in life history.

Although T_0 and G are not strongly correlated phenotypically, they interact functionally to determine geographic patterns of fitness (in our analyses, the mean number of seasonal generations per year, N). Fitness generally declines with increasing T_0 and G, but the strength and pattern of selection varies strongly with latitude. For example, the strength of selection (steepness of the fitness surface) for both traits is greater at higher latitudes, and there is relatively weak selection on T_0 in tropical regions (Fig. 6). These modeling results suggest that selection favoring lower thermal thresholds and more rapid developmental rates is particularly important for seasonal, high latitudes populations, which is consistent with evidence of countergradient selection in many ectotherms (Conover and Schultz 1995).

The developmental traits predict near universal phenological advancements in response to climate change over recent decades, but rates of shifts vary across latitudes and insect orders. Our exclusion of an upper thermal limit for development may have influenced this finding to some degree. Increases in the number of generations are variable, but tend to be somewhat greater at higher latitudes. Increases in the seasonal number of generations generally corresponds to an increase in fitness, but many factors can alter the translation from development rate and phenology into fitness. Differences in phenological advancement among trophic levels can decrease fitness by creating resource mismatches (Miller-Rushing *et al.* 2010). An extensive comparison across UK taxa reveals trophic constraints on phenological advances: plants exhibited pronounced phenological shifts followed by insects with higher tropic levels exhibiting less phenological acceleration (Thackeray *et al.* 2016).

Environmental change, particularly the emergence of environmental novelty, may alter the reliability of seasonal cues resulting in maladaptive development decisions (Pau *et al.* 2011). Larvae of a late summer generation may experience warm conditions that lead them to attempt an additional generation rather than entering diapause. This effect can be particularly pronounced when species have evolved to additionally use photoperiod cues early in their development. Phenological shifts may cause the last generation to experience long summer days early in development before the rapid onset of cool, late season conditions. The cool temperatures can prevent completing development or result in acute mortality, which can be particularly detrimental to species with sequential, non-overlapping generations. Indeed, declines in butterfly populations were observed in regions where a greater proportion of individuals attempted an additional late season generation (Van Dyck *et al.* 2015). Thus, climate change may present an "evolutionary trap" once phenology advances significantly for organisms to attempt additional generations (Hale, Morrongiello and Swearer 2016).

Developmental plasticity may reduce developmental acceleration. For example across an elevation gradient, most grasshopper populations have accelerated development in response to recent climate change. However, a high-elevation population that was previously season limited has delayed development over recent decades, potentially to enable the population to take advantage of the extended season to enable more robust development (Buckley *et al.* 2014). Accelerated life cycles can also lead to increased adult mortality. A climate manipulation experiment found that lizards grew faster, accelerated their onset of reproduction, and increased voltinism in response to warming. However, they experienced decreased adult survivorship, potentially due to warming elevating their metabolic costs (Bestion *et al.* 2015).

Our analysis suggests that phenological advancements generally do not fully compensate for thermal shifts. We investigated whether phenological advancements could lead developing insects to experience cooler, early season temperatures, which could potentially impose thermal stress and survival risk (Inouye 2008; Levy *et al.* 2016). However, we generally predict phenological shifts that are inadequate to expose developing insects to colder temperatures. We do predict that a number of populations will experience cooler temperatures due to phenological shifts, but these temperature shifts were largely non-significant.

More pronounced shifts in phenology and the number of generations in poleward regions may serve to further increase the environmental variability the populations experience, which can reduce fitness (Kingsolver, Diamond and Buckley 2013; Vasseur *et al.* 2014). Documentation of phenological shifts tends to be limited in the tropics, hindering latitudinal comparisons. However, analysis of satellite imagery suggests that phenological advancements have been most pronounced in high latitude regions (Wang *et al.* 2016). Organisms may be more likely to employ photoperiod cues for phenology in high latitude regions where the seasonality is more pronounced. A greater reliance on photoperiod cues at high latitude could limit phenological advances relative to lower latitude regions. Latitudinal gradients in overwintering stages could also alter the potential for phenological advances. Here we assume that all populations overwinter as eggs, but populations with more advanced overwintering stages tend to alter their phenology more (Altermatt 2010; Diamond *et al.* 2011). Low latitude populations may be more likely to overwinter as adults, which could facilitate phenological advancements. Diet choice and breadth also influences phenological shifts (Altermatt 2010; Diamond *et al.* 2011). Low latitude populations may be less likely to have their phenological advancements limited by the seasonality of vegetation.

Phenological shifts have provided extensive evidence of biological responses to climate change (Parmesan and Yohe 2003; Root *et al.* 2003; Poloczanska *et al.* 2013). Here we investigate how developmental traits underlie phenological shifts. Rates of our estimated phenological shifts approximate observed rates in terrestrial systems for multispecies studies [-2.8 (Parmesan and Yohe 2003) and -5.1 (Root *et al.* 2003) days dec^{-1}, see Poloczanska *et al.* (2013) for a broader comparison]. We find that latitudinal gradients in developmental traits lead to systematic shifts in phenology, developmental temperatures, and the number of seasonal generations across latitudes. Further linking mechanistic knowledge of how developmental rates respond to climate change may improve our ability to understand and predict biological responses to climate change. Considering developmental rates highlights the advantages of translating climate change into shifts in the thermal time available to organisms.

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Supplementary data

Supplementary data available at ICB online.

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Figure legends

Fig. 1. Maps of 1^{st} generation phenology (day of year that the 1st generation reaches adulthood, left) and the number of seasonal generations (right) corresponding to constant T_0 (T_0=10) and degree days required (G=300) globally. Some tropical areas are missing data due to inadequate weather station coverage.

Fig. 2. The distribution of developmental data depicting lower developmental temperatures (log(T_0), color) and the degree days required to develop from egg to adult (log(G), size).

Fig. 3. Lower temperature thresholds for development (T_0) tend to decline and the degree days required to complete development (G) tend to increase with absolute latitude, but the relationship among the metrics is weak.

Fig. 4. Across generations within a season, developmental and adult temperatures peak midseason outside the tropics and are relatively flat in the tropics. Generation length generally declines across the season. The seasonal patterns vary across temperate and tropical sites (color: latitude). Some mid-latitude sites are excluded to simplify figure.

Fig. 5. Temporal trends in adult phenology (day of year: J) and developmental temperature for the first seasonal generation and the number of generations (top, slope and standard error of linear regression depicted). The trends are aggregated across and vary across latitude (color). We plot the slope of the relationship between adult phenology, developmental temperature, and the number of generations for each population as a function of absolute latitude (slope and standard error of linear regression depicted). We depict the T_0 for each population (color) and whether or not the temporal trend is significant (solid= significant at $P<0.05$, open= non-significant).

Fig. 6. The average number of generations per season (log scale) varies as a function of lower development threshold (T_0) and the degree days required for development (G). The relationships vary as a function of absolute latitude (plot titles).

Fig. 7. Fitness shifts since 1970 (fitness proxy: number of generations) vary with shifts in developmental temperatures and phenology.