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Elucidating the effects of warming on ectotherms through a trait-based approach:
experimental studies on a pest of stored products

A dissertation submitted in partial satisfaction of the

requirements for the degree Doctor of Philosophy

in Biology

by

Rosa Maria McGuire

2023

ABSTRACT OF THE DISSERTATION

Elucidating the effects of warming on ectotherms through a trait-based approach:

experimental studies on a pest of stored products

by

Rosa Maria McGuire

Doctor of Philosophy in Biology

University of California, Los Angeles, 2023

Professor Priyanga A. Amarasekare, Chair

Temperature is one of the key sources of abiotic variation that affects all communities. Mounting evidence of climate warming makes it doubly important that we understand how perturbations to organisms' typical thermal environment influence population dynamics. My research examines the effects of temperature at individual and population levels on the cowpea seed beetle, *Callosobruchus maculatus*. Through the integration of mathematical

theory and manipulative experiments, my research seeks to address this key gap in our knowledge.

First, I characterized the temperature response of fitness and the fundamental thermal niche (FTN) of *C. maculatus*. I quantified the thermal reaction norms of birth, maturation, and mortality. Through measurements of genetic variation in reaction norms I determined which components of the FTN facilitate vs. constrain its evolution. I found that maturation rate exhibits the least amount of genetic variation, suggesting that it might be a limiting factor in the evolution of the FTN. Using the FTN, I predicted temperature suitability under various climate scenarios. I found that *C. maculatus* would extend its range with warming climate.

Next, I studied the effects of temperature and competition in adult *C. maculatus*. I quantified the temperature response of competition on the per capita birth and growth rates. I found that both rates decline with increase in adult density and that competition exhibits a left-skewed response to temperature. This indicates that the responses of *C. maculatus* populations will differ at low versus high temperature extremes, leaving populations prone to stochastic extinctions.

Finally, I studied the effects of temperature and competition on juvenile *C. maculatus*. I quantified the temperature responses of maturation and juvenile mortality rates as a function of larvae present in host seeds. I found that maturation rate remains constant while juvenile mortality has a positive association with larval density. Furthermore, the temper-

ature response of intraspecific competition on juvenile mortality is left-skewed, indicating a synergistic effect of temperature and competition.

Taken together, this work represents a step forward in understanding ectotherm species' responses under warming. The novel aspect of this research is that it addresses fundamental questions that also have applied significance in food security.

The dissertation of Rosa Maria McGuire is approved.

Kurt Anderson

Nandita Garud

Nathan Jared Boardman Kraft

Van Maurice Savage

Priyanga A. Amarasekare, Chair

University of California, Los Angeles

2023

To my grandmother,

Lucila Olaechea Hernández,

and in loving memory of my grandfather,

Alberto Arellano Greenfield.

Contents

List of Figures

List of Tables

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Curriculum Vitae - Rosa M. McGuire

Education

B.S. in Biology (2015-2018) University of California Riverside

A.S. in Math/Science (2013-2015) Victor Valley College

Publications

1. McGuire, R.M.[*], Hayashi, K.[*], Yan, X.[*], Vaz, M., Cinoğlu, D., Cowen, M., Martínez-Blancas, A., Sullivan, L., Vazquez-Morales, S., and Kandlikar, G.S. (2022). EcoEvoApps: interactive applications for teaching quantitative models in ecology and evolution. *Ecology and Evolution, 12, e9556.* `https://doi.org/10.1002/ece3.9556`

[*]Authors contributed equally

2. Martínez-Blancas, A., Bender, A., Zepeda, V., McGuire, R.M., Tabares, O., Amarasekare, P., Mastretta-Yanes, A., Miriti, M., Santos, A., and Vaz, M.(2022). Surviving racism and sexism in academia: sharing experiences, insights, and perspectives. *Bull Ecol Soc Am 00(00):e02033..* `https://doi.org/10.1002/bes2.2033`

3. Ardelan, A., Tsai, A., Will, S., McGuire, R.M.,and Amarasekare, P. (2023).Increase in heat tolerance following a period of heat stress in a naturally occurring insect species. *Journal of Animal Ecology, 00, 1–13.* `https://doi.org/10.1111/1365-2656.13995`

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- SEEDS Alumni Travel Award, Ecological Society of America (2023)

- UCLA EEB Departmental Research Grant (2019-2020,2022)

- UCLA EEB Halde Conference Travel Grant (2022)

- Eugene V. Cota-Robles Fellowship (2018) $50 000

- NSF Graduate Research Fellowship (2018) $138 000

Teaching and mentoring

Teaching Assistant (2019-2021) UCLA: *Ecology - EEB 122* (3 quarters)

Service and Outreach

SEEDS Alumni Mentor for the Ecological Society of America Annual Meeting. 2023

Moderator and Co-organizer of session "The state of ecosystems across the Global South: Perspectives on ecology, conservation, and environmental justice" Ecological Society of America Annual Meeting . 2022

Co-President of the Bruin Birding Club. 2022-2023

Secretary, ESA Latin American and the Caribbean Chapter. 2021-2022

Organizer, EEB Hacky Hours Committee. 2021-2022

Chapter 1

Genetic variation, thermal adaptation, and the fundamental thermal niche: insights from a cosmopolitan stored product pest

1.1   Introduction

Climate warming is the defining environmental crisis of the 21st century. Ectotherms, which constitute most of biodiversity on earth, are highly vulnerable to warming because their body temperature depends directly on the environmental temperature. A number of large-

scale data analyses show that ectotherms exhibit thermal plasticity in their life history traits (e.g., [1–5]). Plasticity is manifested as a thermal reaction norm, the range of phenotypes exhibited by a given genotype in response to temperature variation [6–8]. The rapid and continuous increase in mean habitat temperature along with the frequency and duration of hot extremes [9, 10] makes in ever more likely that environmental temperatures will exceed the upper limit of thermal plasticity in ectotherms. As a result, warming effects on ectotherms pose the greatest threat to biodiversity loss [11].

Predicting warming effects on ectotherms requires knowing whether they have sufficient plasticity to withstand warming and whether plasticity can evolve fast enough to keep pace with warming. First, determining whether current plasticity levels are sufficient requires quantifying the fundamental thermal niche (FTN), the range of temperature variation over which an ectotherm species can maintain a positive intrinsic growth rate [12]. Doing this requires characterizing the temperature responses (thermal reaction norms) of the underlying life history traits (birth, maturation, mortality). Once we characterize the FTN, we can predict the locations at which a given ectotherm species is likely to persist under current levels of warming. Second, determining whether plasticity can evolve to keep up with warming requires quantifying the genetic variability in the thermal reaction norms of life history traits. Once we have knowledge of genetic variability, we can quantify the genetic variation in fitness (intrinsic growth rate), and identify which fitness components (birth, maturation, mortality) facilitate adaptation and which components constrain it.

Despite their importance in predicting warming effects, intra-specific variation in thermal

plasticity is rarely incorporated into climate change ecology. This is in part due to the dearth of empirical data on genetic variability in thermal reaction norms. Early work in *Drosophila* [13] found substantial between-population variability in reproductive traits. Although there have been recent studies on within-population variability in fish and parasitoid wasps [14, 15] and thermal tolerance across the geographic distribution of marine invertebrates [16], the number of traits measured is limited and relies on inferences based on a handful of metabolic metrics. Virtually no studies have used mechanistic descriptions of trait response functions to quantify the fundamental thermal niche or genetic variance in fitness.

Here we take a step towards filling this key knowledge gap. We use a cosmopolitan stored product pest (the cowpea seed beetle *Callosobruchus maculatus*) as a model system to characterize the temperature responses of life history traits and genetic variation thereof. We utilize this information to quantify the fundamental thermal niche and genetic variation in fitness. The novelty of our framework lies in being able to predict the fundamental thermal niche of ectotherms based solely on trait response data and independently of any population-level information. This framework is also general, and potentially applicable to all multicellular ectotherms. Our focus on a stored product pest allows us to also address warming effects on pest control, and consequences for global food security.

1.2 Conceptual framework

Intrinsic growth rate and fundamental thermal niche

An analytical expression for the temperature response of the intrinsic growth rate in multicellular ectotherms can be derived using a stage-structured delay model of exponential population growth [17]:

$$r(T) = -d_A(T) + \frac{1}{\tau(T)} * W\left[b(T)\tau(T)e^{\tau(T)\left(d_A(T)-d_J(T)\right)}\right] \tag{1.1}$$

where $b(T), d_J(T)$ and $d_A(T)$ are, respectively, the temperature responses of the per capita birth rate, juvenile mortality rate, and adult mortality rate. The quantity $\tau(T)$ is the developmental delay (inverse of the maturation rate $(m(T))$ and W is the positive branch of the Lambert W (product log) function [18].

The fundamental thermal niche is the range of temperatures over which $r(T) > 0$. The advantage of Equation (1.1) is that we can use it to calculate the lower and upper thermal limits below and above which the population goes extinct, and the temperature at which $r(T)$ is maximized. The latter depicts the temperature at which a given ectotherm species can increase fastest from initially low abundances, an important quantity for predicting how ectotherms respond to perturbations in their thermal environment such as hot extremes driven by warming.

Intrinsic growth rate and genetic variance in fitness

The intrinsic growth rate constitutes a measure of fitness [6–8], and the life history traits underlying it (birth, maturation, mortality) constitute fitness components. Predicting whether ectotherms can adapt to climate warming requires determining whether there is sufficient genetic variability in the thermal reaction norms of fitness components.

Thermal adaptation of life history traits involves stabilizing selection towards physiological optima for such environments, resulting in an erosion of genetic variation [7, 19, 20]. However, variants that are selectively neutral could accumulate, particularly at the extremes of the thermal reaction norm [20, 21]. Such cryptic genetic variation [22] may be expressed when organisms are subject to perturbations such as climate warming, allowing species to adapt to novel thermal environments. Determining whether cryptic genetic variation exists at high temperature extremes is therefore critical when quantifying genetic variability in thermal reaction norms of fitness components.

Before we quantify the intrinsic growth rate and genetic variability, we need a mechanistic characterization of life history trait responses based on how temperature affects the underlying biochemical and physiological processes (e.g., enzyme kinetics, neural and hormonal regulation). We do this next.

Temperature responses of life history traits

Several large-scale data analyses have shown that the qualitative nature of the ectotherm trait responses to temperature (e.g.,unimodal, exponential) is conserved across ectotherm taxa [1–3, 23–26]. These trait responses can be categorized into two main types depending on the way temperature affects the underlying biochemical processes. Traits that are driven by rate-controlled processes such as reaction kinetics and enzyme inactivation exhibit phenotypic-level responses that are monotonic increasing/decreasing above a low temperature threshold (e.g., mortality, metabolism) or left-skewed (e.g., maturation, performance traits) [4, 24–28]. On the other hand, traits that are regulated by negative feedback processes that push rate processes towards intermediate optima exhibit phenotypic-level responses that are symmetrically unimodal (e.g., birth and attack rates) [2, 29–31].

The symmetrically unimodal nature of regulatory responses means that a negative deviation from the optimum (i.e., cooler temperatures) has the same detrimental effect as a positive deviation (i.e., warmer temperatures). This suggests that the decline in trait responses at low and high temperature extremes may be driven by similar biochemical constraints. This contrasts with rate-controlled responses that exhibit a faster decline at high temperatures, suggesting that different biochemical constraints may operate at low and high temperature extremes. Empirical data lend support to this suggestion. Low temperature decline of rate-controlled processes typically occurs due to the freezing of body fluids and related phenomena [24–26, 32], which occur more slowly than the rapid high temperature

decline due to protein denaturation and loss of loss of respiratory function [29, 32]. This difference between life history traits responses suggest that warming may operate more strongly through rate-controlled traits than through regulatory traits. The next step therefore is to derive mechanistic descriptions of rate-controlled and regulatory response functions.

We take advantage of a thermodynamical rate process model [33–35] that allows us to characterize both rate-controlled (maturation rate) and regulatory traits (birth rate):

$$X(T) = \frac{\frac{X_{T_{R_X}}T}{T_R}e^{A_{J_X}(\frac{1}{T_{R_X}}-\frac{1}{T})}}{1 + e^{A_{L_X}(\frac{1}{T_{L_X}}-\frac{1}{T})} + e^{A_{H_X}(\frac{1}{T_{H_X}}-\frac{1}{T})}} \tag{1.2}$$

where $X(T)$ is the birth/maturation rate at temperature T (in K), X_{T_R} is the rate at the reference temperature T_{R_X} at which the enzyme is 100% active, A_{J_X} (enthalpy of activation divided by the universal gas constant R) quantifies temperature sensitivity of the trait, A_{L_X} and A_{H_X} are the enthalpy changes related with low and high temperature enzyme inactivation divided by R, and T_{L_X} and T_{H_X} are respectively, the low and high temperatures at which the enzyme is 50 % active [27, 28, 33–36]. Note that when the trait response is regulatory, $A_{L_X} \approx A_{H_X}$; when the trait response is rate-controlled, $A_{L_X} \ll A_{H_X}$. Note also that $A_{L_X} < 0$ and $A_{H_X} > 0$;

Density-independent per capita mortality rate of all ectotherms increases monotonically with temperature above a low temperature threshold [33–36]. This response can be described using a modified Boltzmann-Arrhenius function [24–27]:

$$d(T) = d_{T_R} e^{A_d\left(\frac{1}{T_R} - \frac{1}{T}\right)} \left(1 + e^{-A_{dL}\left(\frac{1}{T_{dL}} - \frac{1}{T}\right)}\right) \tag{1.3}$$

where $d(T)$ is the mortality rate at temperature T (in K), T_R is a reference temperature, and T_{d_L} is the temperature threshold at which mortality increases with decreasing temperature. The parameters A_d (the Arrhenius constant) and A_{d_L} quantify how quickly the mortality rate increases or decreases with increasing or decreasing temperature, respectively ($A_d > 0$ and $A_L < 0$).

1.3   Hypotheses and predictions

Temperature response of the intrinsic growth rate

The intrinsic growth rate (r) is a function of birth, maturation and mortality rates (Equation (1.1)). Since the birth rate is symmetric unimodal, the maturation rate is left-skewed, and mortality increases exponentially with temperature above a low temperature threshold, we expect the temperature response of the intrinsic growth rate ($r(T)$) to be a left-skewed function of temperature. We expect the degree of skewness, as quantified by the difference between the temperatures at which birth and maturation rates are maximized, to be determined by the difference between the Arrhenius constants for high-temperature enzyme inactivation (A_H in Equation (1.2)) for birth and maturation rates. For instance, the higher the A_H for the birth rate compared to the maturation rate, the stronger the regulatory effect

on the birth rate and greater the skew.

If $r(T)$ is left-skewed, we expect the difference between the temperature at which $r(T)$ is maximized $(T_{r_{\max}})$ and upper temperature limit at which $r(T) = 0$ $(T_{\max})$ to be smaller than the difference between $T_{\max}$ and the lower temperature limit at which $T_{\min}$.

Genetic variation in the thermal reaction norms of life history traits

Because they are rate-controlled traits subject to strong biochemical control [27, 28, 33–35], and hence stronger stabilizing selection [7, 19, 20], we expect the thermal reaction norms of maturation and mortality to exhibit less genetic variability compared to the birth rate, which is a regulatory trait driven by feedback processes that prevents the underlying biochemical reactions from proceeding to their maxima (e.g., neural and hormonal regulation [30, 31]).

Given the likelihood of cryptic genetic variation accumulating at temperature extremes outside of the species' typical thermal environment, we expect thermal reaction norms of birth, maturation and mortality rates to exhibit greater genetic variability at hot and cold temperature extremes.

We tested these hypotheses by quantifying the thermal reaction norms for birth, maturation, and mortality (juvenile and adult) rates of the bean beetle *C. maculatus*.

1.4 Methods

Natural History

Callosobruchus maculatus (Coleoptera: Chrysomelidae) is a common pest of stored products such as lentils (*Lens culinaris*), mungbean (*Vigna radiata*), adzuki bean (*Vigna unguilaris*), and cowpea (*Vigna unguiculata*) [37]. *Callosobruchus maculatus* and other members of the subfamily Bruchinae were previously classified as its own family of beetles (Bruchidae), and the subfamily includes other species that require seeds for survival.

Its life history characteristics make *C. maculatus* particularly amenable to experimental manipulation [38]. Eggs adhere to the surface of the seed or bean by a fluid secreted from the ovipositor. Upon emergence, the first-instar larva burrows into the seed. The development time is approximately 21 days at 30 °C, and emerged adults lay eggs for about a week before death, making the total generation time around 28 days at 30 °C [39].

Because of its agricultural and economic importance, numerous studies have elucidated the phylogeographic history of *C. maculatus* and mechanisms of its spread. The region of origin of *C. maculatus* is Africa [40, 41], and several ecotypes have been identified in west Africa [42]. Geographic location, presence of wild hosts, trade, and physical barriers can all affect the genetic structure of *C. maculatus* populations. For instance, there is significant genetic differentiation among geographic regions [43], and populations vary genetically depending on host plant differences [44, 45]. Trade has been identified as a major factor responsible for gene flow between populations [42]. Global trading of host seeds has played

an important role in *C. maculatus*' dispersal [41]. As a result, the species currently has a cosmopolitan distribution.

Beetle Cultures

Cultures of *C. maculatus* reared at 30 °C on mung beans were obtained from Carolina Biological Supply Company. We used these to establish general cultures in the laboratory, which we did by mixing 25 pairs of beetles with 65 grams of cowpea beans (*Vigna unguiculata*). We used cowpea because it is the host species that produces the most beetles under laboratory conditions [38, 46, 47]. The general cultures were maintained at 24 °C, 40 % RH, and 12:12 day:night cycle. New beetle cultures were created every month by mixing individuals from previous general cultures in the same ration as above. We initiated experiments after the beetles had gone through approximately 10 generations at 24 °C.

Experimental Design

We quantified genetic variability in thermal reaction norms using a full-sib design described in Fig. 1.1. We obtained full-sib mating pairs using the following procedure. Beans with adults close to emergence were isolated from the general cultures at 24°C and stored in individual vials. Adults that emerged from these beans were used to form mating pairs. Each mating pair constitutes a family. A total of fifteen families were formed, ten during the first round of experiments (May 2020) and five during the second round (December 2020).

Each mating pair was transferred to a plastic container with 10 grams of cowpea beans and kept at 24 °C. Beans were examined every two days under a dissecting microscope to look for beetle eggs on the surface of the beans. Once the total number of beans with beetle eggs was counted for that mating pair over the two-day period, the beans with eggs were placed in individual vials and distributed between five temperature treatments: 15, 24, 29, 33, or 37 °C for the first round of experiments. Since no adults emerged from the 15 °C treatment during the first round of experiments, the lowest temperature treatment was switched to 18 °C for the second round of experiments. The number of beans taken from each family was replenished to keep the amount of resources constant. This procedure was repeated every other day for each mating pair until female death. Female *C. maculatus* are able to store sperm [48], so no new males were added if the male of a mating pair died before the female. Male and female longevity were recorded for each mating pair.

Offspring of each mating pair (F1 generation, FFig. 1.1) were monitored every two days for adult emergence in all the temperature treatments. Beans with eggs that did not produce adults were examined under a dissecting microscope. If the larva had hatched and burrowed into the bean (revealed by the presence of a small hole), then the bean was dissected and the immature stage at death (larva, pupa, dead adult) was recorded. After recording the date of emergence and sex, each adult that emerged in a given temperature treatment was isolated in a plastic vial and maintained at that same temperature. These adults were used to make full-sib mating pairs for each family, with a maximum of four mating pairs per family per temperature treatment and a total of 143 mating pairs across the five temperature

treatments. Each of these full-sib mating pairs was placed in their own vial with 10 grams of cowpea beans. Number of eggs laid (F2 generation, Fig. 1.1) by each female was recorded in the same way as it was in the parental generation (see above).

Data Analyses

Calculating birth, maturation and mortality rates at each temperature

Data from the F1 generation emerging from eggs laid by the mating pairs were used to quantify birth, maturation and mortality rates for each family in each temperature treatment. One family had to be excluded because of incomplete data, and hence only 14 families were available for this analysis. Since data were collected every two days, the average of the dates between each data collection event was calculated to calculate lifespans and development time using the package lubridate in R [49]. Maturation rate was quantified as the inverse of the development time, the number of days it takes for an egg to develop into an adult. Adult mortality rate was obtained by calculating the inverse of the adult lifespan. Since larvae develop inside the bean, larval lifespan could not be directly measured. We therefore used the instantaneous juvenile mortality rate [50], which we quantified by taking the natural logarithm of the proportion of juveniles surviving to adulthood divided by the average development time for each family at each temperature. Per capita birth rate was calculated by dividing the total number of eggs laid by the female of a F1 mating pair divided by the female's lifespan.

Characterizing thermal reaction norms and quantifying genetic variability

Since each family constitutes a distinct genetic line, we used mean trait values per family per temperature treatment to characterize the thermal reaction norms of birth, maturation and mortality rates. We fitted the mechanistic trait response functions (Equations (1.2) and (1.3)) to these family averages and estimated their parameters using non-linear least squares regression in R (nls.mulstart package; [51]). Given the large number of parameters to be estimated for birth and maturation rates, we first used nls.multstart to fit the high temperature portion of the function, with the lower temperature parameters fixed. Then, following [52], we used a least squares function to find local minima.

Following Stearns & Kawecki [8], Delpuech *et al.* [13], and Dworkin [53], we quantified genetic variability in thermal reaction norms as the coefficient of variation (CV, standard deviation divided by the mean) in trait values across families at each temperature. The CV is a useful metric because it allows comparisons across traits with different mean values.

Trait response parameters estimated for each family were used to quantify the temperature response of the intrinsic growth rate ($r(T)$; Equation (1.1)) for that family. The $r(T)$ thus calculated across families constitutes genetic variance in fitness, with fitness quantified by the intrinsic growth rate [6–8].

We estimated the fundamental thermal niche (FTN) for each family as the range of temperature over which $r(T) > 0$. We calculated the lower and upper temperature limits at which $r(T) = 0$ ($T_{\min}$, $T_{\max}$), and the temperature at which $r(T)$ is maximized ($T_{r_{\max}}$). We

used the average values of these metrics across families as the species-specific parameters of the FTN and used these to to generate thermal suitability maps for *C. maculatus*. Here, a suitable habitat is defined as locations where the estimated value of $r(T)$ is positive. We chose geographic locations that were important in the dispersal of *C. maculatus*. This species is of Afrotropical origin [54], and genetic studies on population differentiation [40] indicate that *C. maculatus* has populations differentiated across three continents: Africa, Asia, and America. We chose California, Nigeria, and Vietnam as our geographic locations. Nigeria and Vietnam are located near the equator and experience tropical climates, while California is located at a higher latitude and has a Mediterranean climate. According to previous research on the distribution and phylogeography of *C. maculatus* [41], Nigeria and Vietnam are located in regions that supported *C. maculatus* colonization routes, while California has a relatively recent population of *C. maculatus*.

Data on the mean annual temperatures for the three locations were obtained from World-Clim [55]. We used two climate datasets for analyses. One is based on current mean annual temperature values for the three locations, and the other uses CMIP6 climate projections [56]. We chose the GFDL-ESM4 model of climate change [57] with an Shared Socioeconomic Path (SSP) scenario of 3-7.0 because it corresponds to the scenario when no climate policies are enacted and global warming of 2 °C would be exceeded by 2100 [58]. We used the parameterized expression for $r(T)$ (Equation (1.1)) in combination with temperature data for each location to calculate $r(T)$ for each location. For each location, we used current and future temperature data (temperatures projected to 2080) at a grid resolution of 2.5 arcminutes.

For each grid cell, the value of temperature was used to calculate maturation, mortality, and birth rates using the parameterized versions of equations (1.2) and (1.3). We used these values to calculate $r(T)$ for the location using equation (1.1). We used these predicted $r(T)$ values to build thermal suitability maps for *C. maculatus* using the package Raster in R [59]. We mapped the predicted $r(T)$ values to the grids of the three locations used, in a similar manner to previous studies on disease vectors [60, 61].

1.5   Results

Temperature responses of life history traits

Consistent with expectations, the birth rate, a regulatory response, exhibits a more symmetric unimodal temperature response compared to the maturation rate, a rate-controlled response (Fig.1.2). Also consistent with expectations, the Arrhenius constant for high-temperature enzyme inactivation (A_H in Equation (1.2)) is greater for the birth rate compared to the maturation rate ($73, 353.92$ vs. 25742.14, Table **??**).

Temperature response of the intrinsic growth rate and the fundamental thermal niche

As expected, the temperature response of the intrinsic growth rate is left-skewed (Fig.1.3). The temperature at which $r(T)$ is maximized ($T_{r_{\max}} = 304.9K(32° \ C)$) is closer to the

upper thermal limit at which $r(T) = 0$ ($T_\mathrm{max} = 312K(39°\ C)$) than to the lower limit ($T_\mathrm{min} = 290K(17°\ C)$).

Genetic variability in thermal reaction norms of life history traits

Consistent with our predictions, genetic variability is lowest for the maturation rate, a rate-controlled trait, and highest for the birth rate, a regulatory trait (Fig.1.4). Juvenile and adult mortality show intermediate levels of variability. The birth rate also shows the greatest variability at temperature extremes, with higher variability at the high temperature extreme compared to the low temperature extreme (Fig.1.4, Fig.A.1). The maturation rate, again, shows the least variability even at temperature extremes.

Predicting habitat suitability under climate warming

We used the metrics of the fundamental thermal niche $(T_\mathrm{min}, T_\mathrm{max}, T_{r\mathrm{max}})$ to generate habitat suitability maps for *C. maculatus* at three locations in three continents: Nigeria, Vietnam, and California (Fig. 1.5). As noted above, Nigeria and Vietnam are closer to the equator and experience tropical climates, while California, which is at a higher latitude, experiences a Mediterranean climate. As a result, the distribution occurs at cooler temperatures in California compared to Nigeria and Vietnam. Because of cooler temperatures, the magnitude of $r(T)$ is also lower in California compared to the more tropical regions whose mean temperatures are closer to the temperature at which $r(T)$ is maximized.

Interestingly, projected distribution under warming (assuming a SSP 3.70 scenario for warming without the implementation of climate policies) shows higher values of $r(T)$ in all locations (Fig.1.5). This increase is greater in California, likely because warming makes the mean habitat temperature closer to the thermal optima for reproduction in currently occupied localities. California also shows a range expansion for *C. maculatus*. In contrast, range limits remain the same under warming in Vietnam and Nigeria despite the increase in $r(T)$.

1.6   Discussion

We investigated the temperature responses of the life history traits of the stored product pest *C. maculatus*, with the goal of quantifying the species' fundamental thermal niche and characterizing genetic variation in thermal reaction norms. The novelty of our approach is that we use mechanistic descriptions of life history trait responses to temperature that are based on thermodynamical principles, and use the parameters of these response functions to predict the fundamental thermal niche and future distribution of the species under climate warming. The fact that we can predict the fundamental thermal niche based solely on trait response data without relying on any population-level information makes this a potentially powerful approach for predicting species' distributions under climate warming.

We report three main findings. First, using the metrics of the fundamental thermal niche to predict future distribution of *C. maculatus* across three continents, we find that warming

allows the species to expand its distribution in the Mediterranean climate of California but not in the tropical climates of Nigeria and Vietnam. A potential explanation for this is as follows. Since *C. maculatus* is a warm-adapted species of subtropical origin, the cooler climate of northern California is likely outside of the species' FTN. A range expansion would be possible if warming increases the mean temperatures in the cooler regions to fall within *C. maculatus*' FTN. The absence of such an expansion in the two tropical localities is likely because the habitat temperatures were already within the species' FTN, and the warming scenario we used did not increase mean temperature to a level that would exceed the upper limit of the FTN.

Our second result is on the genetic variation in thermal reaction norms of *C. maculatus*' life history traits. Consistent with our predictions, we find that rate-controlled traits such as maturation and mortality, which are subject to strong biochemical control [27, 28, 33–35] and hence strong stabilizing selection [7, 19, 20], exhibit lower genetic variability, both within typical temperature range as well as cold and hot extremes, compared to regulatory traits such as the birth rate, which are subject to feedback processes that prevent biochemical reactions from proceeding to their maxima (e.g., neural and hormonal regulation; Long & Fee [30] and Nijhout [31]).

Our third finding is that genetic variation in fitness (intrinsic growth rate) is driven primarily by genetic variability in the thermal reaction norm for the birth rate. The birth rate exhibits both high levels of standing genetic variation within the typical temperature range as well as high level of variability at temperature extremes. This suggests that adaptation

to warmer thermal environments via an increase in thermal plasticity is most likely to occur through the birth rate. However, survival from birth to adulthood in multicellular ectotherms depends crucially on maturation from egg to adult. Even if thermal plasticity in reproduction can increase in response to warming given the higher genetic variability, the near absence of genetic variability in the maturation rate is likely to prevent a concomitant increase in thermal plasiticity of maturation. The important implication is that maturation rate may act a constraint on thermal adaptation in response to warming.

These results have implications that go beyond the study species investigated here. First, the analytical expression for the fundamental thermal niche (FTN) is applicable to all multicellular ectotherms. It is expressed in terms of parameters of life history trait responses to temperature that have been quantified for a large number of ectotherm taxa. This means that it is possible to characterize the FTN of species for which trait response data are already available, and to use the thermal limits to viability, calculated using the FTN, to predict future distributions of these species under any given climate warming scenario. A number of large-scale data analyses [1–3, 23–26] have shown that the qualitative nature of the temperature responses of life history traits (e.g., symmetric unimodal, left-skewed) is conserved across ectotherm taxa, and that their parameters are thermodynamically constrained to take a relatively narrow range of values. Hence, trait data from related species could be used to characterize the FTN of those ectotherm species for which trait response data are not readily available.

Second, it has been known since the 1950s that maturation is a strongly canalized trait

subject to strong stabilizing selection [19]. In addition, the process of maturation (meta-morphosis) is heavily conserved and the mechanisms and hormones are the same across multiple taxa [62–65]. Our finding that the maturation rate has the least genetic variability is therefore likely to be a general phenomenon amongst other ectotherms. Given empirical evidence that the birth rate exhibits a temperature response characteristic of a regulatory trait [66–72], our finding that it has higher genetic variability than maturation or mortality is also likely to be more general. Our finding of the same pattern of genetic variability in the harlequin bug (*Murgantia histrionica*), a free-living Hempipteran herbivore that is only distantly related to *C. maculatus* (McElderry *et al.,* unpublished manuscript), lends support to this idea although more studies are necessary to determine the generality of our findings.

Turning to our study species (*C. maculatus*), we find that warming can allow it to expand its range to cooler climates at higher latitudes while maintaining the integrity of its range limits in warmer tropical climates. Given that legumes and other grains constitute the major source of protein for most countries in the Global South, which are also disproportionately affected by climate warming, greater spread of *C. maculatus* and related stored-product pests could pose a threat to global food security. *Callosobruchus maculatus* is a major pest of stored chickpeas and lentils in Tunisia [44], causing large reductions in germination rates. This reduction can be as high as 80% in chickpea and 33% in lentils. In Africa, where legumes are a major source of protein [42], average loss of cowpea due to infestation by *C. maculatus* 60-70%. The Economic Injury Level, or lowest population size that leads to economic damage has been estimated to be in the range of 60-80 insects per kilogram

[44]. Proposed low cost control methods almost always involve temperature manipulation, including solar heating [73] and exposure of infested seeds to high (50°C) or low temperature extremes $(-14 - 18°C)$ [74]. Our findings of the lower and upper thermal limits to *C. maculatus*' fundamental thermal niche and the temperature at which its intrinsic growth rate is maximized can be used to inform these types of low cost control strategies. For example, we found that exposure of infested seeds to $38 - 40°C$ is sufficient to kill beetle larvae. Given that extreme high temperatures can cause moisture loss, reducing the quality of the beans, using a lower temperature to kill larvae can both reduce heating costs while preserving the quality of the beans. Given that the thermal limits to viability are determined by thermodynamical quantities constrained to take on a narrow range of values (see above), the metrics we have calculated for *C. maculatus*' FTN could be used for controlling other seed product pests in the family Bruchinae.

Because the experiments involved are labor- and time-intensive, our study was conducted across a single generation. We have also measured genetic variability in terms of differences between families in their thermal reaction norms of life history traits rather than through direct genetic studies. Some of the variation we have observed could be epigenetic, i.e., changes such as DNA methylation and genetic code [75–77]. While epigenetic variation can be heritable, demonstrating it requires multi-generational studies. Conducting experiments to determine heritability via parent-offspring regression [78] is an important future direction.

1.7 Tables

Table 1.1: Parameter estimates for life history traits of *C. maculatus*

Parameter	Estimate	Std. Error	p-value
Birth rate $b(T)$			
b_{T_r}	6.492208		
T_r	297.15		
A_b	10367.5721	2260	4.43e-02
A_{L_b}	-100000		
A_{H_b}	73353.9255	21700	7.74e-02
$T_{L/2}$	291.212		
$T_{H/2}$	306.4567	0.736	5.80e-06
Maturation rate $m(T)$			
b_{T_r}	0.02391859		
T_r	297.15		
A_b	15105.3647	4081.364701	3.43e-02
A_{L_b}	-100000		
A_{H_b}	25742.1414	2863.707172	2.91e-03
$T_{L/2}$	288.8152		
$T_{H/2}$	305.2768	2.655463	1.50e-06
Juvenile mortality rate $d_J(T)$			
$d_{J_{T_r}}$	0.009770911		
T_r	297.15		
A_{d_J}	7667.177	117.136900	3.00e-07
Adult mortality rate $d_A(T)$			
$d_{A_{T_r}}$	0.05577638		
T_r	297.15		
A_{d_A}	7848.97	358.416400	2.57e-05

1.8 Figures
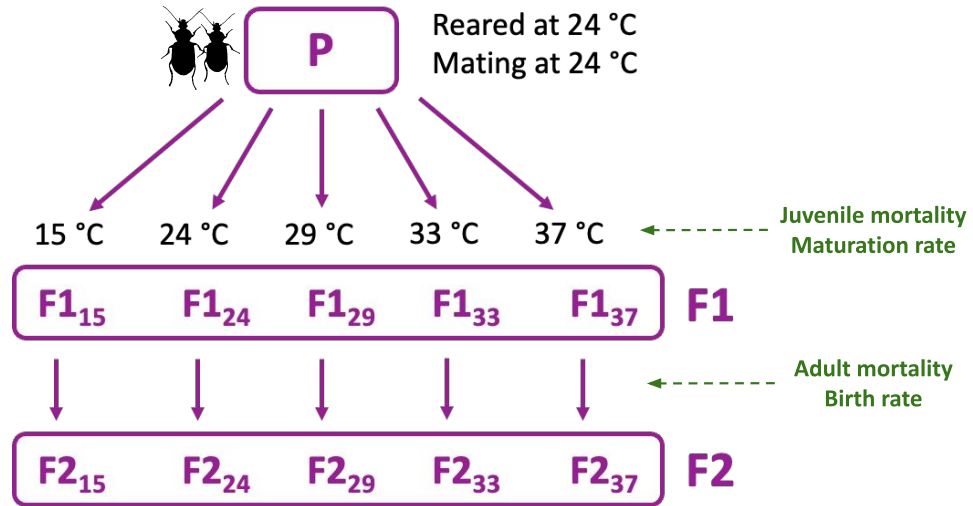
Figure 1.1: Experimental design.
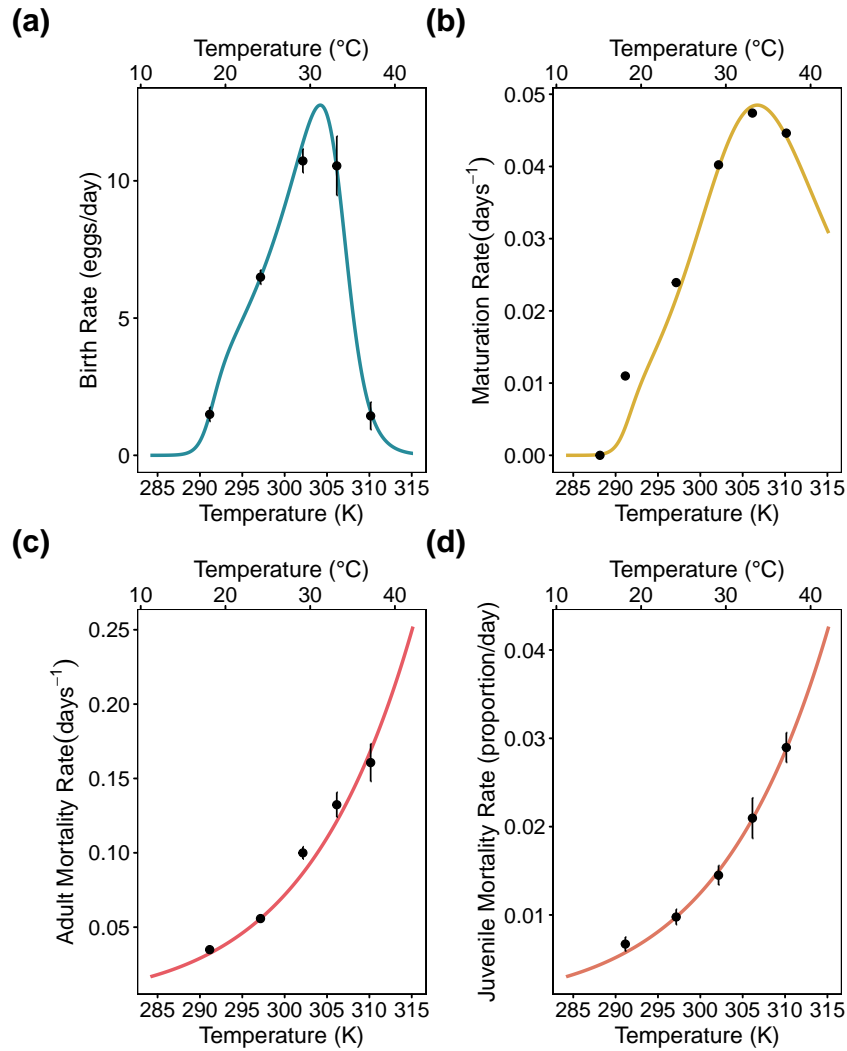
Figure 1.2: Temperature responses of a) birth, b) maturation, c) adult mortality, and d) juvenile mortality of *Callosobruchus maculatus*. The points and error bars depict the mean response (± SE) for each temperature treatment based on data from 12 families. The curves depicted the predicted response using parameter estimates obtained from fitting mechanistic temperature response functions to data. Note that the fitted curves have been extended beyond the experimental temperatures for clarity.
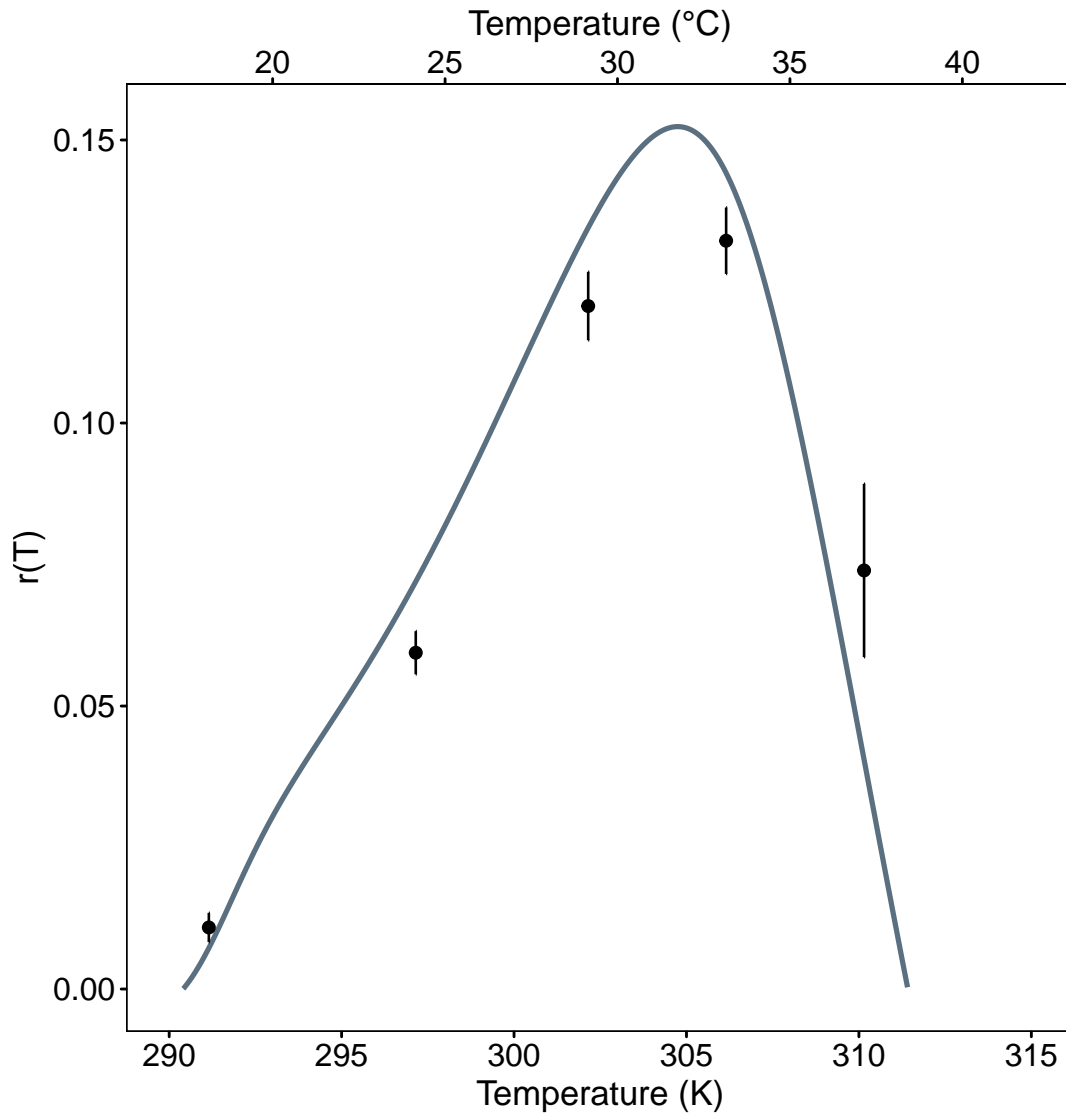
Figure 1.3: Temperature response of the intrinsic growth rate, $r(T)$, of *Callosobruchus maculatus*. The points and error bars depict the mean ($\pm$ SE) of $r(T)$ values for each temperature calculated using experimental data and Equation (1.1). The solid curve depicts the predicted temperature response based incorporating parameter estimates for trait response functions into Equation (1.1), and has been extended beyond the experimental temperatures for clarity.
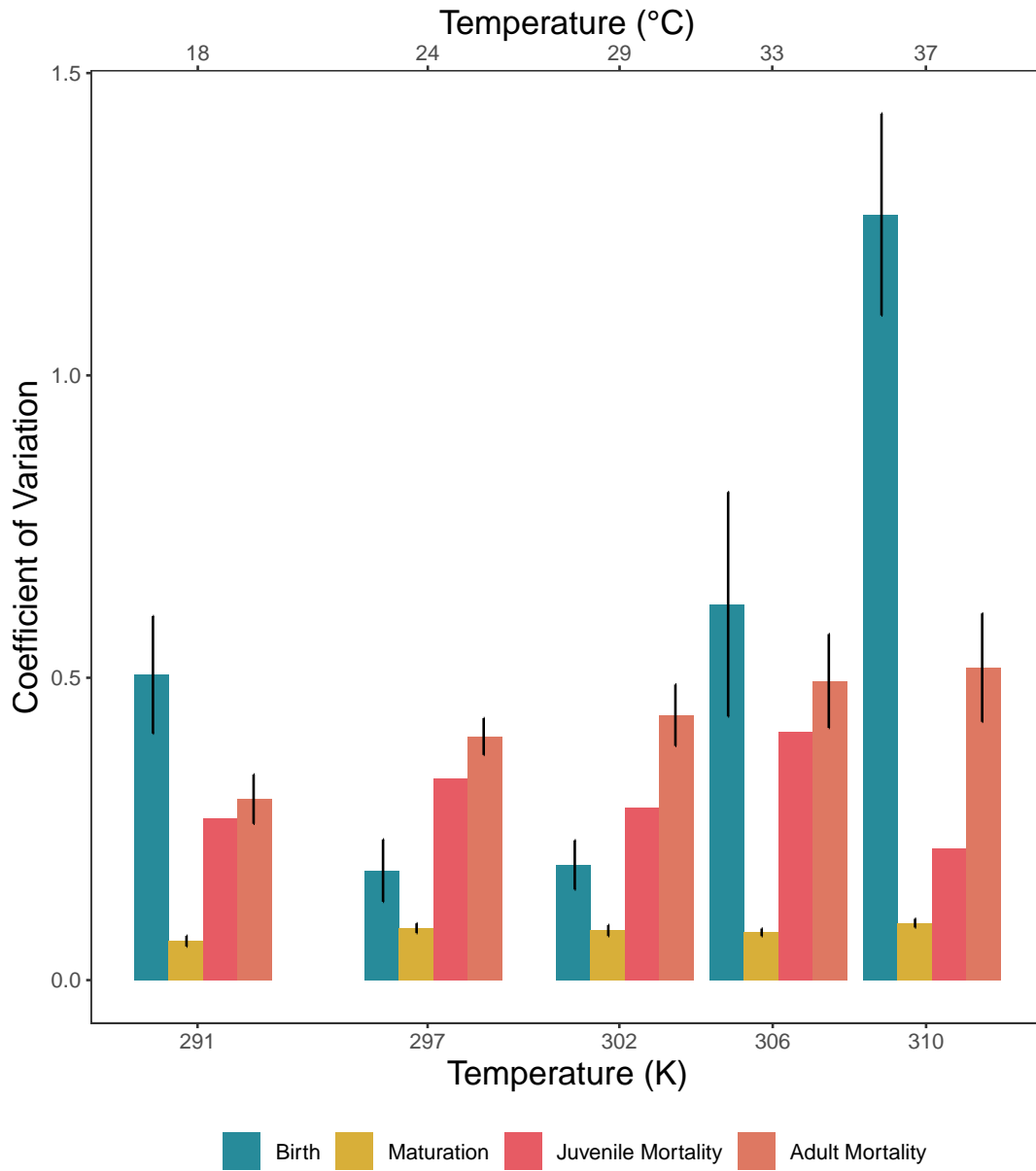
Figure 1.4: Genetic variability in thermal reaction norms birth, maturation adult mortality, and juvenile mortality of *C. maculatus* quantified as the Coefficients of Variation (CV). The solid bars depict the average CV across families and the error bars depict the standard errors.
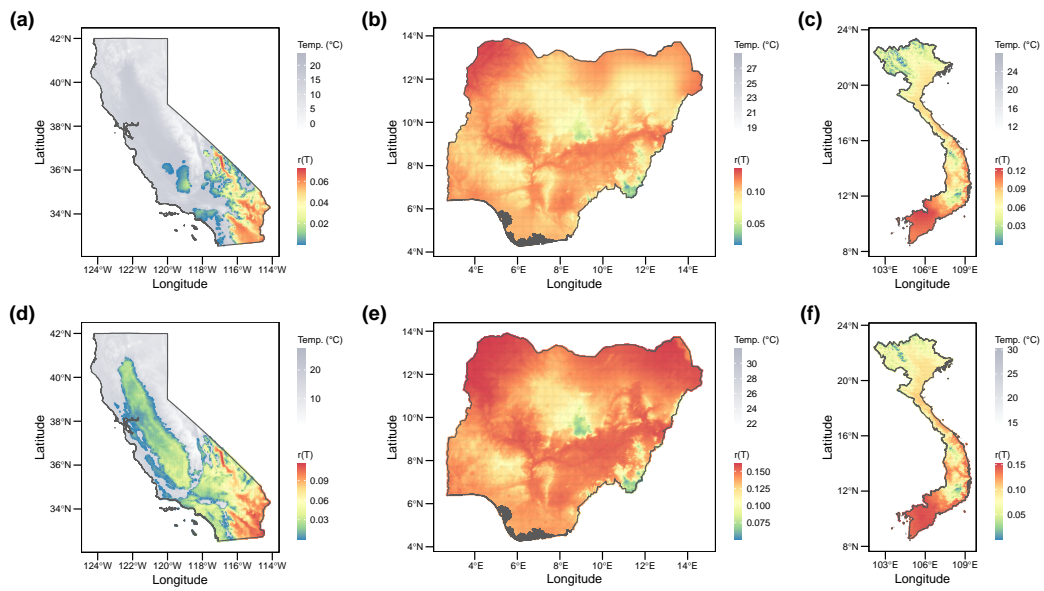
Figure 1.5: Thermal suitability maps for *C. maculatus* for California (a,d), Nigeria (b,e), and Vietnam (c,f). Panels (a)-(c) show suitability estimations based on current mean annual temperatures, while panels (d)-(f) show the potential distributions based on future climate projections (GFDL-ESM4 model, SSP 3.70).

Chapter 2

Effects of temperature on intra-specific competition in adult (*Callosobruchus maculatus*): an experimental study

2.1   Introduction

Population regulation involves the negative feedback processes (e.g., negative density dependence) that allow populations to persist in the long term. Population persistence is a necessary condition for species coexistence and the maintenance of biodiversity. Given that

the vast majority of biodiversity (all organisms except birds and mammals) are ectotherms, elucidating how temperature influences population regulation is a crucial research priority. The overwhelmingly strong evidence for climate warming and the attendant disruption of species' phenology make it all the more important to determine the mechanisms by which temperature affects density-dependent population regulation.

Intraspecific competition (self-limitation) is key to population regulation. In insects, individuals of the same species may compete with a resource that is in short supply, such as space, food, cover, mates, or oviposition sites, resulting in a deleterious effect in mortality and reproduction [79]. For example, it has been shown that individual metabolic rates are negatively correlated with density for a wide range of organisms [80]. The effects of resource limitation are reflected on birth and mortality rates of adult individuals, resulting in a decline in the per capita growth rate.

At the same time, the temperature responses of life history traits are well-explained by how temperature affects the underlying processes such as reaction kinetics and hormonal regulation [4, 5, 27, 28, 31, 33–36]. Several large scale data analyses have shown that the qualitative nature of these trait responses (e.g.,unimodal, exponential) is conserved across ectotherm taxa [1–3, 23–26]. Given that temperature affects the life history traits of ectotherms such as birth and growth rates, temperature can directly affect self-limitation.

There are two hypotheses on how temperature affects intraspecific competition in ectotherms. Both are based on the underlying premise of a limiting resource supply that itself does not change with changing temperature [26, 81, 82]. The first hypothesis is that competi-

tion should be strongest at the physiologically optimal temperature for reproduction because competition for resources is likely to be most intense during the peak reproductive period [81, 83]. It predicts the temperature response of intraspecific competition to be symmetric unimodal (e.g., Gaussian). The second hypothesis posits that the strength of competition should increase with increasing temperature within the biologically relevant temperature range (i.e., the range within which the organism can maintain a viable population; Savage *et al.* [26]).

Empirical evidence of the temperature response of competition is relatively scant. Experimental studies on plankton [84] have found that the strength of competition (quantified as the inverse of the carrying capacity) increased with temperature followed by a rapid decline at high temperature extremes. Studies on multicellular organisms suggest that both response types may be likely. For instance, increasing temperatures increased the strength of density-dependent mortality in grasshoppers [85], while blowflies showed a density dependent decline in fecundity at high temperatures [86]. The single experimental study [81] found temperature response of competition to be symmetric unimodal and competition strength was maximized at the optimal temperature for fecundity. Most recently, Mallard *et al.* [82] found that there was no reproduction at low and high temperature extremes and that reproduction had a unimodal response. The paucity of information on the temperature response of competition in multicellular ectotherms highlights the need for further experiments that can simultaneously test multiple hypotheses for how temperature affects competition.

Here, we report the results of an experimental study that was designed to test the two

competing hypotheses for how temperature affects intraspecific competition. We use the bean beetle, *Callosobruchus maculatus*, as our model organism. Our results provide crucial empirical information in predicting how temperature variation, warming in particular, influences population regulation.

2.2   Conceptual framework

A population is regulated when the per capita growth rate is a decreasing function of density. This can be manifested in one of the rates contributing to the per capita growth rate. In order to calculate a per capita competition coefficient, the vital rate in question is measured under different densities. Examples of traits studied are weight and developmental period [87], body size and longevity [88].

We use a thermodynamical rate process model, first developed by [36] and widely used in thermal ecology since then [27, 28, 33–36, 52, 83, 89, 90] to quantify the temperature response of intraspecific competition :

$$q(T) = \frac{\frac{q_{T_R} T}{T_R} e^{A_q \left(\frac{1}{T_R} - \frac{1}{T} \right)}}{1 + e^{A_L \left(\frac{1}{T_{L/2}} - \frac{1}{T} \right)} + e^{A_H \left(\frac{1}{T_{H/2}} - \frac{1}{T} \right)}} \tag{2.1}$$

where $q(T)$ is the per capita competition coefficient (inverse of carrying capacity) at temperature T (in K), q_{T_R} is the rate at the reference temperature T_R at which the enzyme is 100% active, A_q (enthalpy of activation divided by the universal gas constant R) quantifies temperature sensitivity of the trait, A_L and A_H are the enthalpy changes related with low

and high temperature enzyme inactivation divided by R, and $T_{L/2}$ and $T_{H/2}$ are respectively, the low and high temperatures at which the enzyme is 50 % active [27, 28, 33–36]. Note that $A_L < 0$ and $A_H > 0$.

When the demand for resources is greatest at the optimal temperature for reproduction, we expect $q(T)$ to be symmetrically unimodal. If this is the case, fitting Equation 1.2 to measurements of the competition coefficient at different temperatures should yield estimates for A_L and A_H that are approximately equal in magnitude. When the demand for resources increase with increasing temperature beyond the optimal temperature for reproduction, we expect $q(T)$ to be unimodal and left skewed. If this is the case, fitting Equation 1.2 to data on should yield estimates for A_L and A_H such that $|A_H| \geq |A_L|$.

2.3   Methods

Natural History and Beetle Cultures

Callosobruchus maculatus (Coleoptera: Chrysomelidae) is a common pest of stored products such as lentils (*Lens culinaris*), mungbean (*Vigna radiata*), adzuki bean (*Vigna unguilaris*), and cowpea (*Vigna unguiculata*) [37]. The species currently has a cosmopolitan distribution, and trade has played an important role in *C. maculatus'* dispersal [41] and is a factor responsible for gene flow between populations [42].

C. maculatus is amenable to experimental manipulation due to its life cycle [38]. Females

lay eggs on surface of seeds. Upon emergence, the first-instar larva burrows into the seed and completes its entire development inside the bean. The total generation time is around 28 days at 30 °C [39].

Cultures of *C. maculatus* reared at 30 °C on mung beans were obtained from Carolina Biological Supply Company. These cultures were used to establish new general cultures in the laboratory. Each culture consists of 25 pairs of beetles and 65 grams of cowpea beans. Cowpea (*Vigna unguiculata*) is the host species that produces the most beetles under laboratory conditions [38, 46, 47]. General cultures were maintained at 24 °C, 40 % RH, and 12:12 day:night cycle.

Experimental Procedure

We conducted laboratory experiments to measure the strength of intraspecific competition as a function of temperature. We quantified competition strength at each temperature as the per capita competition coefficient, the slope of the regression of the relevant vital rate (e.g., birth, mortality) on adult density (see Statistical Analyses section below for details). The experiment consisted of seven temperature treatments (18-36 °C, in increments of three), with a minimum of four replicates per temperature. To quantify competition strength at each temperature, mating pairs of adult beetles were assigned to one of five density treatments (1,2,4,8, or 16 pairs).

Adult beetles used in the experiment were obtained using the following rearing procedure.

Cowpea beans with beetles soon to emerge were collected from general cultures and isolated in plastic vials. Adults that emerged from these beans were collected from these vials and assigned at random to one of the seven experimental temperatures. The beetles were grouped by sex and were left at their experimental temperature for 48 hrs to get acclimated. Following the end of the acclimation period, adult beetles were randomly assigned to one of the five density treatments. Beetles from the same replicate (temperature x density treatment) were placed in a 4in x 4in x 4in plastic container with 10 grams of cowpea beans and kept at their respective experimental temperature.

The containers were examined three times a week. On each data collection day, dead adults were removed and death date was recorded. Beans were examined under a dissecting microscope to look for beetle eggs laid on the surface of the beans. Beans with eggs were removed, collected into vials, and incubated at their respective temperature. The number of beans taken was replaced to maintain the resource constant. Containers were checked until the last female in the container died. Vials were checked three times a week for offspring emergence. Date of emergence and sex were recorded.

We quantified two vital rates for each density treatment: per capita birth rate and per capita growth rate. Per capita birth rate was calculated using the number of eggs laid up until the first data collection date in order to avoid confounding effects with parental mortality. The birth rate was calculated by dividing the total number of eggs laid in a container by the number of mating pairs. The per capita growth rate was calculated as $ln(\frac{N_{t+1}}{N_t})$ where N_t is the number of adult individuals at the beginning of the experiment, equivalent to

the parental density, and N_{t+1} is the total number of adult offspring that emerged for an experimental cage.

Statistical Analyses

Calculating the per capita competition coefficient at each temperature

For each temperature we plotted the relationship between each vital rate and parental density. Since the relationships were linear, we calculated the per capita competition coefficient by running a linear regression at each temperature. Slopes, standard errors, and p-values for each linear regression were recorded.

Characterizing the temperature response of intraspecific competition

We fitted the thermodynamical rate process model (Equation 2.1) to data on the per capita competition coefficients at each temperature using non-linear least squares regression in R (nls.mulstart package; Padfield & Matheson [51]). In the case that the slopes were negative, we used the absolute value.

   With seven temperatures and five parameters to estimate from Equation 2.1, the parameter estimation would not converge. Therefore, we fixed the lower temperature parameters (A_L and $T_{L/2}$)to -10000 and 273 K, respectively. Once the high temperature parameters were estimated, we used a least squares function to find local minima and estimate the lower temperature parameters according to Scranton & Amarasekare [52].

A total of 185 replicates were made in this experiment, however, 23 of them were not used in the analyses due to incomplete or missing data. The results of this experiment come from 162 containers across all temperature x density treatments, which yielded approximately 26400 adult offspring.

2.4   Results

Effects of intraspecific competition on the birth rate

Across all temperature treatments except 18 °C, the per capita birth rate decreases linearly with increasing density (Figure 1). This effect is linear and statistically significant (Table 2.1). Of note, the slope of the regression of the birth rate on adult density at each temperature gives the per capita competition coefficient for that temperature. This slope is the steepest (i.e., most negative at 33 °C, suggesting that competition strength is maximized at this temperature.

Fitting the thermodynamical rate process model (Equation 2.1) to the data on competition coefficients shows that the temperature response of intraspecific competition in *C. maculatus* is left-skewed rather than symmetrically unimodal (Figure 2.2). For instance, the magnitude of A_H greatly exceeds that of A_L (98630 vs -100000), and the temperature at which competition is strongest (33 °C) is closer to the upper thermal limit for enzyme denaturation ($T_H = 308.7K$, $p < 0.001$) than to the optimal temperature for reproduction

$(T_{opt_b} = 304.21K)$.

Effects of intraspecific competition on the per capita growth rate

Across all temperatures, the per capita growth rate declines linearly with parental density. This relationship is weakest at the two temperature extremes (18 and 36 °C) and strongest at 33 °C (Figure 2.3).

Fitting the thermodynamical rate process model (Equation 2.1) to the data on competition coefficients (i.e., the slope of the regression on per capita growth rate on parental density) shows that the temperature response of intra-specific competition in *C. maculatus* is left-skewed rather than symmetrically unimodal (Figure 2.4). For instance, the magnitude of A_H greatly exceeds that of A_L (680500 vs -69686.5), and the temperature at which competition is strongest (33 °C) is closer to the upper thermal limit for enzyme denaturation ($T_H = 308.8K$, $p = 0.9998$) than to the optimal temperature for reproduction ($T_{opt_b} = 304.21K$). Note that competition strength is maximal at 33 °C for both per capita birth and growth rates.

2.5 Discussion

In order to predict population dynamics in a warming world, understanding how population regulation responds to temperature is an important research priority. Here, we investigated the temperature response of self limitation in *Callosobruchus maculatus*, a pest of stored products. We studied the temperature response of intraspecific competition by looking at the

per capita growth rate and one of its components, the per capita birth rate and their responses to adult density. The temperature responses of life history traits of ectotherms (e.g., birth, maturation, and mortality rates) have been characterized and quantified for large numbers of ectotherm taxa [3, 24–26], but, data on the temperature response of intraspecific competition have been scarce, thus impending prediction of the population dynamics based on trait responses. This work fills a key gap and provides the opportunity to test predictions made by previous theoretical studies on the qualitative differences between population dynamics when the temperature response of intraspecific competition is symmetric unimodal vs. left skewed.

We find that per capita birth and growth rates display a negative relationship with increasing parental density. Given that our study species spends its whole lifecycle inside seeds, oviposition sites that guarantee offspring survival are a limiting resource. *C. maculatus* beetles are known for distributing their eggs uniformly among host seeds [91]. Moreover, in a species of the same genus, *C. subinnonatus*, females are able to assess egg loads on seeds, and distinguish between seeds with and without eggs [92]. As a result, oviposition and birth rate in *C. maculatus* are traits affected by intraspecific competition with strategies and behaviors modified by the presence of competitors of the same species. For example, under high densities, it has been found that *C. maculatus* females lay wider eggs [93]. Moreover, *C. maculatus* display reproductive behaviors such as host inspection, but their inspecting behavior is reduced at high adult densities [94]. Since birth rate is a component of the per capita growth rate, the per capita growth rate is also affected by intraspecific competition

between adult beetles. In a different seed beetle species, *Acanthoscelides macrophthalmus*, it has been shown that more adult offspring emerge in the absence of competition [95]. Previous theoretical studies on population regulation have found that the mechanisms by which temperature affects competition will dictate the mechanisms of population regulation in ectotherms [83]. Temperature and competition can act antagonistically when competition is strongest around temperatures optimal for reproduction, which can result in complex dynamics. On the other hand, temperature and competition can act synergistically when the strength of competition keeps increasing with temperature beyond the optimal temperature for reproduction, leading to dynamics similar to those when competition is temperature independent.

We find that the temperature response of intraspecific competition in adult bean beetles is left-skewed with competition being strongest at a temperature that exceeds the optimal temperature for reproduction. This suggests that the effects of temperature and competition may be acting synergistically in this species.

According to theoretical studies, synergistic effects of intraspecific competition and temperature enhance nonlinearities in trait responses, leading to an increase in amplitude of population fluctuations [83]. As a result, when competition and temperature act synergistically, populations are at risk of stochastic extinction during periods of low abundances. Our experimental species, *C. maculatus*, is a pest of stored products and can thrive in granaries. Population outbreaks can lead to great economical losses, particularly in nations that rely on legumes as important sources of protein [42]. Since this pest is prone to outbreaks, the

temperature response of competition is not consistent with the behavior of a pest species. One possible explanation of why our study species is able to persist is that its development occurs entirely inside of infested seeds, causing a time lag in population responses to environmental factors [96]. Furthermore, storage conditions that provide metapopulation structure might increase persistence time in pest species [39].

The results from our study can help make predictions for other pest species. Furthermore, since the temperature responses are conserved, our methods are applicable to other multicellular ectotherms. In our experiment, the resource (beans) remained constant throughout the experiment, and was not affected by temperature in this case. However, pest species that attack hosts in the field, which are responding to temperature themselves, might be responding in a similar fashion [97].

An important future direction of this work would be to study *C. maculatus* populations in order to assess the population dynamics over time. Models of insect pests forecasts are already incorporating temperature [98–100]. Developing and testing models that incorporate temperature responses of traits as well as temperature effects on self-limitation will be important to predict insect and pest population persistence in a warming world.

2.6   Tables

Table 2.1: Regression results for per capita birth and growth rates vs. adult density

Temperature (°C)	Per capita birth rate		
	Estimate	Std. Error	p-value
18	-0.08182	0.16677	0.629
21	-0.283	0.1243	0.0353
24	-0.4903	0.164	0.00754
27	-0.2783	0.1353	0.0492
30	-0.3712	0.275	0.191
33	-0.7366	0.1632	0.000143
36	-0.431	0.104	0.000608
	Per capita growth rate		
18	-0.09832	0.00769	<2e-16
21	-0.07803	0.005639	<2e-16
24	-0.066808	0.005085	<2e-16
27	-0.069535	0.006597	<2e-16
30	-0.074415	0.007305	<2e-16
33	-0.083925	0.006158	<2e-16
36	-0.104733	0.008951	<2e-16

Table 2.2: Parameter estimation for the temperature response of intraspecific competition on the per capita birth and growth rates

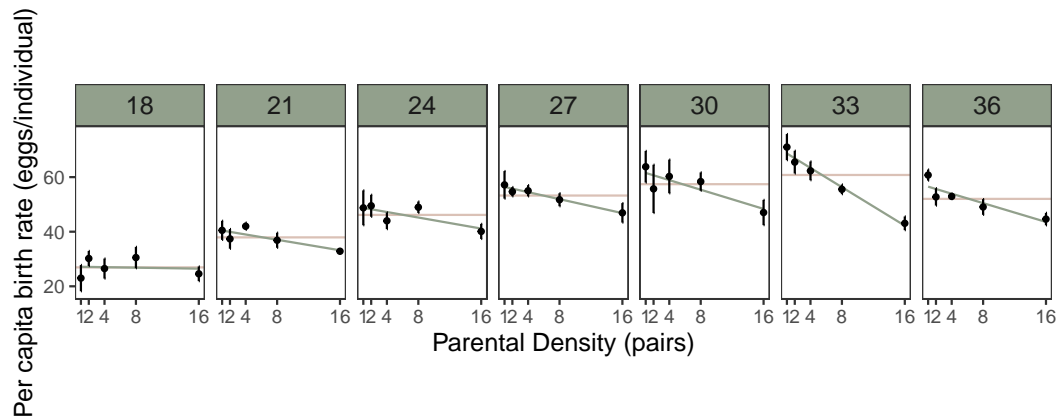| Parameter	Per capita birth rate		
	Estimate	Std. Error	p-value
T_r	297.5		
q_{T_r}	0.50550		
A_q	11660	2899	0.0159
A_L	-100000		
A_H	98630	142100	0.5259
$T_{L/2}$	291.4951		
$H_{L/2}$	308.7	1.223	1.48E-09
	Per capita growth rate		
T_r	297.15		
q_{T_r}	0.023520		
A_q	10610	3046	0.0253
A_L	-69686.5		
A_H	680500	2.505E+12	1
$T_{L/2}$	273		
$H_{L/2}$	308.8	1.24E+06	0.9998

2.7 Figures

Figure 2.1: Per capita birth rate of *C. maculatus* as a function of parental density. Each panel represents an experimental temperature (in °C). In each panel, points represent mean values and bars represent standard error. The pink line corresponds to the mean value for per capita birth rate across all parental densities at each temperature, and the green line corresponds to the best fitting line obtained via linear regression. The average birth rate at each temperature (pink line) increases gradually with increasing temperature and reaches an optimum at 33 °C.

Figure 2.2: Temperature response of the strength of self limitation on the per capita birth rate of *C. maculatus*. Dots represent the slopes from linear regression obtained in Fig. 1 and bars represent standard error of the slope. The solid curve depicts the predicted temperature response based incorporating parameter estimates for the per capita birth rate into Equation (2.1), and has been extended beyond the experimental temperatures for clarity.
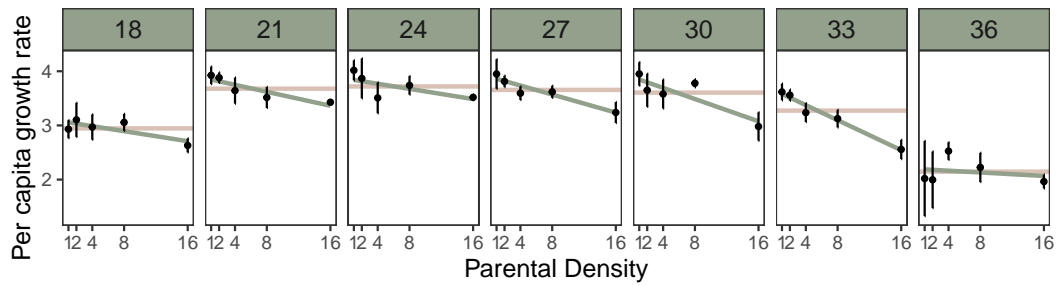
Figure 2.3: Per capita growth rate of *C. maculatus* as a function of parental density. Each panel represents an experimental temperature (in °C). In each panel, points represent mean values and bars represent standard error. The pink line corresponds to the mean value for per capita growth rate across all parental densities at each temperature, and the green line corresponds to the best fitting line obtained via linear regression. The average growth rate at each temperature (pink line) increases gradually with increasing temperature and abruptly declines after 33 °C.
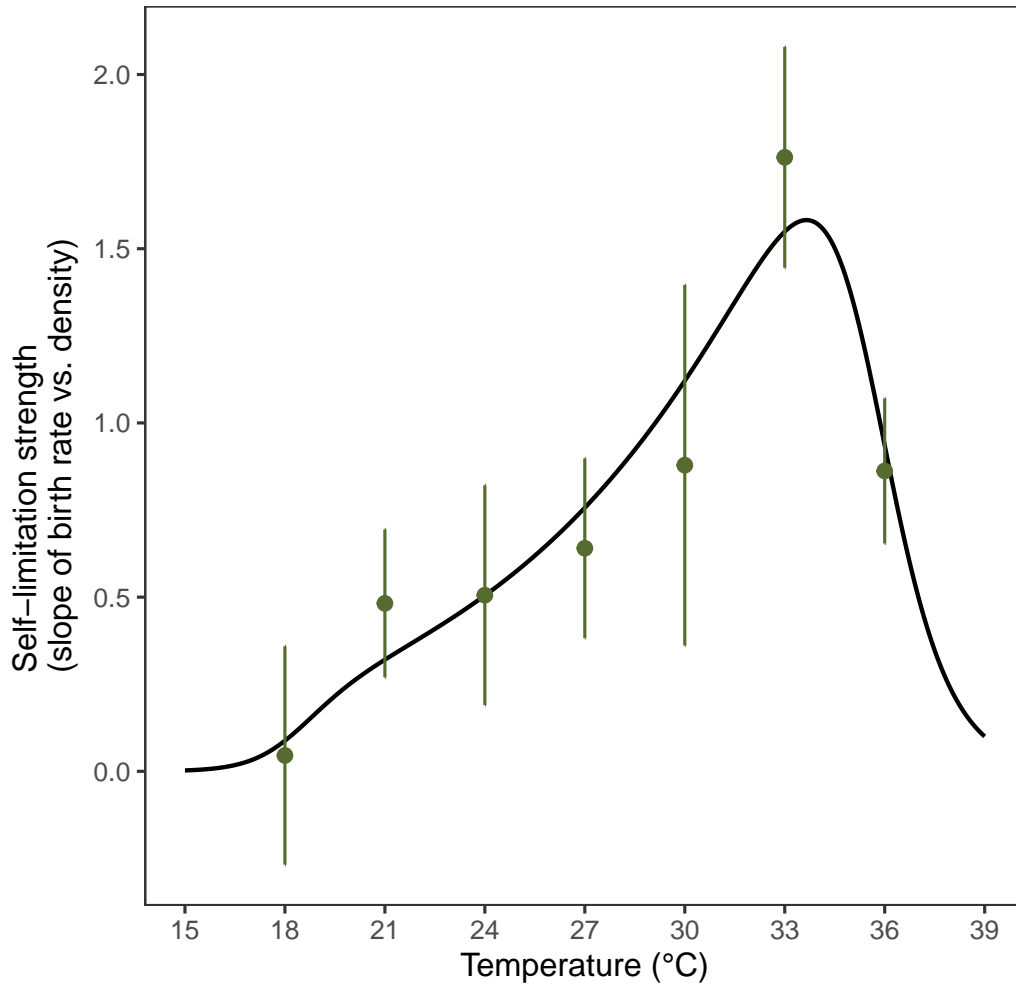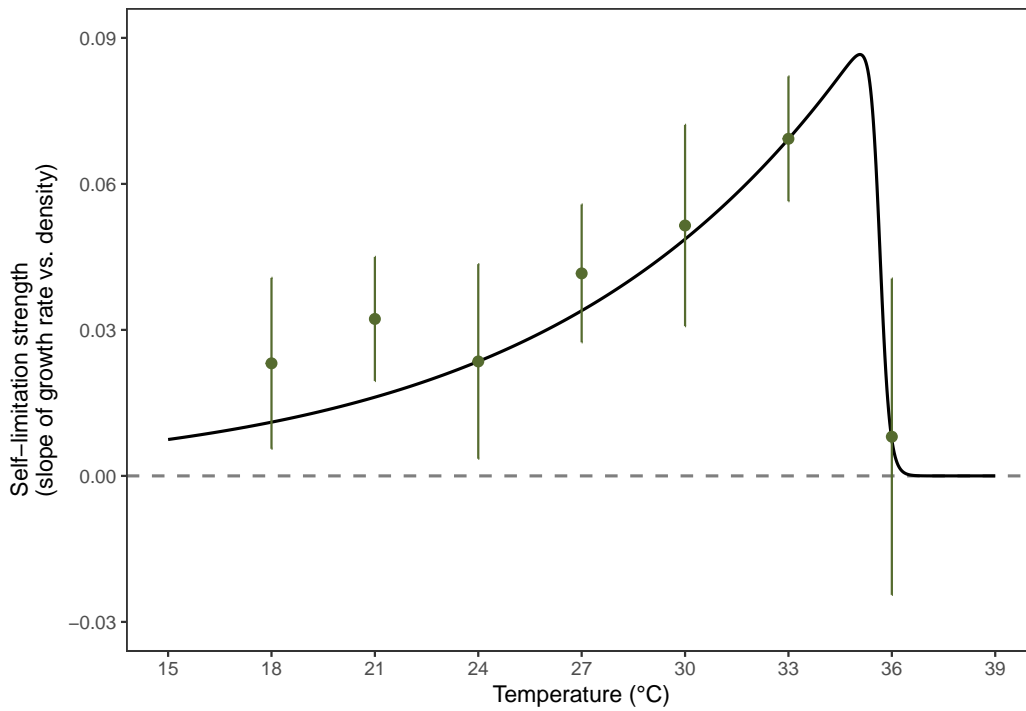
Figure 2.4: Temperature response of the strength of self limitation on the per capita growth rate of *C. maculatus*. Dots represent the slopes from linear regression obtained in Fig. 3 and bars represent standard error of the slope. Dashed grey line added at 0 for clarity. The solid curve depicts the predicted temperature response based incorporating parameter estimates for the per capita growth rate into Equation (1.2), and has been extended beyond the experimental temperatures for clarity.

Chapter 3

Effects of temperature on intraspecific competition in juvenile (*C. maculatus*): an experimental study

3.1 Introduction

The imminent threat of climate change on biodiversity makes it imperative to understand how populations will respond to warming. In particular, ectotherm species, who cannot regulate their body temperature, will especially bear the brunt of rising temperatures. Population regulation is one important process directly associated with population persistence. One of the key mechanisms of population regulation is intraspecific competition. Individuals compete for limiting resources, resulting in negative effects in reproductive and developmen-

tal traits [79].

In ectotherms, there are two hypotheses on how temperature affects intraspecific competition. The response of intraspecific competition can be symmetric unimodal or left-skewed. The first hypothesis predicts the temperature response of intra-specific competition to be symmetric unimodal when competition is strongest at the optimal temperature for reproduction [81, 83]. On the other hand, a left-skewed pattern arises when the strength of competition increases with increasing temperature within the biologically relevant temperature range Savage *et al.* [26].

While theory has been developed, the temperature response of self-limitation remains understudied in experimental settings. Studies on plankton [84] have found that the strength of competition (quantified as the inverse of the carrying capacity) follows a left-skewed response. On the other hand, experimental studies on multicellular organisms have found both symmetrical [81, 82] and left-skewed [85, 86] responses of intraspecific competition to temperature.

Of importance are studies that take a look at development. Most insect species have longer developmental periods relative to reproductive periods. Furthermore, it has been shown that different life stages can differ in their thermal responses [101]. Given that different traits contribute to overall fitness, understanding the temperature responses competition at juvenile stages is important to understand the regulation of populations. In particular, the developmental process is the result of the interactive effects between maturation and juvenile mortality. Maturation rate has important fitness consequences and affects probability of

further survival [102]. Furthermore, it has been shown that temperature can induce tradeoffs between development and juvenile survival in mosquitos [103].

Here, we report the results of an experimental study that intends to investigate how the joint effects of temperature and self-limitation influences the developmental process in a multicellular ectotherm that is also a pest species of economic importance. We use the bean beetle, *Callosobruchus maculatus*, as our model organism to test the two competing hypotheses for how temperature affects intraspecific competition.

3.2   Conceptual framework

To quantify the temperature response of intraspecific competition, we use a thermodynamical rate process model, first developed by [36] and widely used in thermal ecology since then [27, 28, 33–36, 52, 83, 89, 90]

$$q(T) = \frac{\frac{q_{T_R} T}{T_R} e^{A_q(\frac{1}{T_R} - \frac{1}{T})}}{1 + e^{A_L(\frac{1}{T_{L/2}} - \frac{1}{T})} + e^{A_H(\frac{1}{T_{H/2}} - \frac{1}{T})}} \tag{3.1}$$

where $q(T)$ is the per capita competition coefficient (inverse of carrying capacity) at temperature T (in K), q_{T_R} is the rate at the reference temperature T_R at which the enzyme is 100% active, A_q (enthalpy of activation divided by the universal gas constant R) quantifies temperature sensitivity of the trait, A_L and A_H are the enthalpy changes related with low and high temperature enzyme inactivation divided by R, and $T_{L/2}$ and $T_{H/2}$ are respectively,

the low and high temperatures at which the enzyme is 50 % active [27, 28, 33–36]. Note that $A_L < 0$ and $A_H > 0$.

$q(T)$ is expected to be symmetric unimodal when the demand for resources is greatest at the optimal temperature for reproduction. In this case, fitting Equation 3.1 to measurements of the competition coefficient at different temperatures should yield estimates for A_L and A_H that are approximately equal in magnitude. On the other hand, $q(T)$ is expected to be unimodal and left skewed when the demand for resources increase with increasing temperature beyond the optimal temperature for reproduction. In this case, fitting Equation 3.1 to data on should yield estimates for A_L and A_H such that $|A_H| \geq |A_L|$.

3.3 Hypotheses and predictions

The aim of this study is to understand how resource limitation affects the developmental process and how temperature mediates the effects of resource limitation. Development consists of two processes: maturation and juvenile mortality. The first step in understanding how the developmental process is affected by resource limitation is to know whether resource limitation affects one or both traits and if so, determine how temperature may influence the strength of self-limitation for each affected trait.

In *C. maculatus*, we expect the per capita maturation rate to decrease with increasing temperature and the per capita juvenile mortality rate to increase with increasing temperature. If the temperature response of self-limitation is symmetric unimodal, we expect the

strength of density-dependence (slope of the regression of per capita maturation/mortality rate on juvenile density) to increase with temperature to a maximum around the optimal temperature for reproduction (at which the juvenile density should be maximal) and decline thereafter. Alternatively, if the temperature response of self-limitation is left-skewed, we expect the strength of density-dependence to increase to a maximum at a temperature above the optimum for the birth rate and decline thereafter.

3.4   Methods

Experimental Procedure

Callosobruchus maculatus (Coleoptera: Chrysomelidae) is a common pest of stored products such as lentils, mungbean, adzuki bean, and cowpea (Varma and Anandhi, 2010). *C. maculatus* and other members of the subfamily Bruchinae were previously classified as its own family of beetles (Bruchidae), and the subfamily includes other species that require seeds for survival. Its life history characteristics make *C. maculatus* particularly amenable to experimental manipulation [38]. Eggs adhere to the surface of the seed or bean by a liquid secreted from the ovipositor. Upon emergence, the first-instar larva burrows into the seed. The development time is approximately three weeks, and emerged adults lay eggs for about a week before death, making the total generation time around four weeks [39]. This species is cosmopolitan, and dispersal into the Americas may have occurred as a result of global

trading of host seeds from Africa and Asia [41].

The experiment consisted of seven temperature treatments (18-36 °C, in increments of three), with five density treatments (1,2,4,8, or 16 pairs of adult beetles). Newly emerged, unmated adults were collected from general cultures and assigned at random to one of the seven experimental temperatures. Following the end of the acclimation period (48 hrs), the adults were randomly assigned to one of the five density treatments. The beetles were placed in a plastic container (4in x 4in x 4in) with 10 grams of cowpea beans. The containers were examined three times a week. On each data collection day, all beans in a container were examined to look for beetle eggs. Beans with eggs were removed and incubated at their respective temperature.

For this experiment, we used beans from at least two replicates of each density x temperature treatment. From these replicates, we randomly sampled half of the beans with eggs that were collected on the first data collection date for that replicate. These beans were incubated at their respective experimental temperature. After a period of time equivalent to one third of the average development time at that temperature, the beans were examined under a dissecting scope. All eggs were removed using a teasing needle, and the number of larva that burrowed inside each bean was quantified and recorded as the number of holes present on the surface of the bean after egg removal. Each bean was then placed into a 24-well plate, with each well covered with a piece of foam. Adult beetle emergence from each well-plate was recorded three times a week. Sex and date of emergence of each adult was recorded.

We quantified two vital rates for all beans: maturation rate and juvenile mortality rate. The maturation rate was calculated as the inverse of the development time, or the time between an egg was laid and adult came out. Since the data collection occurred every three days, we calculated average development time using the R package Lubridate.

The juvenile mortality rate was calculated by subtracting the number of emerged adults from number of larvae inside a bean and dividing by the average development time at that temperature.

Statistical Analyses

Calculating the per capita competition coefficient at each temperature

For each temperature we plotted the relationship between each vital rate and larval density. Since the relationships were linear, we calculated the per capita competition coefficient by running a linear regression at each temperature. Slopes, standard errors, and p-values were recorded.

Characterizing the temperature response of intraspecific competition

We fitted the thermodynamical rate process model 3.1 to data on the per capita competition coefficients at each temperature using non-linear least squares regression in R (nls.mulstart package; Padfield & Matheson [51]).

With seven temperatures and five parameters to estimate from Equation 3.1, the param-

eter estimation would not converge. Therefore, we fixed the lower temperature parameters (A_L and $T_{L/2}$)to -10000 and 273 K, respectively. Once the high temperature parameters were estimated, we used a least squares function to find local minima and estimate the lower temperature parameters according to [52].

The results of this experiments were obtained total of 77 replicates across all density x temperature treatments, adding to about 1400 beans, resulting in 4400 adult beetles.

sectionResults

Effects of intraspecific competition on the maturation rate

Across most temperatures, the relationship between maturation rate and larval density is weak (Figure 3.1). Of note, the relationship is slightly positive at 30° C and negative 24 °C(Figure 1, Table 1). Overall, maturation rate remained constant despite an increase in larval competition. The slope of the regression of maturation rate on larval density at each temperature gives the per capita competition coefficient at that temperature (Figure 3.2). We find that the slopes remain close to zero except for 36 °C. Given that the relationship was almost nonexistent we did not fit the thermodynamical rate process model to these data.

Effects of intraspecific competition on the juvenile mortality rate

Across all temperatures, the juvenile mortality rate increased with larval density (Figure 3.3). The relationship is positively linear and statistically significant (Table 1). The relationship is

weakest at the cold temperature extreme (18 °C) and is the strongest at 36 °C (Figure 3.3). The slope of the regression of juvenile mortality rate on larval density at each temperature gives the per capita competition coefficient at that temperature (Figure 3.4).

Fitting the thermodynamical rate process model (Equation 3.1) to the data on competition coefficients (i.e., the slope of the regression on juvenile mortality rate on larval density) shows that the temperature response of intra-specific competition in *C. maculatus* is left-skewed rather than symmetrically unimodal (Figure 4). For instance, the magnitude of A_H greatly exceeds that of A_L (39127.168 ± 63205.735 vs -61722.2), and the temperature at which competition is strongest (36 °C) is closer to the upper thermal limit for enzyme denaturation ($T_H = 310.079K$, $p < 0.001$) than to the optimal temperature for reproduction ($T_{opt_b} = 304.21K$, data from Chapter 1).

3.5 Discussion

We studied the temperature response of self-limitation development using *Callosobruchus maculatus*, a pest of stored products. We investigated the temperature response of intraspecific competition in the two components of development: maturation and juvenile mortality rates and their responses to larval density. Our competition experiments test multiple hypotheses for the temperature response of intraspecific competition (symmetric vs. left-skewed). While the temperature responses of life history traits of ectotherms have been studied in multiple ectotherm taxa [3, 24–26], experimental data on the temperature re-

sponse of intraspecific competition have been scarce. Therefore, this work stands to provide much-needed information on how the effects of temperature and density interact in multi-cellular ectotherms, particularly insects. It has direct applications for the management of stored product pests, by determining the temperatures at which competition may limit pest numbers.

We report two key findings. The first one is that maturation is not affected by larval density. This is consistent with other pest species. In a single temperature study, Giga & Smith [104] found that larval density did not affect development time in two *Callosobruchus* species. In *C. maculatus*, development occurs entirely inside of host seeds. As a result, competition for resource can be intense. Individuals die before having the chance to mature into the next developmental stage. Subsequently, surviving individuals experience less resource limitation and can therefore mature into the next stage without the developmental process being hampered by resource limitation. *C. maculatus* engage in scramble-like competition, as they can feed at lower satiation levels to reduce larval encounters inside the host seeds [105]. However, interference competition is still prevalent, with female larvae more likely to interfere with competitors compared to male larvae [106].

Our second key finding is that juvenile mortality increased with increasing larval density in *C. maculatus*, displaying a strong linear and positive relationship (Table 1). This pattern is seen in other insect taxa like mosquitoes [107]. Most importantly, however, this pattern is seen in insect species that have a similar life history (developing inside a host). For example, the spruce cone maggot *Strobilonmyia neanthracina*, exhibits lower individual survival when

more eggs are hatched per cone [108]. In a similar way, the fly *Rhagoletis pomonella*, larval survivorship declines with more larvae growing per fruit [109]. Our results indicate that juvenile mortality, not maturation rate, is the component driving intraspecific competition in juvenile *C. maculatus*.

Theory predicts that the manner in which temperature affects intraspecific competition has consequences on the mechanisms of population regulation. If competition is strongest at temperature optimal for reproduction, then temperature and competition act in a synergistic fashion, leading to complex population dynamics which in the case of pest species would mean prone to outbreaks. On the other hand, when competition is strongest at temperatures beyond what is optimal for reproduction, the dynamics of a population are similar to those when competition is temperature independent [83].

We find that the response of self-limitation in the juvenile mortality of *C. maculatus* is left-skewed, and that the temperature at which competition is strongest is beyond the optimal temperature for reproduction. As a result, theory predicts that the population will be left prone to stochastic extinction. Nevertheless, our experiment only covered a single generation of beetles since the experimental work is both labor and time intensive. In experimental settings, another bean beetle species, *Callosobruchus chinensis*, has displayed oscillatory dynamics caused by overlapping generations and delayed density dependence [110]. Experiments that examine population dynamics over time at different temperatures will help determine if the population dynamics adhere to the theoretical expectations.

Our research has applications to agriculture, the economy, and food security. Harmful,

non-native species respond to climate change in a different way than native species do. Research has shown that warming can act synergistically with biological invasions [111–113] and that many pest species can expand their range as temperatures rise [114–116]. An important future direction of this work include studying possible fitness effects on the survivors of larval competition. By using *C. maculatus*, a pest of stored products, our results can shed light into the effects of climate change on pest species.

3.6 Tables

Table 3.1: Regression results for maturation and juvenile mortality rates vs. larval density

	Maturation Rate		
Temperature (°C)	Estimate	Std. Error	p-value
18	0.00002957	0.00002465	0.231
21	0.00006566	0.00001613	0.0000529
24	-0.0004469	0.00004099	¡2e-16
27	0.00007659	0.00002764	0.00574
30	0.0014164	0.000108	¡2e-16
33	-0.0001071	0.00004928	0.0301
36	-0.008052	0.0032494	0.807
	Juvenile Mortality Rate		
18	0.0071273	0.0002696	¡ 2e-16
21	0.0104316	0.0002778	¡2e-16
24	0.010327	0.0006165	¡2e-16
27	0.020241	0.000738	¡ 2e-16
30	0.022664	0.001067	¡ 2e-16
33	0.0264788	0.0008642	¡ 2e-16
36	0.029179	0.001064	¡ 2e-16

Table 3.2: Parameter estimation for the temperature response of intraspecific competition on the juvenile mortality rate

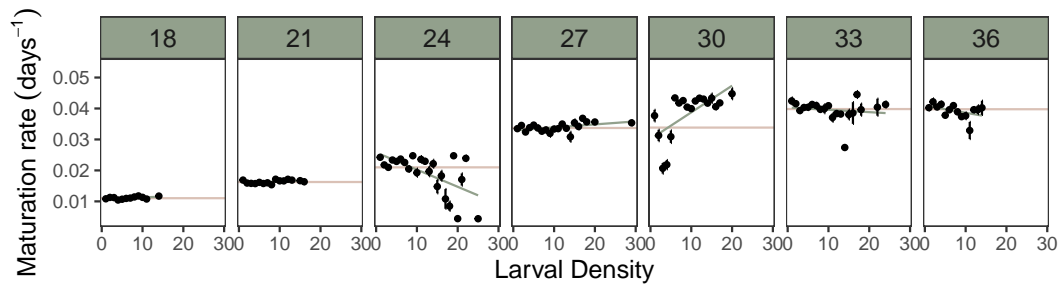|	Juvenile mortality rate		
Parameter	**Estimate**	**Std. Error**	**p-value**
T_r	297.15		
q_{T_r}	0.010327		
A_q	11554.077	5805.683	0.117
A_L	-61722.28		
A_H	39127.168	63205.735	0.569
$T_{L/2}$	273.00		
$T_{H/2}$	310.079	1.223	1.48E-09

3.7 Figures

Figure 3.1: Maturation rate of *C. maculatus* as a function of larval density. Each panel represents an experimental temperature (in °C). In each panel, points represent mean values and bars represent standard error. The pink line corresponds to the mean value for the maturation rate across all parental densities at each temperature, and the green line corresponds to the best fitting line obtained via linear regression. The average maturation at each temperature (pink line) increases gradually with increasing temperature and reaches an optimum at 33 °C.
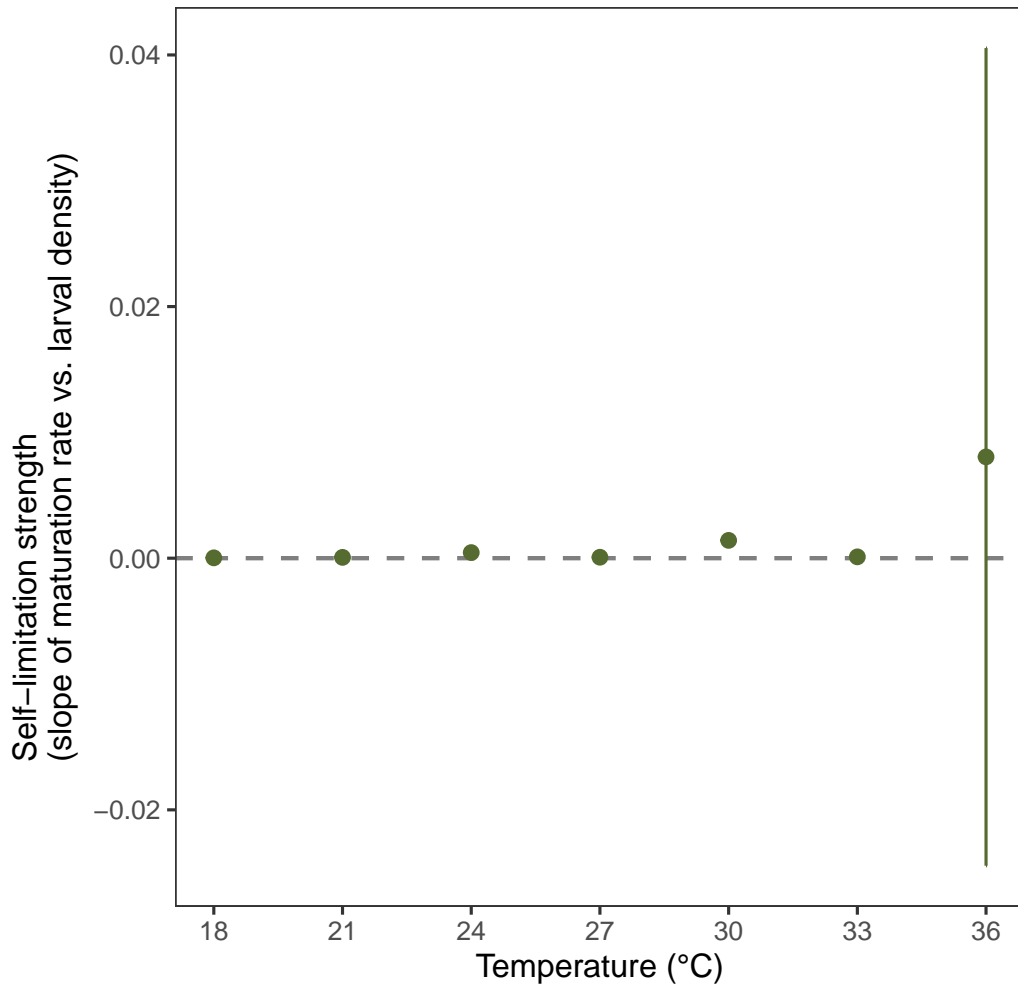
Figure 3.2: Temperature response of the strength of self limitation on the maturation rate of *C. maculatus*. Dots represent the slopes from linear regression obtained in Fig. 1 and bars represent standard error of the slope. Dashed grey line added at 0 for clarity.
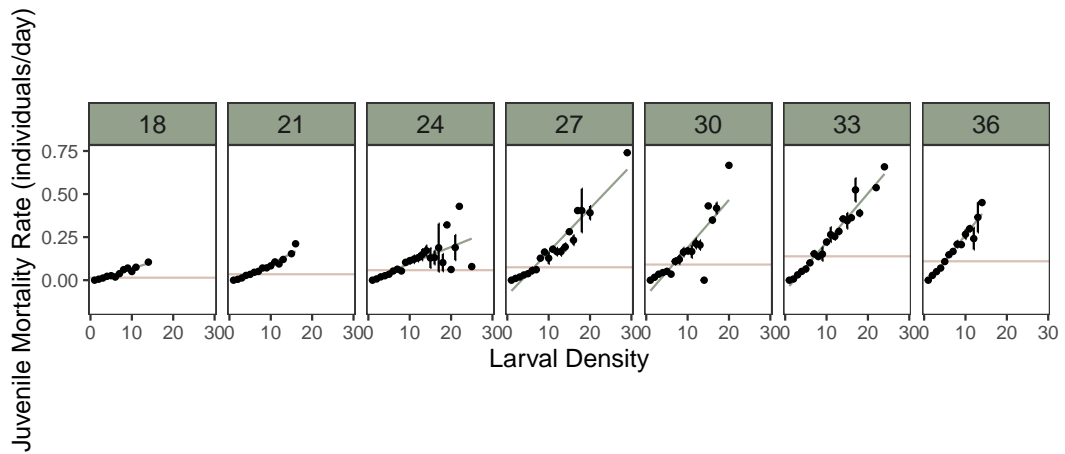
Figure 3.3: Juvenile mortality rate of *C. maculatus* as a function of larval density. Each panel represents an experimental temperature (in °C). In each panel, points represent mean values and bars represent standard error. The pink line corresponds to the mean value for the maturation rate across all parental densities at each temperature, and the green line corresponds to the best fitting line obtained via linear regression. The average maturation at each temperature (pink line) increases gradually with increasing temperature and reaches an optimum at 33 °C.
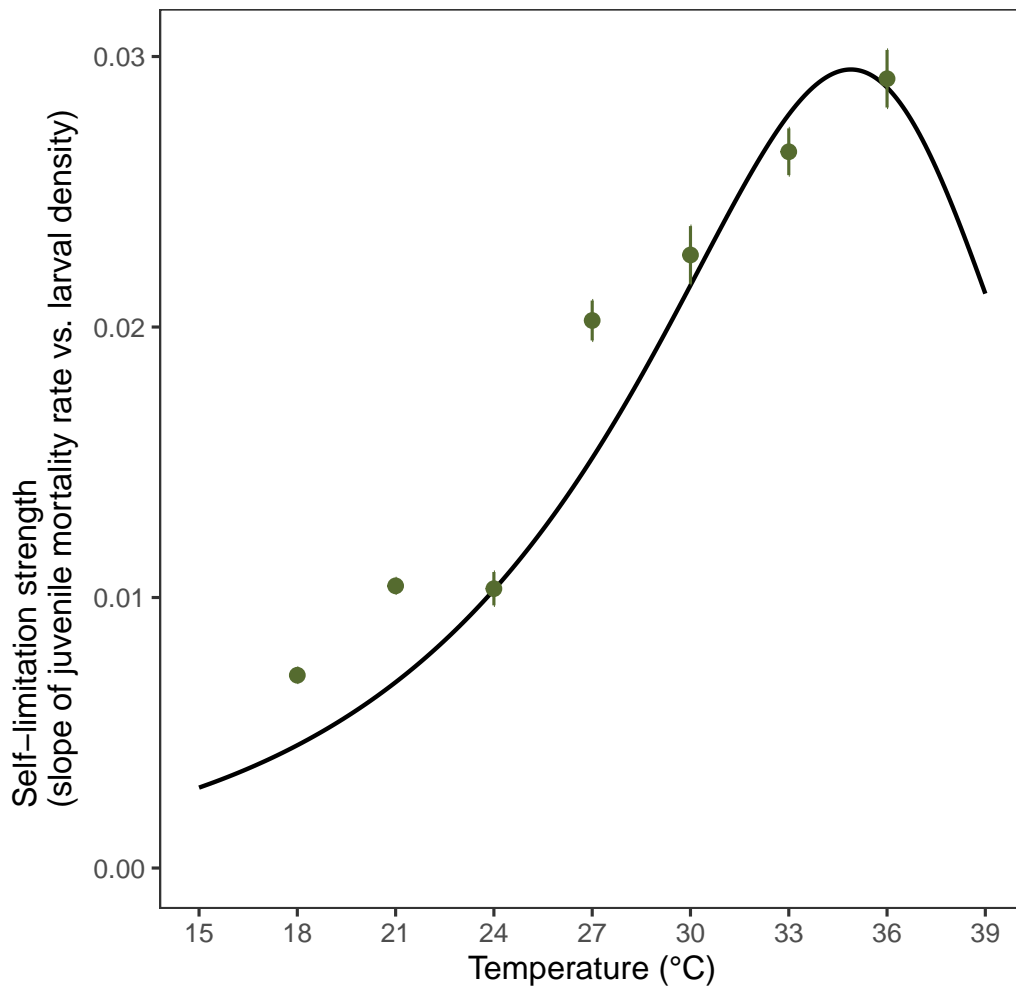
Figure 3.4: Temperature response of the strength of self limitation on the juvenile mortality rate of *C. maculatus*. Dots represent the slopes from linear regression obtained in Fig. 3 and bars represent standard error of the slope. The solid curve depicts the predicted temperature response based incorporating parameter estimates for the per capita growth rate into Equation (3.1), and has been extended beyond the experimental temperatures for clarity.

Appendix A

Supplement for Chapter 1

A.1 Appendix S1: Genetic variation in thermal reaction norms of life history traits and fitness (intrinsic growth rate)

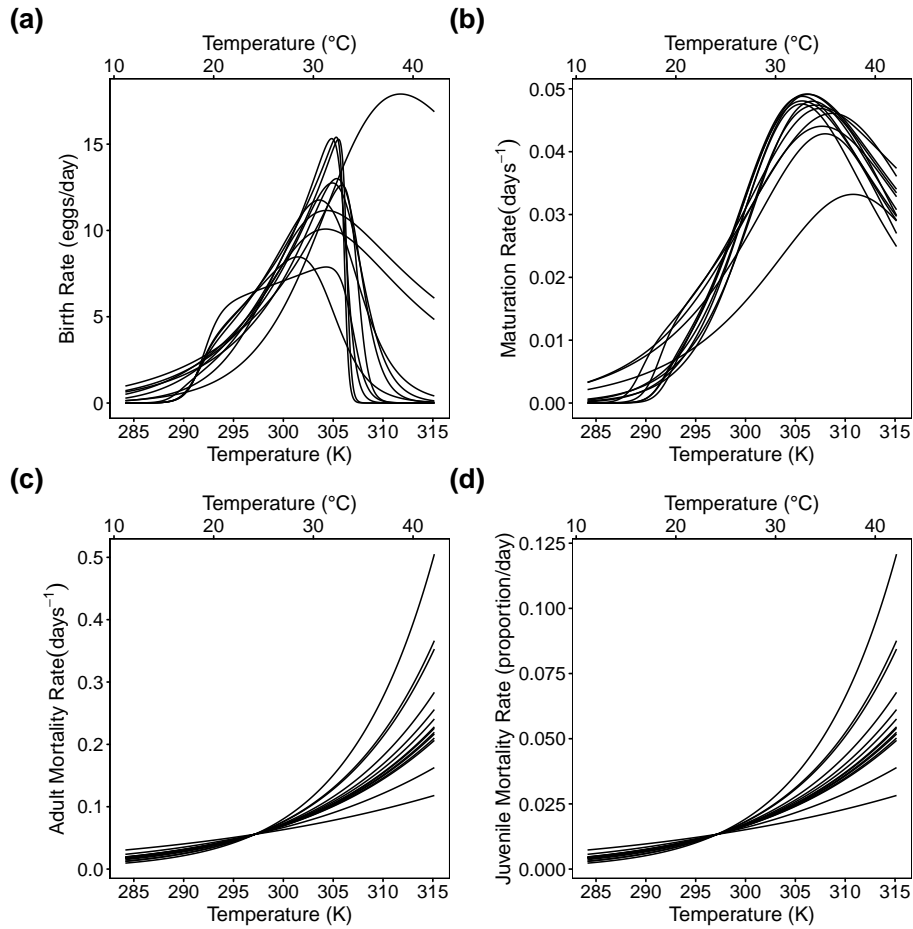**Figure A.1:** Thermal reaction norms of a) birth, b) maturation, c) adult mortality, and d)juvenile mortality of *Callosobruchus maculatus* for each experimental family as predicted by fitting mechanistic temperature response functions to experimental data. Each curve represents a different genetic line (family). Given the large number of genetic lines, the data points have been omitted for clarity.
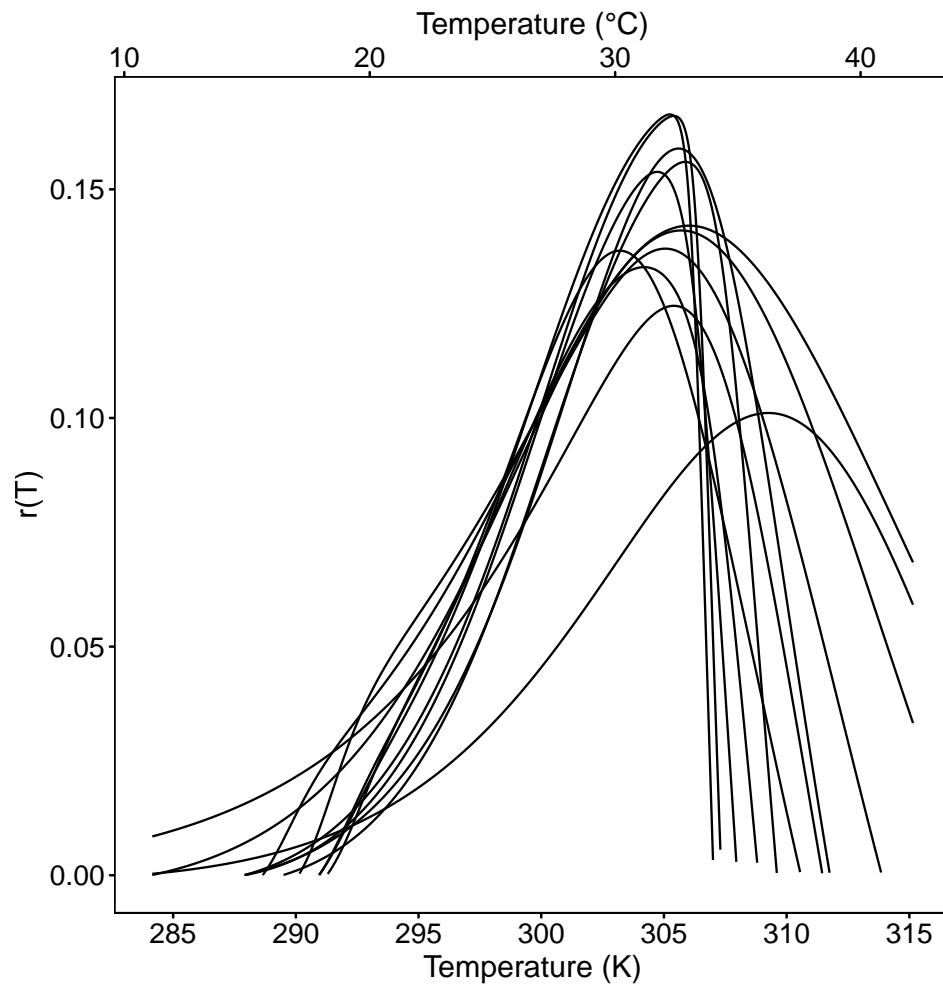
Figure A.2: Temperature response of the intrinsic growth rate, $r(T)$, of *Callosobruchus maculatus* for each experimental family. Each curve represents a different genetic line (family). Curves show predictions from the fit to temperature response functions (data points have been omitted for clarity) and have been extended beyond the experimental temperatures for better visualization.

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