

MODELING THE TEMPERATURE- AND NUTRIENT-DEPENDENCE OF LARVAL DEVELOPMENT RATE, EGG-TO-ADULT SURVIVAL, AND ADULT SIZE IN *CULEX* MOSQUITOES

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Abstract. Understanding mosquitoes better is the mission of many concerned with disease transmission and global public health. The larval life stage is of particular interest because larval rearing conditions can influence the developmental process and subsequent effects can carry over into adulthood. Both nutrition and temperature are essential factors in this stage that fluctuate in natural environments: nutrient availability has been observed to influence development time, survival, and resulting adult body size and, because mosquitoes are ectotherms, their biological processes depend on external temperature. We explored how life history traits, specifically egg-to-adult survival, larval development rate, and adult size, respond to a range of temperatures and whether these responses differ between natural and artificial nutrient regimes. We collected data from published laboratory studies reporting these life history traits for *Culex* mosquitoes at various temperatures, and under natural and artificial nutrient regimes. We then fit linear and nonlinear, unimodal models to the data for each trait and the corresponding subsets of nutrient categories to determine the best fit model. Our findings indicate that all three traits are temperature-dependent in unique, nonlinear ways, thus challenging the conventional population growth formulae that incorporate them statically. Our results reveal the need for more laboratory experiments to use natural nutrient regimes and to be conducted at thermal extremes for a better understanding of how these traits respond at critical thermal thresholds.

INTRODUCTION

The *Culex* genus is widely-distributed throughout the world and the adult *Culex* mosquitoes are known to vector illnesses such as West Nile Virus, posing a threat to human health. To better understand mosquito development, survival, reproduction, and disease transmission, scientists have explored the factors that may influence traits at different life history stages. The abiotic and biotic conditions of mosquito larval habitats have been the subjects of extensive research in particular because these rearing conditions can help or hinder development and these effects can then carry over into adulthood and influence broader population dynamics and disease transmission. Various studies have focused on the roles of conditions such as temperature (Bowler et al. 2008; Grech et al. 2015; Mordecai et al. 2013; Ragland and Kingsolver et al. 2008a, 2008b; Davies et al. 2016; Christiansen-Jucht et al. 2015), inter- and intraspecific competition (Alto et al. 2012; Bédhomme et al. 2005, Gardner et al. 2015), predation (Alto et al. 2005; Grigaltchik et al. 2016; Fischer et al. 2012; Silberbush et al. 2015), diet (Padmanabha et al. 2008a, 2008b; Yahouédo et al. 2014; Phelan et al. 2013; Yee and Skiff 2014), and pollution (Chaves et al. 2010; Kibuthu et al. 2016) in larval habitats and their effects on various life-history traits. However, many of these

conditions are interrelated and the responding life history traits may involve trade-offs, making the observed effects highly context-dependent.

Substantial evidence has been amassed indicating that thermal conditions and nutrition in the larval habitat, both of which fluctuate in natural environments, play a large role in mosquito development and, as a result, in overall adult fitness (Padmanabha et al. 2008a, 2008b; Davies et al. 2016; Dodson et al. 2011). Increased nutrient availability in larval environments has been shown to shorten development time and to increase larval survival and adult size (Phelan et al. 2013). These effects on adult size are important because there is a strong correlation between female body size and fecundity: the greater the adult body size, the greater the number of ovarioles (van den Heuvel 1963) and thus the greater amount of eggs the female is able to lay. Nutrient limitation has been observed to increase competition pressure, slow development rate, limit survivorship, decrease body size, and skew the population sex ratio (Alto et al. 2012; Lounibos and Escher 2008).

Similarly, the temperature at which larvae are reared has been noted to influence development and the rate at which it proceeds: lower mean temperatures contribute to slower development, and higher to faster (Ragland and Kingsolver 2008b). Higher temperature during the larval stage has been shown to lead to smaller larvae and adults (Christiansen-Jucht et al. 2015). Mosquitoes are ectotherms, meaning that they rely on the external environment for their body heat; their biological processes are therefore temperature-sensitive, having a critical maximum of around 40 °C (Neven 2000), after which protein denaturation occurs and mortality ensues. Temperature impacts life history traits during mosquito larval stages and beyond: the temperature at which adults were reared as larvae has been observed to affect the incubation period of their first egg lay (Christiansen-Jucht et al. 2015).

Furthermore, temperature and nutrition are seen as being interrelated: Phelan et al. (2013) recognized that as temperatures rise within a range, food requirements tend to increase along with development rate. Padmanabha and his team (2011a) have suggested that nutrient and thermal conditions in larval habitats work in tandem to affect the development process. Mosquito development, and thus mosquito survival and reproductive ability, is sensitive to a combination of nutrient and thermal conditions, each influencing the other.

In the literature review involved in this project, we noticed a division in the nutrient regimes used for laboratory experiments: most research teams used artificial nutrients such as Tetramin fish food (El-Sayed and El-Bassiony 2016) and rat chow (Smith et al. 1995) but others used natural nutrients such as detritus (Allgood and Yee 2014) and plant infusions (Gardner et al. 2015). Very few studies have investigated the effects of different nutrient types on larval development. We are interested in how the life history traits of larval development rate, egg-to-adult survival, and adult size of *Culex* mosquitoes respond across a range of temperature and whether there is a difference in thermal response based on the type of nutrient regime used. We conducted a statistical modeling project based on a meta-analysis of primary literature. We were able to visually demonstrate the temperature-sensitivity of these traits by fitting linear and nonlinear models to them. Each life history trait was fit with three models -- a linear fit, a quadratic curve, and a Briere curve -- and the best fit of the three was determined using statistical information and logic. The best model was then applied to each of the subsets of natural and artificial nutrient regimes for the life history trait.

We predicted that the natural nutrient regime, consisting of materials that mosquito larvae would be consuming and assimilating in most field environments, would lead to higher performance in each life history trait: a higher proportion of survival, faster rate of development, and greater body size. We expected the nonlinear Briere model to best fit survival and development rate data, as these types of traits have an optimal that, once surpassed, will lead to increased mortality. We predicted body size to have a linear relationship to temperature because it tends to decrease with an increase in temperature (Christiansen-Jucht et al. 2015).

METHODS

Data Collection

We collected data from a variety of laboratory studies that dealt with *Culex* larvae at a range of constant temperatures and that reported at least one of these life history traits of interest (larval development rate, proportion of survival to adulthood, and female adult body size as wing length) as well as the type of food provided to the larvae. Laboratory studies were used in order to control for the additional confounding variables that a field study could contain. A constant temperature was required because this was the manner by which we were able to create a plot with distinct values from various studies over a range of temperature.

We used the Metagear package in RStudio to narrow down the original literature search results to the more viable options (Lajeunesse 2016; Figure 1: 1A, 1B). DataThief III was then used to extract data that were graphically represented (Tummers 2006; Figure 1: 2A). Data from the research papers that fit our criteria were recorded directly in our publicly-accessible Google spreadsheet. Overall, ten species of the *Culex* genus were used in all of the papers we collected data from, the most data points being attributable to *Culex pipiens* and *Culex quinquefasciatus* (Figure 1: 1C). The data for both size and survival were used in their raw form; the data for the rate of development were transformed once they were collected. Specifically, the raw data for development rate were originally in the form of days until adulthood or pupation and we simply took the inverse of the number of days to get the rate of development (instead of time to development). These were the final values we plotted and fit models to for this trait.

We encountered some issues when it came to standardization of data: wing length was often reported as being a measurement taken from the alular notch to the distal margin excluding the fringe scales but occasionally the wing length values varied from this standard. We marked these inconsistencies accordingly on the spreadsheet so as to allow for them to be removed if they seemed to be biasing the data. Similarly, the data we collected for development rate were more or less split between time to pupation and time to adulthood, making these values difficult to standardize into one dataset for this life history trait. We decided to add 2 days to the “time to pupation” values to incorporate them into the “time to adulthood” data. After testing the dataset with and without these values, we decided to include them because they did not alter the best statistical model for the data, which remained the quadratic for each test.

Modeling

All modeling was done using RStudio. The data for each life history trait were plotted accordingly on three separate graphs and then three models were fitted to each (Figure 1: 3A). The models we fit to the data were a linear fit (Figure 1: 3B), a quadratic fit (Figure 1: 3C), and a Briere curve (Briere et al. 1999; Figure 1: 3D). We chose to use a linear fit because this model is conventionally used for life history traits though recently there have been calls for more nuanced models to accurately depict these temperature-dependent relationships (Mordecai et al. 2012); we wanted to compare the linear fit to the other, nonlinear models (Figure 1: 3B). The formula for the linear fit is $y = mx + b$. We employed the quadratic fit as one of the unimodal, nonlinear models so as to provide for the possibility that the life history traits could show a rise and a fall that are equidistant from the peak (Figure 1: 3C). The formula for the quadratic curve is $y = qx^2 + rx + s$. We used the Briere curve, which was proposed as a rate model of temperature-dependent development for arthropods (Briere et al. 1999), as the second unimodal, nonlinear model (Figure 1: 3D). The equation for this model is $y = CT(T - T_{min})(T_{max} - T)^{1/2}$ and is rooted in the quadratic formula but tweaked to account for temperature-dependence, which gives it the elongated left tail and the rapid drop-off after the peak. The Briere curve's x-intercepts represent the thermal minimum (T_{min}) and maximum (T_{max}). The "C" in the formula is a rate constant. This curve predicts an increase with temperature as the rate of biochemical processes increases, a peak at an optimal temperature at which these processes are functioning maximally, then a drop-off as temperature exceeds the optimum and the processes are compromised when proteins denature.

The best statistical fit for each life history trait was determined using the AIC (Akaike Information Criterion) values, which assess the relative quality of each model for the given dataset. The smaller the AIC value is, the better the fit. Once we determined the best fit model for a particular life history trait, we broke that plot down into the nutrient regime subsets, of which there could have been the artificial or natural nutrient regimes or a combination of the two. We then applied the model from the best fit for the overall trait to each of the nutrient regime subsets to visualize whether there was a difference between their thermal responses.

RESULTS

All of the life history traits showed variation across the temperature range, reinforcing that they are temperature-sensitive. All of the temperature-trait relationships were best fit by nonlinear, unimodal models; the linear model was never the best fit model for any of the life history traits.

We were unable to interpret the results of the different nutrient regime models due to data-deficiency. In two of the three life history trait datasets (survival and size) we were unable to fit the best model (a quadratic curve in both cases) to the natural nutrient regime because there weren't enough data and the few points that we did have plotted for the subset gave an upward concave curve. This model would not be reasonable because it essentially proposes that those larvae provided with a natural nutrient regime are experiencing one hundred percent survivorship at a low temperature, that the proportion then declines and reaches a minimum around where the optimal temperature range for many traits is suspected to be, and then rises and reaches one hundred percent survivorship again near the thermal maximum, where survival is actually compromised. Similarly, with adult body size, this would mean that the largest sizes, which are

desirable for females, would result at the thermal extremes though these thermal extremes cause physical stress and a higher temperature also leads to a faster development rate, which can result in a smaller body size. For these reasons, we exempted the quadratic fits to the natural nutrient data subset from the figures (Figure 6; Figure 8).

Rate of Development

The rate of development life history data were fit with all three models (Figure 2); the AIC values deemed the quadratic fit to be the best, followed by the Briere and finally the linear model (Table 1). However, we decided that the best fit for the rate of development was in fact the Briere curve because the quadratic curve is not reasonable in that it dramatically overshoots the thermal maximum. We are confident with this decision because the Briere and quadratic curve AIC values are comparable (Table 1) and Mordecai et al. (2012) determined that the best fit for the rate of development for *Anopheles* mosquitoes was a Briere curve. We also see that if the Briere curve is allowed a higher T_{\max} (at 44 °C instead of 40 °C), it becomes the best statistical fit (Figure 3). The development rate data for the two nutrient categories were each fitted with a Briere curve, the natural having the higher mean development rate at the optimal temperature (Figure 4).

Larval Survival

The life history trait of larval survival to adulthood was fit with all three models (Figure 4), of which the quadratic curve was the best statistical fit according to the AIC values (Table 1). The Briere curve was the second best fit and the linear the third. The proportion of survival is thus seen as increasing after its posited thermal minimum, around 5 °C, until reaching a peak that spans from around 30-40 °C, and then decreasing back down to total mortality around its thermal maximum, which is depicted as being around 43 °C here. This result is supported by another study: Mordecai et al. (2012) also found the quadratic fit to be the best for survival across a range of temperature for the *Anopheles* genus.

We were unable to fit quadratic curves to the natural and combination nutrient regime subsets due to data-deficiency, but we were able to plot a reasonable quadratic curve for the artificial nutrient regime subset (Figure 5).

Adult Size

Adult body size (as proxied by wing length) was fit by all three models, the best fit being the quadratic followed by the linear and finally the Briere curve (Table 1; Figure 6). We were unable to fit a quadratic curve to the natural nutrient subset due to data-deficiency. The artificial nutrient regime, however, fits a quadratic curve well (Figure 7).

DISCUSSION

The rate of development data being best fit by a Briere curve seems biologically reasonable because an increase in temperature (within a range in which survival is viable) generally leads to an increase in the rates at which biological processes are able to proceed, leading to a gradual rise in rates along with the

rise in temperature. These processes, including larval development, would thus take place at a faster and faster rate along the range of temperature until they were functioning as efficiently as possible at an optimal range of temperature. After this range of temperature was surpassed, however, these essential biological processes would be compromised as animal proteins denature, leading to the drop-off that can be seen with the Briere curve (Figure 2). We see that the Briere curve also becomes the statistical best fit once its upper parameter, the T_{MAX} , has been increased, suggesting that the statistical ambiguity is taking place at this end of the temperature range and that more data near the suspected T_{MAX} would strengthen the model and make the results less ambiguous (Figure 3).

The quadratic curve was determined to be the best fit for the larval survival to adulthood data, both statistically and logically because the areas where it intercepts the x axis (indicating no survival at those temperatures) are close to the estimated thermal minimum and maximum (Figure 5). We had originally predicted the Briere curve to be the best fit for larval survival, meaning that larval survivorship would slowly increase until it reached its optimum at a certain temperature and quickly drop back down to total mortality after the optimum temperature was surpassed. However, the quadratic curve offers a more apt explanation because as soon as the larvae are within a certain temperature range where biological processes are able to proceed, no matter the rate, there will indeed be larval survival. The highest survival rates will occur at the optimal temperature, where these processes are being facilitated, but it is reasonable that this trait would be less susceptible to changes in temperature (within a hospitable range) than development rate and other traits that could be better described using a Briere curve.

The quadratic curve fit to the artificial subset of the larval survival data seems reasonable: the second quadratic intercept at the higher temperatures meets the x-axis right around where the estimated thermal maximum is located (Figure 6). This serves as a reiteration of how well this model fits this life history trait.

The adult size data were best fit by the quadratic curve (Figure 7). We know that wing length will never actually have a value of 0 before the thermal maximum because, as long as development and survival are being facilitated, the emerging adults will have some quantifiable form of wings. We can then understand why the Briere curve, which drops to 0 before the thermal maximum, does not fit these data well and is the worst statistical model for this trait according to the AIC values (Table 1). We had originally expected the best fit for adult body size to be the linear model because of the established relationship between temperature, development, and size: adult body size tends to decrease along with an increase in temperature (Christiansen-Jucht et al. 2015; Padmanabha et al. 2011b; Phelan et al. 2013; Mohammed and Chadee 2011; Grech et al. 2015; Mordecai et al. 2013) since higher temperatures speed up biochemical processes, leading to a shorter development time (and thus less time to assimilate nutrients and dedicate energy and matter to physical growth), which results in a smaller adult body size. The quadratic fit, however, seems to offer a reasonable, nuanced biological explanation for the size-temperature relationship that accounts for both the stress that the thermal extremes induce (the linear does not).

This relationship can also be visualized in the artificial nutrient subset plot for adult body size, which is fitted with a quadratic curve. Each end slopes downwards after the peak, which is around 10-20 °C, but we see that the lowest projected value within the viable temperature range is located at the thermal

maximum. This projected outcome seems reasonable due to a combination of the stress induced at thermal extremes and the smaller body size associated with faster development rate at these higher temperatures.

By nature of the meta-analysis approach of this project, we were able to better understand not just these *Culex* life history traits but how laboratory experiments dealing with this subject are commonly conducted and how they could be improved. For example, reporting raw data and standardizing data such as how wing length is measured and whether survival is until pupation or adulthood is essential in sharing information and making results available for future meta-analyses.

In addition, we are able to see that there are simply not enough data at the thermal extremes (Figure 9), making a comprehensive understanding of how these traits behave across a full range of temperature nearly impossible. This data-deficiency can lead to statistical ambiguity and make fitting a proper model much more difficult as it did for our development rate dataset, which only had 5 data points past 30 °C, thus obfuscating exactly how development rate can respond at higher temperatures (Figure 2; Figure 3). Our models would have been strengthened by more data at these extremes. More laboratory experiments need to include larval rearing temperatures at the thermal minimum and maximum.

In terms of further data-deficiency, it is also evident that artificial nutrient regimes are much more commonly provided to *Culex* larvae than natural nutrient regimes. This results in the data-deficiency and subsequent statistical ambiguity seen in the natural nutrient subsets for the life history traits (Figure 6; Figure 8). In almost exclusively employing artificial nutrient regimes in laboratory experiments, we could be overlooking how mosquitoes are actually developing in the field with naturally-occurring nutrient conditions. It is unclear whether or not there is a significant difference in the effects of each nutrient regime on different life history traits because not enough studies have used the natural regime.

As it is, collecting data from such a wide range of research papers that all together contain many confounding variables means that the patterns we do see can be quite striking. *Culex* larval development rate, survival, and body size are all temperature-dependent in unique ways. Each trait shows nonlinear, unimodal temperature-dependence, thus supporting other studies that have observed similar patterns (Mordecai et al. 2012) and challenging conventional linear models that simplify and overlook the nuance involved in these relationships.

This is also relevant in terms of population growth rate formulae and the tendency to incorporate such traits statically. The formula for the estimation of per capita rate of change in reproductive cohorts (Livdahl and Sugihara 1984) does not incorporate any temperature sensitivity:

$$r = \frac{\ln \frac{1}{N_0} \sum A_x f(\bar{w}_x)}{D + \frac{\sum x A_x f(\bar{w}_x)}{\sum A_x f(\bar{w}_x)}}$$

In other words, if r (the intrinsic growth rate of the population that this formula aims to estimate) were plotted against temperature, the relationship would be a flat line without any increase or decrease in its

projected values as temperature increases along the x axis. As we see, however, traits such as body size (which is related to fecundity, or f as seen in the formula) that are regularly incorporated, vary across a range of temperature and should thus be treated accordingly in order to make the output as accurate as possible. Studies have continually supported that temperature substantially influences life history traits and population dynamics (Christiansen-Jucht et al. 2015; Davies and Lyons 2016; Mordecai et al. 2013; Padmanabha et al. 2011a, 2011b; Ragland and Kingsolver 2008a, 2008b). Temperatures are projected to rise and mosquito life history traits will be affected by this change, which will in turn impact mosquito and vector-borne disease prevalence and distribution. Additionally, disease transmission factors such as human biting rate and vector competence are likely to shift in a changing environment (Lima et al. 2017). More realistic and nuanced temperature-sensitive models of population growth rate need to be created, especially in the context of global climate change, in order to achieve a better understanding of these intricately connected moving parts on individual, population, and global levels.

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APPENDIX

TABLE 1. Model strength for each of the life history traits. Equations for each model are listed in the text. Tests for the significance of the Briere models still need to be conducted (currently blank).

Life History Trait	Model Type	Parameters	AIC	Significance
Rate of development (per day)	Linear	m = 0.003 b = 0.007	-728.366	P-value: 6.62e-12 R-squared: 0.251
	Quadratic	q = -0.122 r = 0.247 s = 0.075	-741.497	P-value: 3.716e-14 R-squared: 0.316
	Briere	C = 2.229e-05 T ₀ = 5.102 T _M = 40.000	-739.367	
Larval survival (until adulthood)	Linear	m = 0.002 b = 0.474	111.154	P-value: 0.726 R-squared: 0.00059
	Quadratic	q = -1.128 r = 0.617 s = 0.510	107.170	P-value: 0.049 R-squared: 0.029
	Briere	C = 1.230e-04 T ₀ = 0.000 T _M = 39.300	109.617	

TABLE 1 - continued

Life History Trait	Model Type	Parameters	AIC	Significance
Adult size (wing length)	Linear	$m = 4.471$; $b = -0.039$	127.815	P-value: $8.124e-06$ R-squared: 0.157
	Quadratic	$q = -2.743$ $r = -2.792$ $s = 3.410$	123.178	P-value: $1.954e-06$ R-squared: 0.203
	Briere	$C = 0.001$ $T_0 = 0.000$ $T_M = 36.451$	236.617	

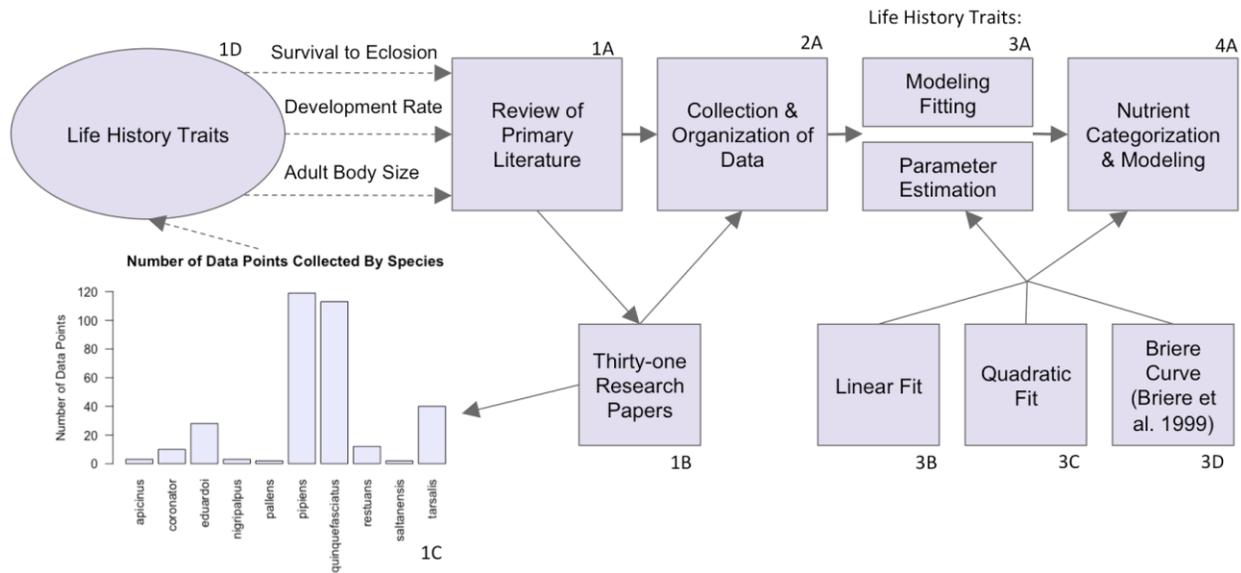


FIGURE 1. Methods Flowchart describing the meta-analysis and modeling processes. 1A depicts the initial review of primary literature, of which there were thirty-one research papers we collected and used data from (1B). 1C is a bar plot of the species that were profiled in the papers. The life history traits in 1D are those that belong to the species in 1C and that are observed and quantified in the literature in 1A. 2A shows the collection and organization process that took place on a Google spreadsheet. Statistical modeling took place in 3A and 4A, dealing first with overall life history traits then nutrient category subsets, respectively. The three models used in this process are as seen in 3B, 3C, and 3D.

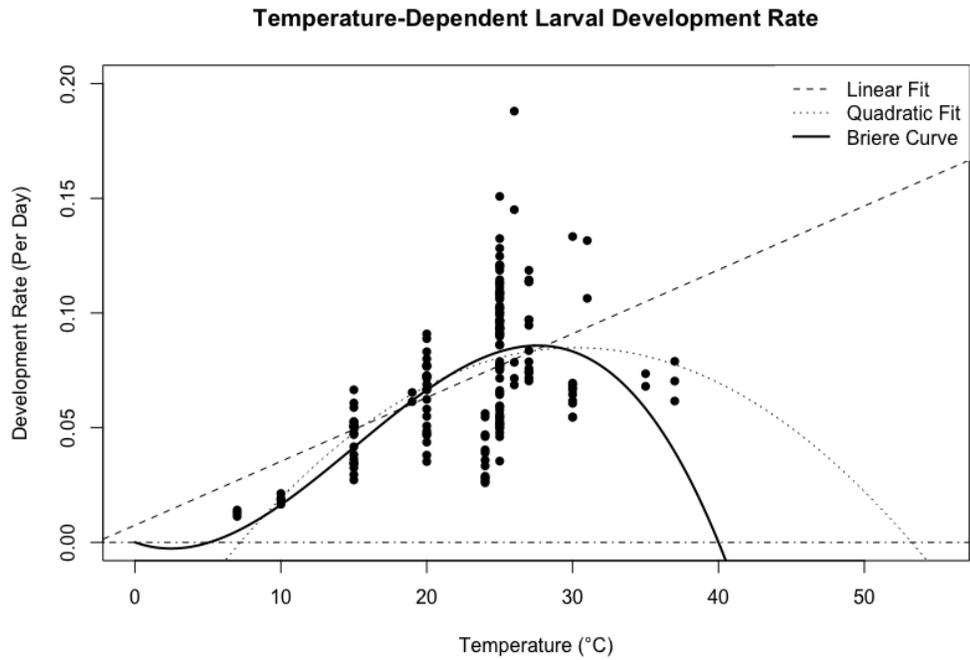


FIGURE 2. Temperature-Dependent Larval Development Rate

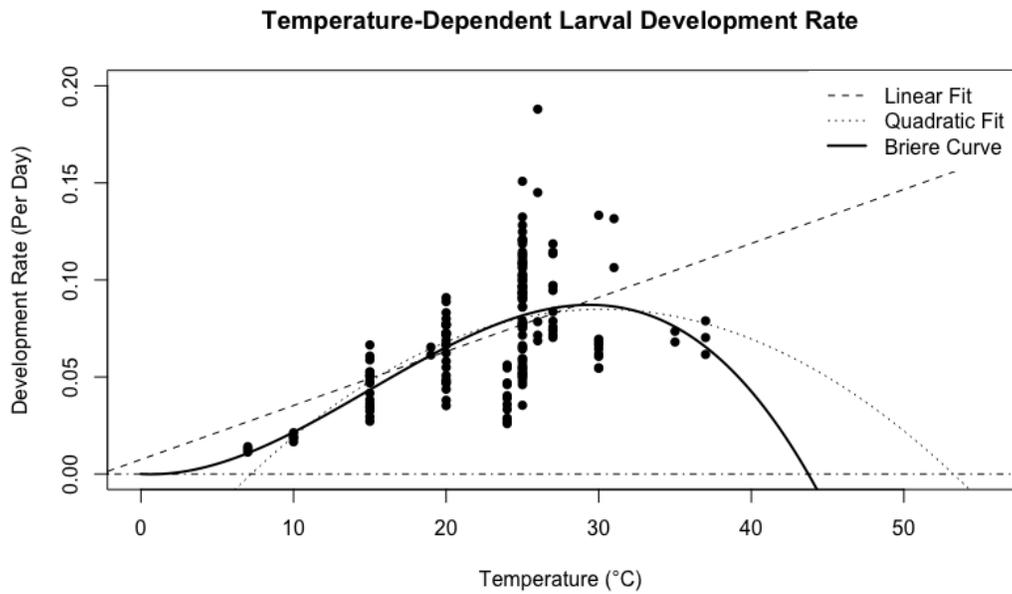


FIGURE 3. Temperature-Dependent Larval Development Rate with an Altered T_{max} (44 instead of 40 °C) for the Briere Curve. This tweak in the thermal maximum value for the Briere curve makes it the best statistical model according to the AIC values (of which the Briere is -744.672, the quadratic is -741.497, and the linear is -728.366).

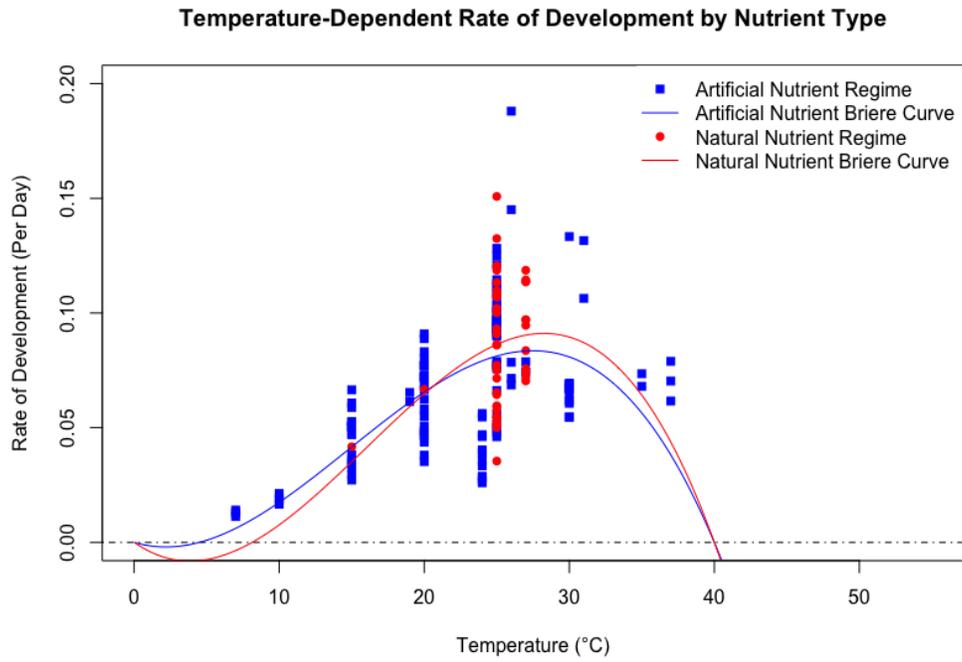


FIGURE 4. Temperature-Dependent Larval Development Rate by Nutrient Type

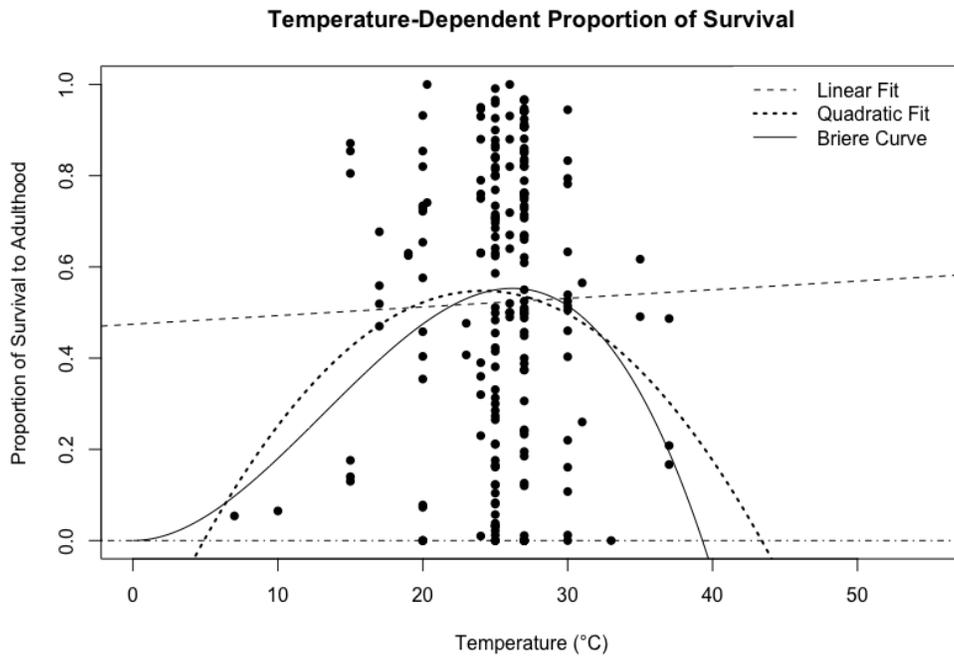


FIGURE 5. Temperature-Dependent Proportion of Survival

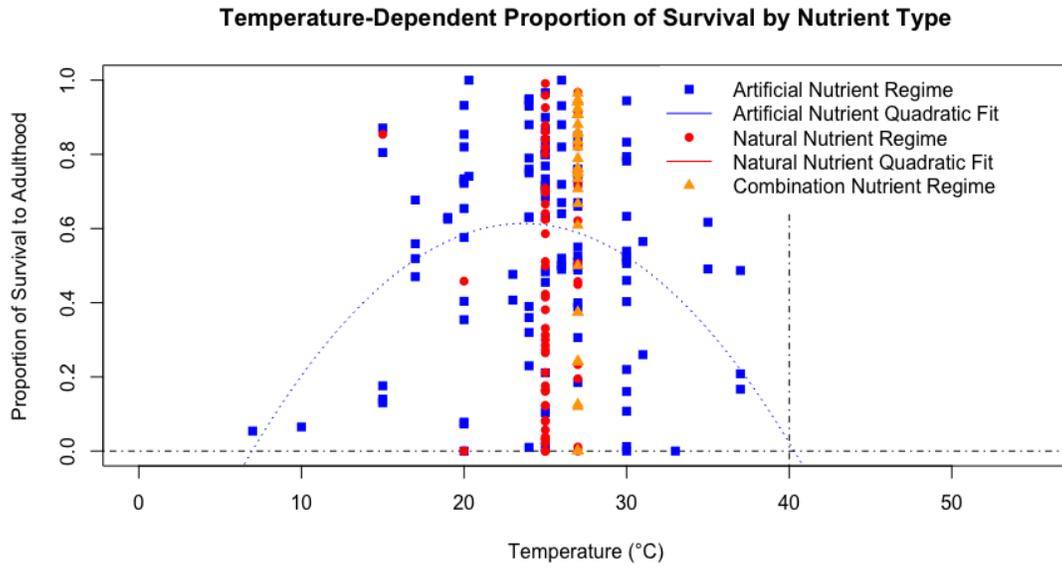


FIGURE 6. Temperature-Dependent Proportion of Survival by Nutrient Type. The dashed and dotted line at the 40 °C mark represents the thermal maximum.

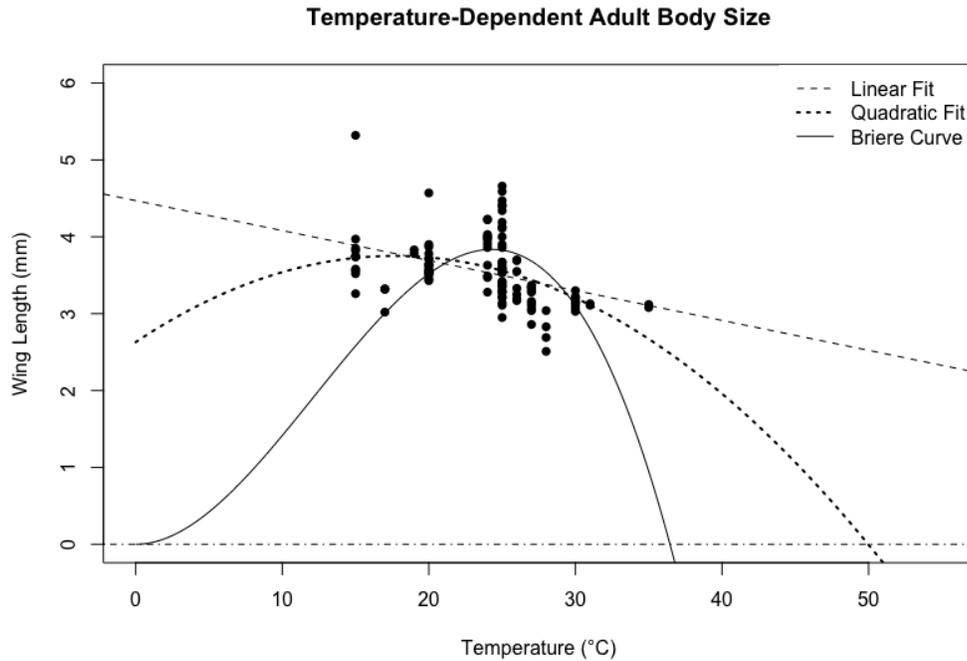


FIGURE 7. Temperature-Dependent Adult Body Size

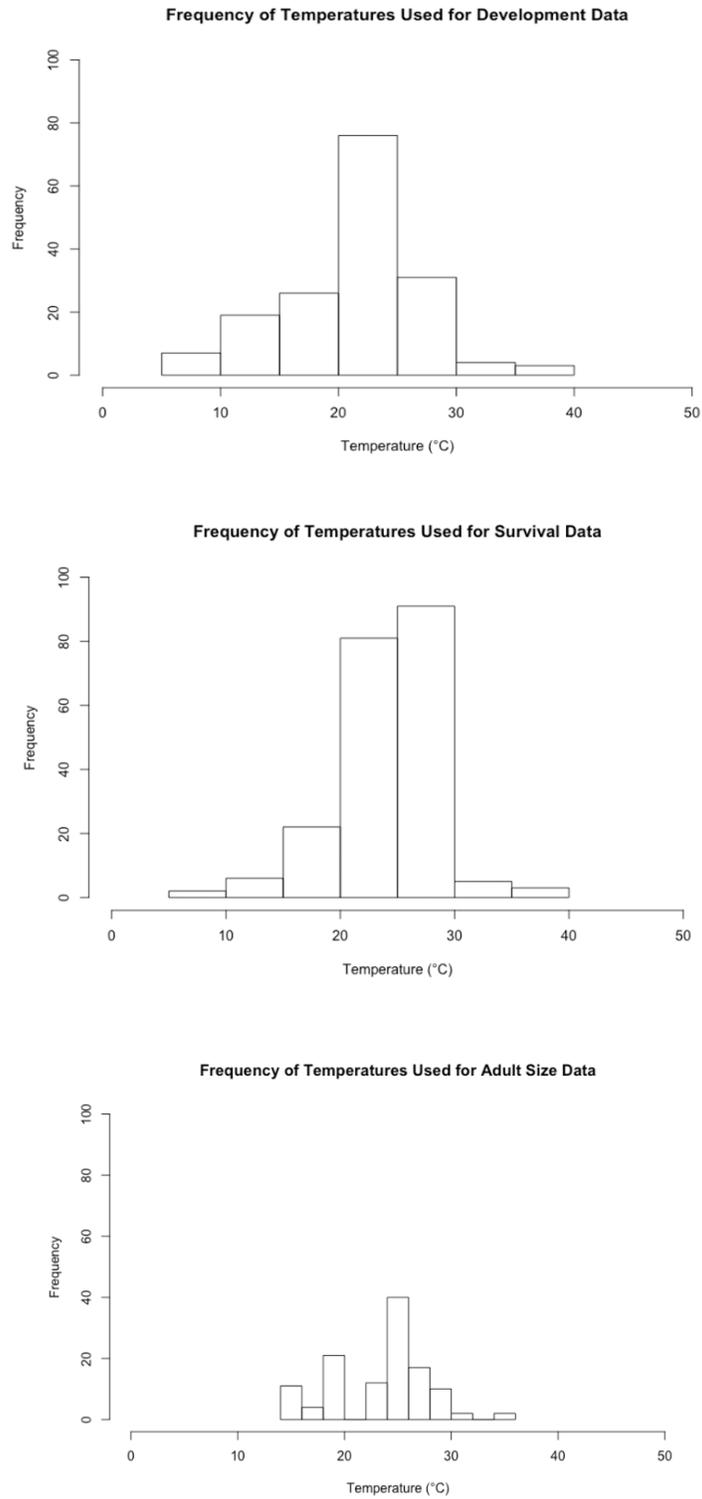


FIGURE 9. Barplots for the frequency of temperatures used for each life history trait, demonstrating the data-deficiency at the thermal extremes.