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Temperature Sensitivity of Fitness Components across Life Cycles Drives Insect Responses to Climate Change

Christopher A. Johnson,[1,2,*] **Rachael Ren,**[1] **and Lauren B. Buckley**[1,2]

1. Department of Biology, University of Washington, Seattle, Washington 98195; 2. eScience Institute, University of Washington, Seattle, Washington 98195

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ABSTRACT: Thermal performance curves (TPCs) are increasingly used as a convenient approach to predict climate change impacts on ectotherms that accounts for organismal thermal sensitivity; however, directly applying TPCs to temperature data to estimate fitness has yielded contrasting predictions depending on assumptions regarding climate variability. We compare direct application of TPCs to an approach integrating TPCs for different fitness components (e.g., per capita birth rate, adult life span) across ectotherm life cycles into a population dynamic model, which we independently validated with census data and applied to hemipteran insect populations across latitude. The population model predicted that climate change will reduce insect fitness more at higher latitudes due to its effects on survival but will reduce net reproductive rate more at lower latitudes due to its effects on fecundity. Directly applying TPCs underestimated climate change impacts on fitness relative to incorporating the TPCs into the population model due to simplifying survival dynamics across the life cycle. The population model predicted that climate change will reduce mean insect density and increase population variability at higher latitudes via reduced survival, despite faster development and a longer activity period. Our study highlights the importance of considering how multiple fitness components respond to climate variability across the life cycle to better understand and anticipate the ecological consequence of climate change.

Keywords: climate change, demographics, population dynamics, thermal performance curves.

Introduction

Research considering the physiological sensitivity of organisms to climate change has questioned the initial logic that organisms will be most strongly impacted by climate change at high latitudes experiencing more extreme climate change (Ghalambor et al. 2006; Deutsch et al. 2008; Huey et al. 2012; Buckley and Kingsolver 2021). Thermal performance curves (TPCs) offer an expedient way to characterize organismal sensitivity (Angilletta 2009). TPCs describing the temperature dependence of fitness have been increasingly used to predict climate change impacts on ectotherms along latitudinal climate gradients characterized by high mean annual temperatures and low seasonal temperature variability at lower latitudes and the converse at higher latitudes (Deutsch et al. 2008; Dillon et al. 2010; Kingsolver et al. 2013; Sunday et al. 2014; Vasseur et al. 2014).

TPCs have generated diverse and sometimes contrasting predictions about the ecological impacts of climate change depending on underlying assumptions. Some studies predict that tropical ectotherms will be more vulnerable to climate change than species at higher latitudes (Deutsch et al. 2008; Dillon et al. 2010; Sunday et al. 2014) because their TPCs are specialized to relatively constant thermal conditions and their climates are already near the temperatures at which fitness declines precipitously (points in fig. 1*A*, 1*B*). Other studies emphasize the importance of temperature variation, predicting that midlatitude species will be similarly or more vulnerable to climate change because of their relatively specialized TPCs combined with much greater temperature fluctuations and more extreme climate warming (Kingsolver et al. 2013; Vasseur et al. 2014). High-latitude species are generally predicted to be less sensitive to climate change impacts because of their more generalized TPCs (Deutsch et al. 2008; Kingsolver et al. 2013). How accurately TPCs predict climate change impacts, however, remains an important question (Kingsolver et al. 2013; Vasseur et al. 2014; Sinclair et al. 2016; Buckley and Kingsolver 2021).

TPCs are typically constructed by fitting nonlinear curves (black lines in fig. 1) to laboratory data on species' fitness or performance across a range of constant temperatures. Integrating the TPC over a biologically realistic temperature

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[*] Corresponding author; email: cjohns21@uw.edu.

ORCIDs: Johnson, https://orcid.org/0000-0001-6388-8770; Ren, https://orcid.org/0000-0003-3950-7178; Buckley, https://orcid.org/0000-0003-1315-3818.

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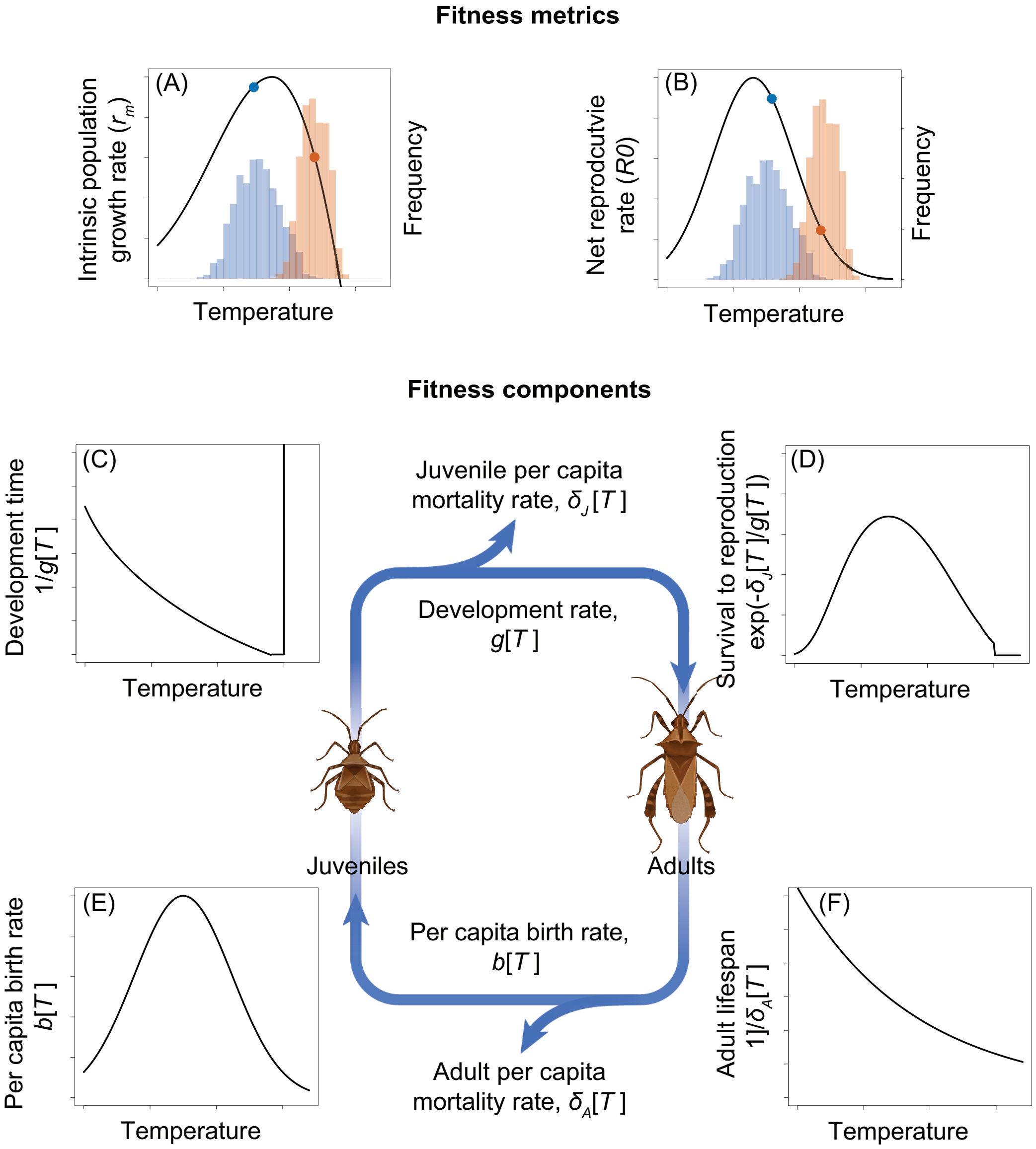

Figure 1: Thermal performance curves (TPCs) predict climate change impacts on two fitness metrics—intrinsic population growth rate, r_m (*A*), and net reproductive rate, R_0 (*B*)—of *Clavigralla shadabi* in Benin (*top panels*). Integrating TPCs (black curves) directly over seasonal temperature variation (depicted by histograms) yields the mean fitness in that climate. Blue points are mean values in the recent climate (1980–1985; blue histogram), and orange points are mean values in the future climate (2095–2100; orange histogram). A schematic of the population model (*bottom panels*) depicts hypothetical TPCs characteristic of the different fitness components—development time (*C*), survival to reproduction (*D*), per capita birth rate (*E*), and adult life span (*F*)—over the life cycle. The insect icons were illustrated by Julie Johnson (Life Science Studios).

regime—either body temperature or environmental temperature as a proxy (histograms in fig. 1*A*, 1*B*)—yields an estimate of a species' mean fitness or performance in that climate (points in fig. 1*A*, 1*B*). A recent review (Sinclair et al. 2016), however, highlights biologically questionable assumptions required to use TPCs to directly estimate ectotherm responses to climate change. We assessed the assumptions that (1) population dynamics can be ignored, (2) fitness TPCs can predict species' responses to temperature variation without considering the components of fitness, and (3) organisms respond similarly to environmental variation across their life cycle (Sinclair et al. 2016). Specifically, we predicted climate change impacts on ectotherm population dynamics (TPC assumption 1) using a mathematical framework that explicitly considers the thermal responses of fitness components (TPC assumption 2) and mechanistically incorporates temperature-dependent developmental delays between life stages (TPC assumption 3). We evaluated how climate change responses predicted by the population model, which integrates TPCs for multiple fitness components accounting for complex life cycles, differ from those produced by integrating TPCs directly. Models that avoid common TPC assumptions by considering temperature effects on fitness components (e.g., fig. 1*C*–1*F*) across life stages may better predict climate change impacts on fitness, and its components, than does direct application of fitness TPCs (Kingsolver et al. 2011; Levy et al. 2015; Kingsolver and Buckley 2020; Buckley et al. 2021).

We fit TPCs for two fitness metrics (intrinsic population growth rate, r_m, and net reproductive rate, R_0) and four fitness components (survival to reproduction, per capita birth rate, development time, adult life span) using laboratory data for 21 populations of hemipteran insects (Barlow 1962; Deloach 1974; Asante et al. 1991; Dreyer and Baumgartner 1996; Wang et al. 1997; Tsai and Liu 1998; Xia et al. 1999; Morgan et al. 2001; Dabire et al. 2005; Lu et al. 2009, 2010; Conti et al. 2010; Jandricic et al. 2010). Hemipteran insects are an excellent study system because they are relatively well-studied ectotherms inhabiting a wide range of climates across latitude (table S1). We incorporated fitness component TPCs into our population model and simulated the dynamics of each population in both its recent climate (using historical data from nearby climate stations) and its future climate (using CMIP6 climate model projections for 2025–2100). We investigated four key questions. First, how accurately can population dynamics be predicted by models incorporating temperature responses of multiple fitness components and accounting for complex life cycles? Second, how does climate change influence fitness and its constituent components for ectotherm populations inhabiting different climate regimes across latitude? Third, how accurately are these climate change impacts predicted by the direct application of TPCs? Fourth, how will climate change affect ectotherm population dynamics along latitudinal climate gradients? Taken together, these questions probe how the temperature sensitivities of different fitness components (Buckley et al. 2021) across multiple demographic life stages (Kingsolver et al. 2011; Levy et al. 2015; Buckley 2022) contribute to ectotherm responses to climate change.

Methods

TPCs for Fitness Metrics and Fitness Components

TPCs have been frequently used to quantify fitness or performance as a function of temperature. Although body temperature is the appropriate temperature metric (Huey et al. 2012), we used habitat temperature as a proxy, which is reasonable for small-bodied insects on plants above the soil surface (Stevenson 1985; Deutsch et al. 2008). We built TPCs for fitness metrics and their components by fitting functions to laboratory data via nonlinear least squares regression using the nls function in R. (See "Fitting TPCs" in the supplemental PDF for more details).

We examined two common metrics for fitness: the intrinsic population growth rate, r_m, which is a direct measure of Darwinian fitness, and net reproductive rate, R_0, which is the number of viable offspring that each individual produces over its lifetime. For many ectotherms, r_m increases to a maximum value at an optimal temperature, beyond which it declines rapidly and becomes negative at high temperatures (fig. 1*A*). This left-skewed thermal response arises because of temperature effects on fitness components (Amarasekare and Savage 2012). From the various functions used to describe r_m (e.g., Dell et al. 2011; Amarasekare and Savage 2012), we adopted a widely used formula (Deutsch et al. 2008; Vasseur et al. 2014) in which the rise in r_m is described by a Gaussian function and its decline is described by a parabolic function:

$$r_m = \begin{cases} \exp\left(-\dfrac{(T - T_{\mathrm{opt},r})^2}{2\sigma_r^2}\right) & T \le T_{\mathrm{opt},r}, \\ 1 - \left(\dfrac{T - T_{\mathrm{opt},r}}{T_{\mathrm{opt},r} - T_{\mathrm{max},r}}\right)^2 & T > T_{\mathrm{opt},r}, \end{cases} \tag{1a}$$

where T is the habitat temperature (in kelvins), $T_{\mathrm{opt},r}$ is the optimal temperature, $T_{\mathrm{max},r}$ is the maximum temperature above which r_m is negative, and σ_r gives the steepness of the rising portion of r_m.

Net reproductive rate, R_0, typically exhibits a symmetrical thermal response (fig. 1*B*; Huey and Berrigan 2001; Kingsolver et al. 2013) that is well described by a Gaussian function:

$$R_0 = \exp\left(-\frac{(T - T_{\mathrm{opt},R_0})^2}{2\sigma_{R_0}^2}\right), \tag{1b}$$

where T_{opt,R_0} is the optimum temperature for R_0 and σ_{R_0} gives the variability about the optimum. Both r_m and R_0 were scaled relative to their maximum values to facilitate comparisons across different populations. We used equations (1a) and (1b) to quantify climate change impacts on fitness by integrating the TPCs directly; these equations were not incorporated into the population model.

TPCs for fitness components are generally well understood (Angilletta 2009; Kingsolver 2009; Kingsolver et al. 2011) and can be described by functions derived from first principles of thermodynamics. The per capita birth rate, $b[T]$, exhibits a unimodal and symmetric temperature response (fig. 1*E*) due to temperature effects on underlying biochemical regulatory processes (Dell et al. 2011; Amarasekare and Savage 2012) and is well described by a Gaussian function:

$$b[T] = b_{T_{\mathrm{opt}}} \exp\left(-\frac{(T - T_{\mathrm{opt},b})^2}{2\sigma_b^2}\right), \tag{2a}$$

where $b_{T_{\mathrm{opt}}}$ is the maximum per capita birth rate at an optimal temperature $T_{\mathrm{opt},b}$ and σ_b gives the variability about the optimum.

The per capita mortality rate of life stage i, $\delta_i[T]$, exhibits a monotonic thermal response (fig. 1*F*) due to temperature effects on biochemical rate processes (Gillooly et al. 2001; Brown et al. 2004; Savage et al. 2004), which is well described by the Boltzmann-Arrhenius function:

$$\delta_i[T] = \delta_{i,T_R} \exp\left(A_i\left(\frac{1}{T_R} - \frac{1}{T}\right)\right), \tag{2b}$$

where δ_{i,T_R} is the per capita mortality rate of life stage i ($i = J$ for juveniles and $i = A$ for adults) at a reference temperature T_R and A_i is its Arrhenius constant, quantifying how rapidly mortality increases with rising temperature. Adult life span is the inverse of adult mortality rate, $1/\delta_A[T]$.

The development rate, $g[T]$, is reduced at both low and high temperatures due to enzyme inactivation (Van der Have and De Jong 1996; Kingsolver et al. 2011), which is often described by the thermodynamic rate process model (eq. [S1]). There were often insufficient data, however, for us to robustly parameterize this function. By setting the optimal ($T_{\mathrm{opt},g}$) and maximum ($T_{\max,g}$) temperatures for development directly from the data, we fit the remaining parameters for the temperature response of the development rate for the following piecewise function:

$$g[T] = \begin{cases} \dfrac{g_{T_R}\left(\dfrac{T}{T_R}\right)\exp\left(A_g\left(\dfrac{1}{T_R} - \dfrac{1}{T}\right)\right)}{1 + \exp\left(A_L\left(\dfrac{1}{T_L} - \dfrac{1}{T}\right)\right)} & T \le T_{\mathrm{opt},g}, \\ g_{\max} & T_{\mathrm{opt},g} < T \le T_{\max,g}, \\ 0 & T > T_{\max,g}, \end{cases} \tag{2c}$$

where $g_{\max}$ is given by evaluating $g[T]$ at the optimal temperature, $T_{\mathrm{opt},g}$. Below the optimal temperature, $T_{\mathrm{opt},g}$, development rate is given by a simplified thermodynamic rate process model (eq. [S1]), where g_{T_R} is the development rate at the reference temperature, T_R; A_g is its Arrhenius constant (quantifying how rapidly development rate increases with increasing temperature when enzymes are 100% active); and T_L and A_L give the low temperature at which enzymes are 50% active and its Arrhenius constant, respectively. Development rate is at its maximum value, $g_{\max}$, between the optimum temperature, $T_{\mathrm{opt},g}$, and the maximum temperature, $T_{\max,g}$, above which it is zero. Development time is the inverse of the development rate, $1/g[T]$ (fig. 1*C*).

Finally, we quantify survival as the fraction of individuals that survive to the age of first reproduction. Survival often exhibits an inverted U-shaped temperature response (Kingsolver 2009; Amarasekare and Sifuentes 2012) with sharp thresholds at both low and high temperatures (fig. 1*D*) and is quantified from the TPCs of the juvenile per capita mortality rate (eq. [2b]) and the development rate (eq. [2c]) as $\exp(-\delta_J[T]/g[T])$ (Gurney and Nisbet 1998).

We quantified climate change impacts on fitness metrics (r_m and R_0) and components (survival to reproduction, per capita birth rate, development time, and adult life span) from TPCs directly by integrating each TPC over each species' site-specific seasonal habitat temperature for 5 years in the recent and future climates (see "Climate Data") using the cubintegrate function with the hcubature argument in R. TPCs of the per capita birth rate, stage-specific mortality rates, and development rate were incorporated directly into the population model.

Population Model

We developed a population model to investigate how multiple fitness components across life stages affect insect fitness and population dynamics with climate change. The model is based on a framework (Scranton and Amarasekare 2017) that models temperature effects on insect demographics using temperature-dependent delay differential equations, which mechanistically describe the population dynamics of species with complex life cycles (Nisbet and Gurney 1983; Murdoch et al. 1987; Nisbet 1997). The model (fig. 1*C*–1*F*) has two life stages, juveniles (density J) and adults (density A); incorporates TPCs of fitness components (eqq. [2a]–[2c]); and explicitly considers overwintering (supplemental PDF). Model dynamics are given by

$$\frac{dJ}{dt} = b[T]Ae^{-\alpha[T]A} - R(t) - \delta_J[T]J, \tag{3a}$$

$$\frac{dA}{dt} = R(t) - \delta_A[T]A. \tag{3b}$$

The function $b[T]$ gives the temperature response of the per capita birth rate (eq. [2a]), while $\delta_J[T]$ and $\delta_A[T]$ describe the temperature responses of the per capita mortality rate of the juvenile (prereproductive) and adult life stages (eq. [2b]), all of which are the same as their TPCs. The function $\alpha[T]$ gives the temperature response of intraspecific competition, which is assumed to act on the per capita birth rate, as is widely observed in insects (Murdoch et al. 2003), and is described as a Gaussian function very similar to that of the per capita birth rate (eq. [S2]; see "Temperature response of intraspecific competition" in the supplemental PDF). The function $R(t)$ gives the number of individuals recruiting from the juvenile to the adult stage at time t, which based on theory of dynamically varying time delays (Nisbet and Gurney 1983) is given by

$$R(t) = \left(b[T(t-\tau)]A(t-\tau)e^{-\alpha[T(t-\tau)]A(t-\tau)}\right) \times \left(\frac{g[T(t)]}{g[T(t-\tau)]}S\right), \tag{4a}$$

where $t - \tau$ is the time (day) when maturing individuals were born and τ is their development time. Importantly, because development time is temperature dependent, τ changes over time as temperatures vary. The function $R(t)$ therefore gives the number of individuals born τ time ago (first bracket of eq. [4a]) that survived through the juvenile stage given the temperature response of their development rate (second bracket of eq. [4a]), where the developmental time delay τ and juvenile survival S are themselves time-varying differential equations (Nisbet and Gurney 1983):

$$\frac{d\tau}{dt} = 1 - \frac{g[T(t)]}{g[T(t-\tau)]}, \tag{4b}$$

$$\frac{dS}{dt} = S\left(\frac{g[T(t)]}{g[T(t-\tau)]}\delta_J[T(t-\tau)] - \delta_J[T(t)]\right). \tag{4c}$$

We numerically solved the population model in Python (Python Core Development Team 2019) using the JiTCDDE package (Ansmann 2018). For simplicity, we used a constant initial history ($J = 100$ and $A = 10$ for time $t - \tau < 0$) and ensured that the model was run for sufficiently long to avoid transient dynamics. We incorporated overwintering into the model by setting the per capita birth rate to zero and increasing the adult mortality rate when temperatures were below a population-specific threshold, $T_{\min}$, estimated by extrapolating the linear portion of the development rate TPC to the temperature at which it was zero (Dixon et al. 2009; see “Insect overwintering” in the supplemental PDF for more details). All variables and parameters are summarized in table S2.

Seasonal Temperature Variation

Climate change affects both the mean habitat temperature and its seasonal variability (Field et al. 2012), which we included in our analyses by setting $T = T(t)$ in equations (1)–(4) and modeling seasonal temperature variation, $T(t)$, using the following sinusoidal function:

$$T(t) = (M_{T,x} + \Delta_{M,x}t) - (A_{T,x} + \Delta_{A,x}t)\cos(2\pi(t + S_{T,x})/365), \tag{5}$$

where $M_{T,x}$ is the mean temperature, $A_{T,x}$ is the amplitude of seasonal temperature variation, and $S_{T,x}$ is the shift in the timing of the warmest temperatures. The subscript x denotes the time period for which equation (5) was fitted to data on mean daily near-surface air temperature (see “Climate Data”), which was done to capture temperature variation during the recent climates ($x = r$; pre-2020) and future climates ($x = f$; 2025–2100). For simplicity, we used linear functions to describe long-term climate changes in mean temperature, $\Delta_{M,x}$, and in the amplitude of seasonal temperature variation, $\Delta_{A,x}$. To facilitate comparisons between populations that may have been studied decades apart, we set $\Delta_{M,r}$ and $\Delta_{A,r}$ to zero in the recent climate and analyzed the model from 1980 to 1985, which was roughly halfway through the average historical climate data. We set $\Delta_{M,f}$ and $\Delta_{A,f}$ to zero in the future climate when the fit to climate data yielded $P > .05$ and analyzed the model from 2095 to 2100. Using a continuous function rather than the temperature data themselves was necessary to incorporate seasonal temperature variation into the continuous-time population model. It also effectively reduced the impacts of short-term climate extremes while capturing the effects of longer-term extreme events (Vasseur et al. 2014).

Climate Data

For each insect population (see “Insect Data”), we used the KNMI Climate Explorer (http://climexp.knmi.nl) to obtain historical daily temperature maxima and minima from the nearest monitoring station in the Global Historical Climatology Network (table S3). We obtained CMIP6 climate model projections (O’Neill et al. 2016) of daily maximum and minima near-surface air temperatures for the years 2025–2100 using the Copernicus Climate Data Store (http://cds.climate.copernicus.eu), under the CMIP6 licensing agreement. We used the Shared Socioeconomic Pathway experiments SSP3-7.0 scenario, which simulates high climate change mitigation and adaptation challenges and a radiative forcing of 7.0 W/m^2 in the year 2100. We used the CESM2 model from the National Center for Atmospheric Research (Danabasoglu 2019), which affords a spatial resolution of 1°. Using mean daily near-surface air temperature is reasonable because the small-bodied insects in our database are typically active in the morning and generally remain on host plants near the soil surface (Stevenson 1985; Deutsch et al. 2008).

Insect Data

We compiled a worldwide database of the temperature responses of 21 distinct populations (17 species) of hemipteran insects spanning an 89° latitudinal range (table S1). Data were sourced from the published literature using Google Scholar and the Web of Science. The database was not meant to be exhaustive but to include populations from different climates. We restricted our analyses to studies that reported temperature effects on the per capita birth rate or fecundity rate, development rate or time, juvenile survival or mortality rate, and adult life span or mortality rate. For model fitting, we generally required studies to have measured traits across at least five constant temperatures. To facilitate comparisons between populations, we also restricted our analyses to two suborders of Hemiptera: Heteroptera and Sternorrhyncha (and within the infraorder Aphidomorpha). All species in our dataset are herbivores. We included data from only one host plant species or cultivar for the few studies that reported performance on different host plants. Studies in our database were published between 1962 and 2010 (table S1).

Insect Case Studies

There were two populations in our dataset for which census data were also available, offering us a rare opportunity to independently validate model dynamics. The tropical species is *Clavigralla shadabi*, a pod-sucking bug (Hemiptera: Coreidae) that is a major pest of legumes in the tropics (Dreyer and Baumgartner 1996). The temperate species is *Apolygus lucorum* (also referred to as *Lygus lucorum*), a plant bug (Hemiptera: Miridae) that has become a key pest of transgenic (Bt) cotton in China (Lu et al. 2008). We parameterized the population model (eq. [3]) by fitting equations (2a)–(2c) to temperature response data (for *C. shadabi*, Dreyer and Baumgartner 1996; for *A. lucorum*, Lu et al. 2010). We validated the population models using field census data that were entirely independent from those data used to parameterize the model. For the tropical species, we quantified mean adult density from census data collected in large field plots of cowpea (*Vigna unguiculata*) during two growing seasons in 1991 (assumed to start in mid-May and September) at an agricultural station in Aborney-Calavi in southern Benin (fig. 4*A*, 4*B* of Dreyer et al. 1994). For the temperate species, we obtained census data collected from 2005 to 2006 in the Dafeng region of China (fig. 2 in Lu et al. 2008). Because this insect becomes active earlier in the year than the fields were planted in the study (Li et al. 2010), there was an inherent lag between the model dynamics and the census data. We therefore assumed that individuals in the model become active only after the date on which the fields were planted in the study, which we implemented by setting $T_{\min}$ to the temperature in mid-May (day 137) when the fields were planted (i.e., $T_{\min} = T(137)$). We imposed this constraint only for model validation and not for the subsequent analyses. Finally, because juvenile and adult densities were not reported separately in this study, we also assumed for tractability that the vast majority of individuals observed in the census were the larger and more conspicuous adults, such that we could compare adult dynamics predicted by the model directly with the census data reported in the study. Model simulations were run for 10 years with the last 2 years coinciding with the censuses (1982–1992 for *C. shadabi* and 1996–2006 for *A. lucorum*).

Model Analyses and Comparisons with TPCs

We assessed the ability of the population model to predict census data by using linear least squares regressions of adult density predicted by the model against that observed in the field. For each population in our database, we quantified the effects of climate change as the difference in the mean fitness or fitness component between the recent and future climates. To facilitate comparisons across populations, mean values were quantified by integrating over the same 5 years of model projections (last 2 years of density-independent population dynamics for r_m) in the recent (1980–1985) and future (2095–2100) climates and by integrating TPCs directly over seasonal temperature variation (via eq. [5]). This is because nonlinear thermal responses in the population model and TPCs mean that the values at the mean temperature do not equal the mean of the values across variable temperatures due to Jensen's inequality (Dowd et al. 2015). We used linear least squares regression to assess latitudinal patterns in these climate change impacts. We evaluated whether directly applying TPCs over- or underestimated the decline in fitness or its components with climate change via the slopes of linear least squares regressions of direct applications of TPCs and predictions from the population model. Finally, we quantified changes in mean adult density, population variability (coefficient of variation of adult density), and activity period (fraction of the year in which habitat temperatures exceeded the minimum temperature for development, $T_{\min}$) between model predictions in the recent and future climates. We used linear least squares regressions to evaluate latitudinal patterns in these metrics.

Results

Insect Case Studies

We independently validated the population model for a tropical species (*Clavigralla shadabi*), which experiences high mean temperatures but small seasonal fluctuations (fig. 2*A*), and a temperate species (*Apolygus lucorum*), which experiences low mean temperatures but large seasonal fluctuations (fig. 2*B*). Climate change in the tropical region is predicted to increase mean annual temperature by 0.9°C by 2100 relative to the historical climate during the census but actually reduce seasonal fluctuations by 0.4°C (fig. 2*A*). Climate change in the temperate region is

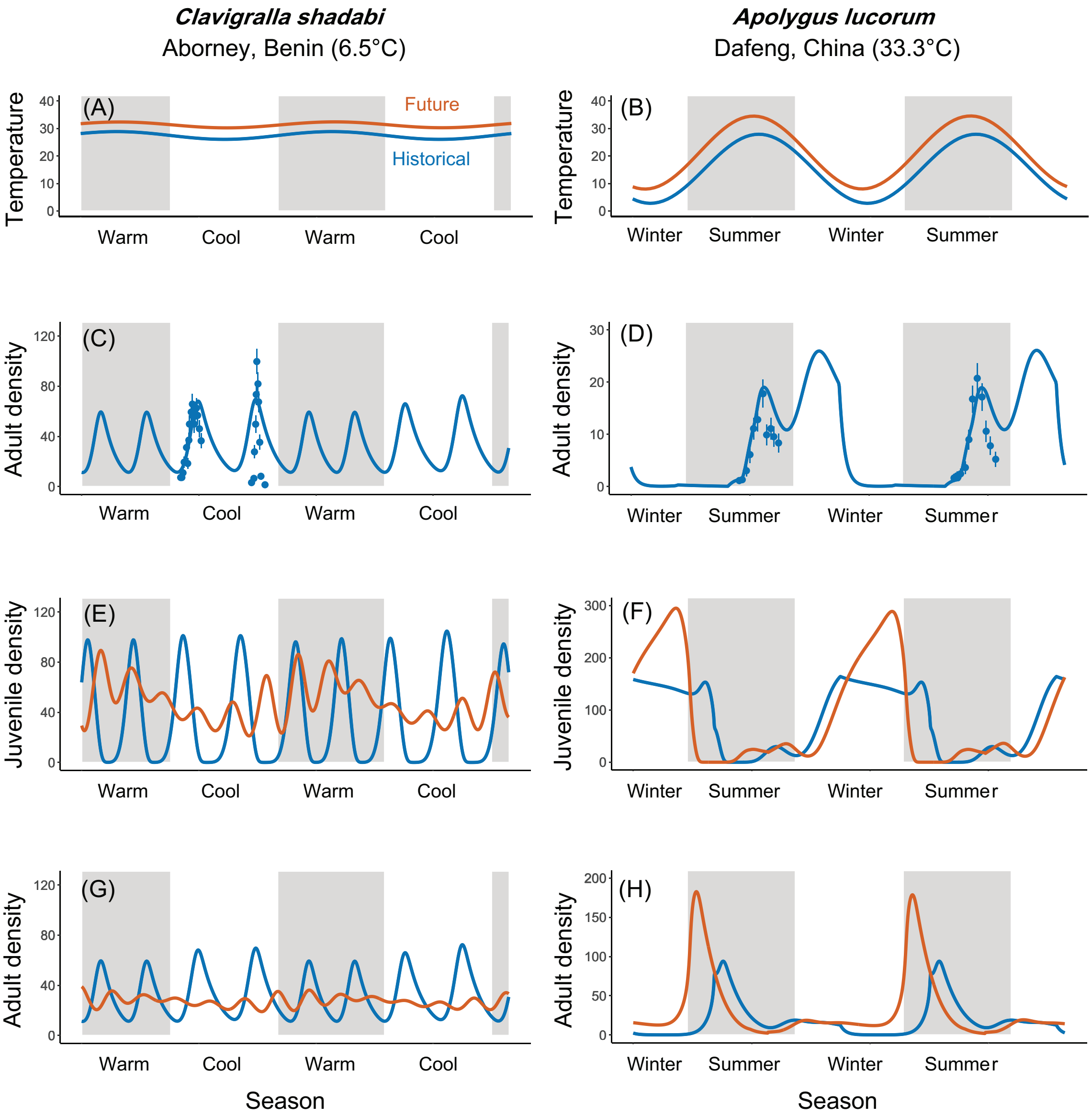

Figure 2: Predicted population dynamics of a tropical species (*Clavigralla shadabi*; *left panels*) and a temperate species (*Apolygus lucorum*; *right panels*) in the recent (blue; 1991–1992 for *C. shadabi* and 2005–2006 for *A. lucorum*) and future (orange; 2099–2100) climates (*A*, *B*). Gray regions indicate the warmer half of the year in the recent climates. Model projections of adult density correspond well to independent field data (*C*, *D*; points are mean density per 50 host plants ± SD). Shifts in juvenile (*E*, *F*) and adult (*G*, *H*) population dynamics in response to climate change are projected to differ between the tropical and temperate species.

predicted to increase mean annual temperature by 3.9°C and seasonal fluctuations by 0.2°C by 2100, with peak temperatures occurring ~10 days earlier in the year (fig. 2*B*). The population model very accurately predicted the field census data of both the tropical species (fig. 2*C*; $n = 28$, $R^2 = 0.78$, $t = 9.99$, $P < .001$) and temperate species (fig. 2*D*; $n = 22$, $R^2 = 0.90$, $t = 14.3$, $P < .001$).

The model predicted that climate change will drive the tropical species to exhibit greater oscillatory frequency, but of lower amplitude (fig. 2*E*, 2*G*). For the temperate species, the model predicted that climate change will cause juvenile density to increase dramatically in winter (fig. 2*F*) and peaks in adult density to be higher and occur earlier (fig. 2*H*). Climate change was predicted to lower mean adult density and population variability of the tropical species (fig. 2*G*) but increase mean adult density and population variability of the temperate species (fig. 2*H*).

Climate Change Impacts across Latitude

When applied across populations, the population model predicted that climate change will reduce intrinsic growth rate, r_m, more at higher than at lower latitudes, as revealed by linear regression (fig. 3*A*; $n = 21$, $t = 2.06$, $P = .05$), but the net reproductive rate, R_0, exhibited the converse trend (fig. 3*B*; $n = 21$, $t = 2.24$, $P = .04$). Based on linear regressions, lower-latitude populations suffered greater declines in per capita birth rate (fig. 3*D*; $n = 21$, $t = 2.30$, $P = .03$) and adult life span (fig. 3*F*; $n = 21$, $t = 6.03$, $P < .001$) with climate change, ultimately reducing R_0 more than at higher latitudes (fig. 3*B*). Conversely, greater reductions in survival to reproduction

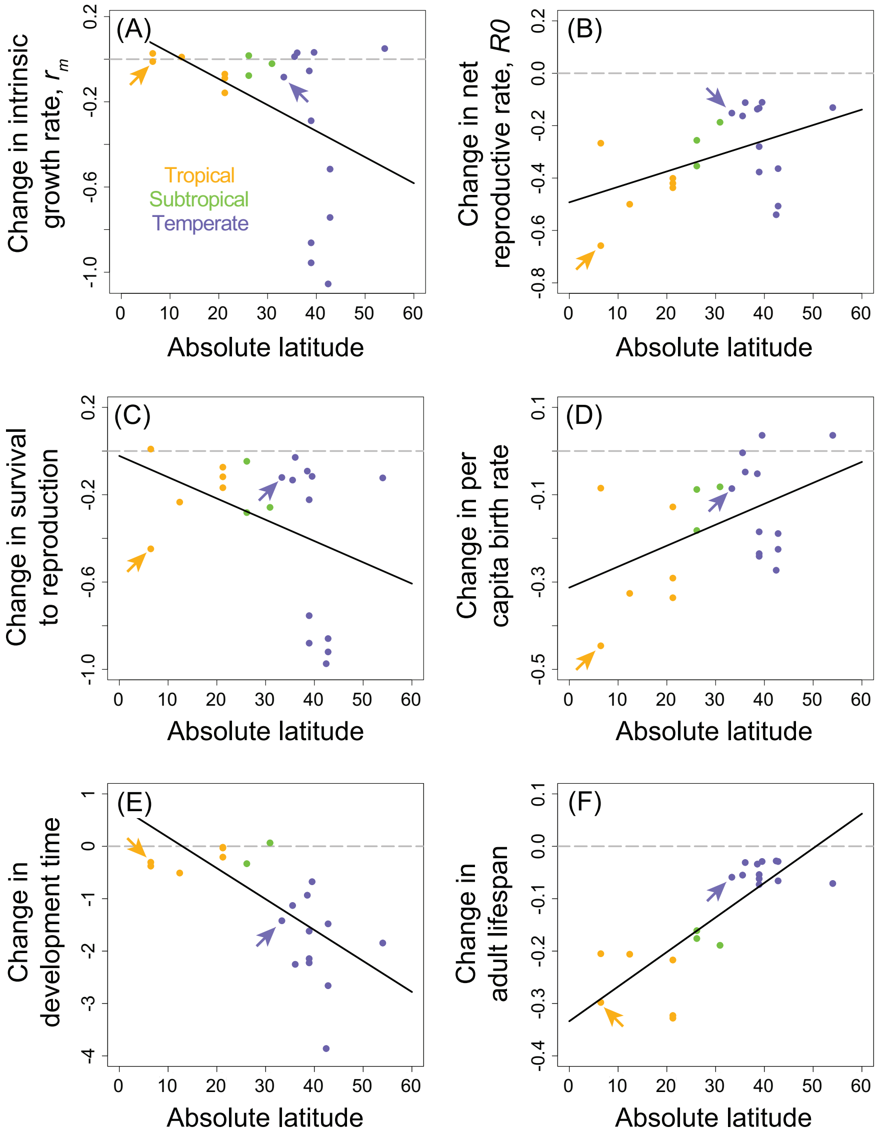

Figure 3: Model predictions of climate change impacts on fitness metrics and components across latitude. Panels show changes in the intrinsic growth rate, r_m (*A*); net reproductive rate, R_0 (*B*); survival to reproduction (*C*); per capita birth rate (*D*); development time (*E*); and adult life span (*F*) for tropical (orange), subtropical (green), and temperate (purple) populations. Climate change impacts are quantified as the change in mean value over 5 years (2 years for r_m) of simulated, site-specific recent (1980–1985) and future (2095–2100) climates. Lines shows the best fit of least squares linear regressions. Metrics are scaled to facilitate comparisons between populations (supplemental PDF). Colors indicate climate type and not statistical groups. Arrows denote case studies in figure 2.

(fig. 3*C*; $n = 21$, $t = 1.83$, $P = .08$) at higher latitudes ultimately reduced fitness more than at lower latitudes (fig. 3*A*) despite lesser declines in per capita birth rate and adult life span (fig. 3*C*, 3*F*) and greater reductions in development time (fig. 3*E*; $n = 21$, $t = 3.58$, $P = .002$).

TPC and Population Model Predictions

Typically, studies project fitness responses to climate change by directly applying a single TPC for fitness or performance to temperature data. By comparing fitness metrics and components quantified by directly applying TPCs versus incorporating TPCs in the population model, we assessed how much different fitness components and life stages contributed to species' overall responses to climate change. Applying TPCs directly systematically underestimated projected declines in fitness metrics and their components, as estimates from directly applying TPCs were correlated with population model projections with slopes shallower than 1 (fig. 4; table S4). Projections for changes in the per capita birth rate and adult life span were not altered by including TPCs in the population model because they are unaffected by density dependence or time delays within the population model.

Climate Change Impacts on Insect Population Dynamics

The population model predicted variable climate change impacts on mean adult density across latitude. The greatest projected declines, however, were concentrated between 30° and 45° (fig. 5*A*), and the five populations predicted to become extinct with climate change are all within these latitudes (*Macrosiphum euphorbiae* and *Myzus persicae* in Canada and *Aulacorthum solani*, *Brevicoryne brassicae*, and *Myzus persicae* in the United States; table S1). Climate

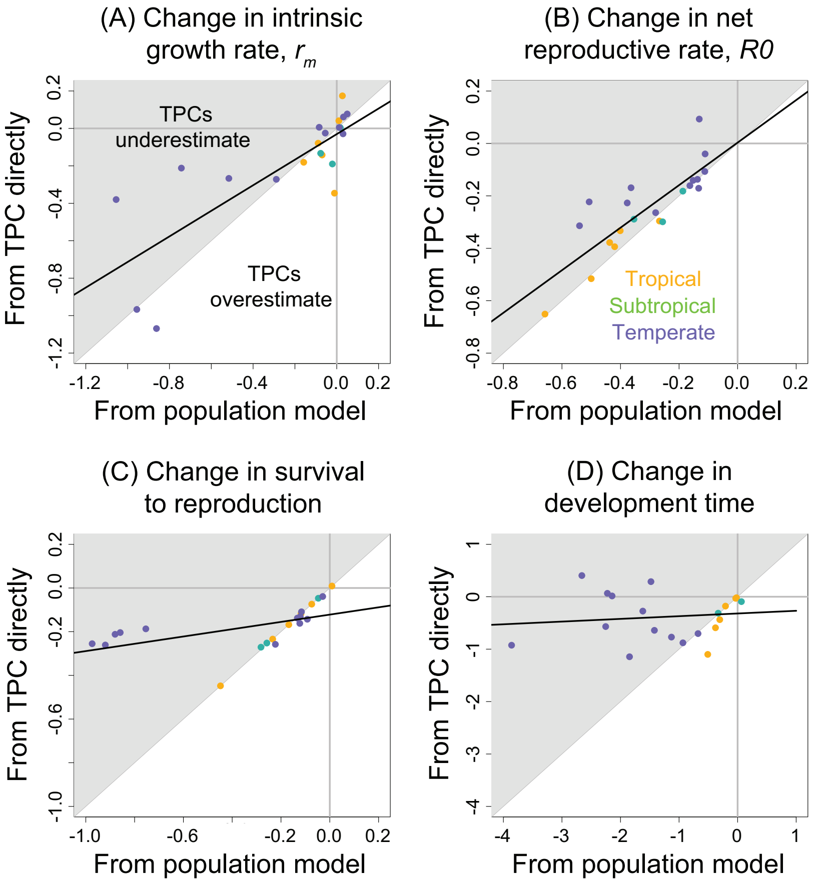

Figure 4: Climate change impacts on fitness metrics and components estimated from applying thermal performance curves (TPCs) directly (*y*-axes) versus from the population model (*x*-axes). Directly applying TPCs underestimated (gray regions) climate change–driven declines in the intrinsic growth rate, r_m (*A*); net reproductive rate, R_0 (*B*); survival to reproduction (*C*); and development time (*D*) relative to population model predictions. Lines show the best fit of least squares linear regressions. Colors indicate climate type and not statistical groups.

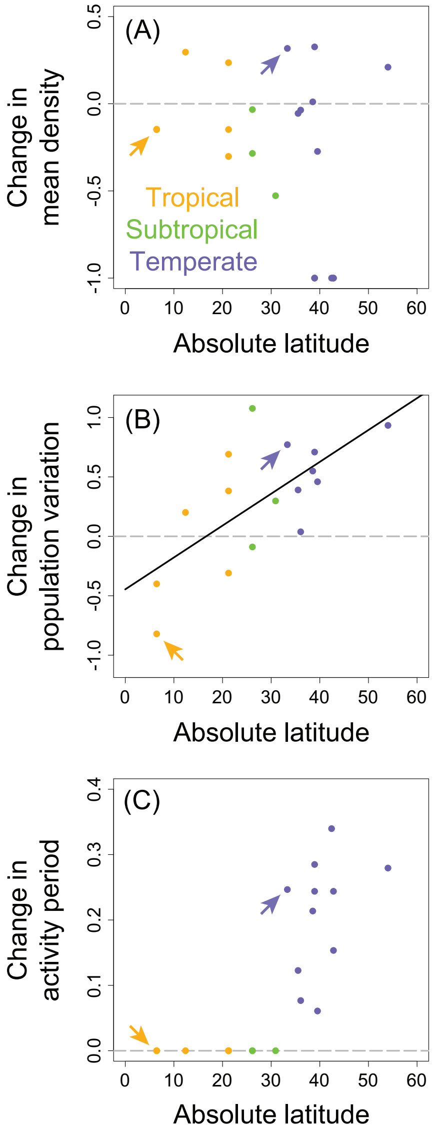

Figure 5: The population model projects that climate change will alter mean adult density (*A*), population variability (*B*; coefficient of variation of adult density), and activity period (*C*; fraction of the year when temperatures exceed the minimum temperature for development, T_{min}) across latitudes. All values are estimated over 5 years of simulated, site-specific recent (1980–1985) and future (2095–2100) climates. The line in *B* shows the best fit of a least squares linear regression. Mean adult density and population variability are quantified over the active period. Colors indicate climate type and not statistical groups. Arrows denote case studies in figure 2.

change was predicted to drive significantly greater increases in population variability at higher latitudes than at lower latitudes, based on linear regression (fig. 5*B*; $n = 21$, $t = 3.40$, $P = .004$). The activity periods of temperate populations were also predicted to increase as a result of climate change (fig. 5*C*).

Discussion

Our study revealed how differences in thermal sensitivity across fitness components and life cycles influence climate change responses, allowing us to address our four objectives. First, we successfully validated our population model for a tropical and a temperate insect species (fig. 2*C*, 2*D*). The model projected that climate change will reduce mean adult density and population variability of the tropical species but will increase mean adult density and population variability of the temperate species (fig. 2*E*–2*H*). These results extend predictions that 3°C–6°C increases in mean temperature alone will reduce the tropical, and increase the temperate, species' mean adult density (Scranton and Amarasekare 2017). Model validation by predicting field population dynamics is extremely rare (but see Johnson et al. 2015), but it is critical for accurately forecasting climate change impacts (Wheatley et al. 2017).

Second, our study revealed opposing latitudinal trends in the fitness metrics, which may help to reconcile opposing findings from directly applying TPCs. Our predictions that climate change will reduce fitness, r_m, more strongly at higher latitudes, particularly between 35° and 45° (fig. 3*A*), align with some past projections from directly applying TPCs (Kingsolver et al. 2013; Vasseur et al. 2014). Midlatitude species (20°–40°) may be particularly vulnerable to climate change because their TPCs are specialized to relatively narrow temperature ranges compared with high-latitude species, but they can experience pronounced climate variability (Kingsolver et al. 2013). Our population model found that greater fitness declines at higher latitudes in our dataset are attributable to much greater reductions in survival to reproduction (fig. 3*C*). Conversely, our model predicted that climate change will reduce the net reproductive rate, R_0, more at low latitudes (fig. 3*B*) due to greater declines in both reproduction and adult life span (fig. 3*D*, 3*F*). Our results highlight the importance of considering multiple fitness components (Buckley et al. 2021).

Third, projections from direct applications of TPCs often linearly correlated with those from the population model, suggesting that directly applying TPCs can coarsely estimate relative climate change impacts. Applying TPCs directly, however, consistently underestimated climate change impacts on fitness metrics and components (fig. 4). The underestimates resulted from simplifying survival dynamics across the life cycle. The population model mechanistically considers the temperature sensitivity of survival through the juvenile stage (eq. [4c]) over a developmental period (eq. [4b]) that is itself temperature dependent. If development of the thermally sensitive juvenile stage coincides with a warm period, exponential increases in juvenile mortality with increasing temperatures (eq. [2b]) can impact population dynamics substantially. We project that for many species, accelerated development with climate change will not compensate for elevated mortality rates, particularly at midlatitudes (20°–40°; fig. 3*C*). Directly applying TPCs omits how developmental timing can, for example, result in substantial juvenile mortality during warm periods, underestimating climate change impacts on survival and fitness (fig. 4*A*–4*C*). More generally, these results emphasize the importance of the survival component of fitness (Buckley et al. 2021) and how shifts in development rates can expose sensitive life stages to thermal stress (Kingsolver et al. 2011; Colinet et al. 2015; Levy et al. 2015; Ma et al. 2021; Buckley 2022).

Fourth, our population model predicted that climate change will often reduce mean adult density and increase population variability, particularly at midlatitudes (20°–40°; fig. 5). Thermal variability at these latitudes intersperses periods of population growth and decline (e.g., fig. 2*F*, 2*H*). Climate change can transform optimal periods of the year traditionally characterized by high population growth into periods of substantial population decline, often via reduced survival. Increased thermal opportunity with warming associated with higher fecundity and longer activity periods (fig. 5*C*) is irrelevant if insects cannot survive warm periods to capitalize on them (Sinervo et al. 2010). Lower mean densities and greater population variability associated with mortality events may even predispose midlatitude (20°–40°) populations to extinction during periods of low density (Kingsolver et al. 2013).

Such dynamics emphasize a critical need to move beyond fitness projections based on directly applying TPCs describing aggregate responses to estimate how climate change will alter fitness components and demography (Kingsolver and Woods 2016; Sinclair et al. 2016; Buckley and Kingsolver 2021). By comparing climate change impacts predicted by a population model with those estimated by applying TPCs directly, we show that population dynamics can be accurately predicted and can shape climate change responses. Furthermore, directly applying fitness TPCs can underestimate climate change impacts by omitting differential shifts in fitness components as well as how different demographic life stages experience climate variability.

Our findings suggest that resolving demographic responses to climate change will require considering how climate variability influences both the fecundity and the survival components of fitness (Buckley et al. 2021), the timescale of fitness or performance relative to those of environmental variation (Kingsolver and Woods 2016), and how the cumulative effects of thermal exposure influence performance and fitness (Rezende et al. 2020). These insights, based on data from hemipteran insects, may apply more generally to other organisms with multiple life stages with different temperature sensitivities, such as other ectotherms or even plants, fungi, and some endotherms. For example, while plants are underrepresented in TPC studies (Angilletta 2009; Sinclair et al. 2016), TPCs of plant fitness and components such as germination, survival, and flowering could predict plant sensitivity to climate change and forecast plant range shifts (Wooliver et al. 2022). For these organisms, studies that explicitly consider temperature effects on fitness components across life cycles (e.g., on seedlings and reproductive plants; DeMarche et al. 2018) may better predict climate change impacts than applying TPCs directly.

Like most studies, we use TPCs estimated across constant temperatures. A key challenge is to incorporate responses to variable temperatures and to understand how temperature variation affects ectotherm fitness and performance (Helmuth et al. 2014; Colinet et al. 2015; Sinclair et al. 2016; Ma et al. 2021; Marshall et al. 2021). Our framework could also be modified to explore additional processes important to climate change responses, including behavior, phenotypic variation and plasticity, and evolution (Angilletta 2009; Huey et al. 2012; Sunday et al. 2014; Woods et al. 2015; Sgrò et al. 2016; Sinclair et al. 2016; Williams et al. 2016). Finally, it is critical to study how organisms will respond to shifts in climate factors beyond just temperature (Gunderson et al. 2016; Sinclair et al. 2016; Buckley and Kingsolver 2021). Our population model is flexible enough to incorporate variability in other climate factors, which would be difficult to study by directly applying TPCs. More generally, our framework points to the importance of considering how temporal climate variability impacts fitness components across the life cycle (Buckley et al. 2021; Buckley 2022). Such considerations will become increasingly important as climate change increases climate variability and the incidence of climate extremes (Colinet et al. 2015; Williams et al. 2016; Buckley and Kingsolver 2021; Ma et al. 2021).

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Statement of Authorship

C.A.J. and L.B.B. conceptualized the research. C.A.J. and R.R. obtained and analyzed the climate data, and C.A.J. collected and analyzed the insect temperature response data. C.A.J. developed the mathematical models and performed the statistical analyses with feedback from L.B.B. C.A.J. and L.B.B. wrote the manuscript with feedback from all authors.

Data and Code Availability

Data and code are available in Zenodo (https://zenodo.org/badge/latestdoi/637424730; Johnson et al. 2023). The population model was constructed in Python (ver. 3.8.8), and the data were analyzed in R (ver. 4.1.2).

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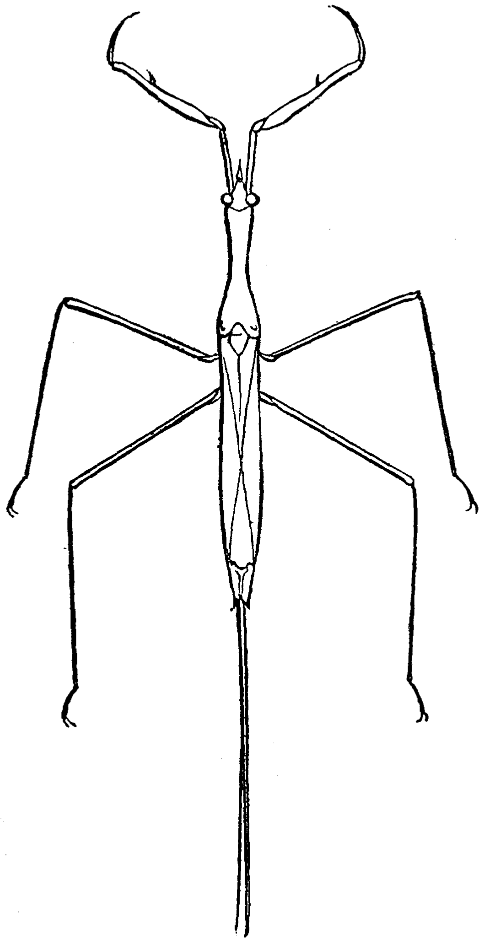

“Another insect-hunter is the singular *Ranatra fusca* ([figured], from Sanborn). It is light brown in color, with a long respiratory tube which it raises above the surface of the water when it wishes to breathe.” From “The Insects of August” by A. S. Packard Jr. (*The American Naturalist*, 1867, 1:327–330).