Title: The effect of resource limitation on the temperature dependence of mosquito population fitness

Data accessibility statement:

Data will be made publicly available at publication from the Dryad Digital Repository.

ABSTRACT

1. Laboratory-derived temperature-dependencies of life history traits are increasingly being used to make mechanistic predictions for how climatic warming will affect the abundance of disease vectors. These laboratory data are typically from populations reared on optimal resource supply, even though natural populations are expected to experience fluctuations in resource availability.
2. Using laboratory experiments and stage-structured population projection modelling, here we ask how resource limitation affects temperature-dependence of life history traits and emergent fitness of a principal arbovirus vector, *Aedes aegypti*, across a temperature range it typically experiences (22–32°C).
3. We show that low-resource supply significantly depresses the vector's maximal population growth rate (r_{max}) across the entire temperature range and causes it to peak at a lower temperature, than under high-resource supply. This difference is driven by the fact that resource limitation significantly increases juvenile mortality, slows development, and reduces lifespan and size at maturity (which then decreases fecundity in adults). These results show that resource supply can significantly affect the temperature-dependence of population-level fitness of disease vectors by modifying the thermal responses of underlying traits.
4. Our study suggests that by ignoring resource limitation, projections of vector abundance and disease transmission based on laboratory studies are likely to substantially underestimate the effect of temperature on development time and juvenile survival, and overestimate the effect of temperature on lifespan, size and fecundity.
5. Our results provide compelling evidence for future studies to consider resource supply when making predictions about the effects of climate and habitat change on disease vectors. More generally, our results point at the need to consider the effects of resource limitation on temperature-dependence of life history traits to further advance Ecological Metabolic Theory and improve its utility for predicting the responses of holometabolous insects to climate change.

KEY WORDS: climatic warming, Ecological Metabolic Theory, environmental temperature, population-level fitness, population projection matrices, resource limitation, size-temperature rule, vector-borne disease

INTRODUCTION

The global public health burden of some vector-borne diseases has increased substantially in recent decades (Stanaway et al. 2016, World Health Organization 2014). The geographical distribution and abundance of vectors is strongly linked to transmission patterns of these diseases (Li et al. 2019, Ng et al. 2018). Climate and land-use change, coupled with rapid globalization, are thought to have contributed to shifts in both the distributions of vector species and the diseases they transmit (Brown, Medlock & Murray 2013, Kraemer et al. 2019, Lambin et al. 2010, Wilder-Smith & Gubler 2008). However, mechanistic models that account for how fundamental environmental drivers (temperature, rainfall and resource supply) may independently and interactively affect population-level vector fitness are largely absent (Mordecai et al. 2019).

Ecological Metabolic Theory (EMT) links body size and environmental temperature through metabolic rate to individual-level trait performance and population-level fitness (Brown et al., 2004, Savage et al. 2004). For example, within an ectotherm's operational thermal range, biological rates (e.g. metabolic, development, mortality) increase approximately exponentially with temperature to affect population growth in a similar way (Gillooly et al. 2001, Gillooly, Charnov & West 2002, Savage et al. 2004). While this core EMT prediction is well-supported, it has not yet been tested across varying levels of resource supply. This is because EMT models linking metabolic rates to population-level fitness assume that resource supply is not a limiting factor (Savage et al. 2004).

Temperature and resource supply may interact to significantly affect fitness and its component traits, because the energy cost of somatic maintenance, development and growth generally increases with temperature (Kooijman, 1988, 2000; Marshall et al. 2020). The ability to meet this increasing demand is influenced by resource supply from an individual's environment. If the resources available to an individual do not keep pace with these increasing maintenance and growth requirements, its growth, development, and survival should be compromised. Ultimately, these effects should negatively affect fitness, and the severity of these effects should increase with temperature.

The thermal responses of individual traits have been used extensively in the rapidly expanding body of research on the responses of disease transmission rates to climate change (Bhatt et al. 2013, Iwamura, Guzman-holst & Murray 2020, Mordecai et al. 2013, 2017; Parham & Michael 2010). The classical EMT framework has recently provided important

contributions in this area (Kirk et al. 2018, 2019; Molnár et al. 2013), including vector-borne diseases (Mordecai et al. 2013, 2017). However, despite the potential importance of resource supply, very little is known about how it interacts with temperature to influence vector demographics and transmission capacity (Mordecai et al. 2019). For example, recently, Mordecai et al. (2013, 2017; Ryan et al. 2019) used a EMT trait-based framework to predict the temperature dependence of R_0, but all the parameterisations for the temperature dependence of component traits come from mosquitoes provided with optimal food quantities. Thus, the question of whether and how temperature and resource supply may together modulate disease transmission through underlying traits remains open.

Additionally, temperature indirectly affects ectotherm fitness by determining size at maturity. Generally, size at maturity decreases with rising temperature (the size-temperature rule, Atkinson, 1994; Pettersen et al. 2019), which also applies to disease vectors, such as mosquitoes (Rueda et al. 1990). For vectors specifically, female size is demographically and epidemiologically important because it is associated with longevity, fecundity, and biting behaviour. For example, individuals reared at warmer temperatures emerge earlier and are smaller, shorter-living and less fecund than conspecifics reared at cooler temperatures (Costanzo et al. 2018, Rueda et al. 1990). Reduced development time, due to increased temperature, can increase fitness, but cooler temperatures yield larger, more fecund and longer-living females, which are all traits that generally increase fitness (Birch 1948, Costanzo et al. 2018, Livdahl & Sugihara 1984). Furthermore, since larger females live longer, they are more likely to outlive a pathogen's external incubation period, and hence have greater transmission potential than smaller individuals (Clements & Paterson 1981). However, smaller females may bite more frequently, which can increase transmission probability (Scott et al. 2000). All these lines of evidence underline the importance of understanding the governing physiological mechanism(s) of the size-temperature rule and determining how it relates to mosquito fitness and disease transmission. However, it remains largely untested under resource limitation (Atkinson 1994, Forster et al. 2012).

Studies on the effects of resource availability on mosquito traits generally report a positive association between food level and immature development and survival (Agnew et al. 2002, Couret et al. 2014, Romeo Aznar et al. 2018), as well as adult body size, nutritional reserves and fecundity (Briegel 1990, Colless & Chellapah 1960, Steinwascher 1982). Many studies have examined how resource quantity effects fitness in interaction with larval density, as competition for limited resources between larvae is generally believed to be a major regulator

of adult mosquito abundance (Dye 1982, 1984; Gilpin & McClelland 1979, Southwood et al. 1972). However, studies on the effects of resource supply on fitness have not generally included temperature.

Given that wild mosquitoes are likely to experience variations of temperature and resource availability (Arrivillaga & Barrera 2004, Barrera, Amador & Clark 2006, Walsh et al. 2011), measuring the effects of both variables directly is important for predicting their population dynamics. In this study, we investigated whether and how fitness and its component traits are affected by the interaction between realistic temperature and resource supply variation and interactions between these two factors in *Aedes aegypti*; a principal mosquito vector of human arboviruses (e.g. dengue, yellow fever and zika; Brady & Hay 2020). We show that these factors can both, act alone, and interact to significantly modify the responses of body size, life history traits and fitness to temperature.

METHODS

To investigate the effects of temperature and resource supply on mosquito life history, we employed a 3 × 2 factorial design comprised of three temperatures (22, 26, and 32°C) and two resource supply levels: 0.1 (low-resource supply) and 1 mg/larva/day (high-resource supply). These experimental temperatures span the range of average annual temperatures that this strain of *Ae. aegypti* is likely to experience in the wild (Fort Meyer, FL; Arguez et al. 2012). This particular low-resource supply level was chosen because previous work has demonstrated that it is the lowest resource limitation that can be applied to this species without resulting in almost complete juvenile mortality; a level of limitation often experienced by wild populations (Barrera et al. 2006, Arrivillaga & Barrera 2004). The high-resource supply level corresponds to the upper mid-range of the high resource supply levels used in Arrivillaga & Barrera (2004) and Barrera et al. (2006), and is consistent with the levels of resource supply commonly used in laboratory studies on this species (Couret et al. 2014, Rueda et al. 1990).

Batches of approximately 300 *Ae. aegypti* (F16-19) eggs were randomly assigned to one of the three experimental temperatures and immersed in plastic tubs containing 150 ml of tap water. Each tub was provided with a pinch of powdered fish food (Cichlid Gold®, Hikari, Kyrin Food Industries Ltd., Japan) to stimulate overnight hatching. The tubs were then submerged in water baths (Grant Instruments: JAB Academy) set at either 22, 26, or 32°C. Water baths were situated in a 20°C climate-controlled insectary with a 12L:12D photoperiod

and 30 minutes of gradual transition of light levels to simulate sunrise and sunset. On the following day, first instar larvae were separated into cohorts of 30 and held in tubs containing 150 ml of water. We created three replicate tubs per treatment (90 individuals/treatment). Low-resource supply treatments were provided 3 mg of powdered fish food and high-resource supply treatments received 30 mg. Thereafter, resource levels were adjusted daily according to the number of living individuals in each tub prior to feeding each day such that resource levels were maintained at an approximately constant level during the juvenile lifespan. Water volumes were also adjusted daily in accordance with mortality to maintain larval density (0.2 larvae × ml^{-1}).

Fitness calculation

To calculate population-level fitness, we used our data to parameterise age-structured (Leslie) population projection matrices (Caswell 1989), which describe change in a population over time:

$$\mathbf{N}_{t+1} = \mathbf{A}\mathbf{N}_t, \qquad (1)$$

where $\mathbf{N}_t$ is a vector of the age structure at time t and $\mathbf{A}$ is the population projection matrix. The first row of elements in $\mathbf{A}$ is populated with fecundity data. Fecundity is the number of female offspring produced per female at age i. The sub-diagonal of $\mathbf{A}$ is populated with the probability of survival from age i to age $i + 1$. Multiplying the transition matrix ($\mathbf{A}$; eqn. 1) and age-structured population size vector ($\mathbf{N}_t$; eqn. 1) sequentially across time intervals yields population dynamics. Once the stable age (stage) distribution of the abundance vector is reached, the dominant eigenvalue of the system is the finite population rate of increase (λ) (Caswell 1989). Then, the intrinsic rate of population growth,

$$r_{\max} = \log(\lambda).$$

This is a population's inherent capacity to reproduce, and therefore a measure of population-level fitness (Birch 1948, Cole 1954, Savage et al. 2004). Negative $r_{\max}$ values indicate decline and positive ones, growth. The projection matrices were built and analysed using the `popbio` R package (R Core Team 2018, Stubben & Milligan 2007).

Parameterisation

Immature development time and immature and adult survival probabilities

Matrix survival elements (the sub-diagonal of the matrix **A**; eqn. 1) were populated with continuous survival probabilities derived from the Kaplan-Meier survival function in the `survival` R package (Therneau 2020, R Core Team 2018). We assumed life stage duration (i.e. larva-to-pupa-to-adult) was the mean duration of transitioning into and out of that stage, and a fixed age of adult emergence at the mean age of emergence. Adult survival elements were populated with the Kaplan-Meier probabilities. Hatching-to-adult development times were calculated by recording the day and time that egg eclosion, pupation and adult emergence occurred for each individual. Upon pupation, mosquitoes were held in individual falcon tubes containing 5ml of tap water. This enabled pupa-to-adult development durations and the lifespans of individual starved adults to be recorded. In the absence of food, this condition forces adults to metabolise the nutritional reserves accumulated during larval development. Therefore, starved adult lifespan is a useful indicator of the carry over effects of temperature and resource availability in the larval habitat (Agnew et al. 2002, Briegel 1990).

Fecundity (the first row of **A**; eqn. 1)

As a proxy for body size, wing length (L in eqn. 3) was measured to the nearest 0.01 mm from the alula to the wing tip, excluding the apical fringe (van Handel & Day 1989). Wings (one per female) were removed, mounted onto glass slides, photographed using a dissecting microscope and then measured with ImageJ software (Schneider et al. 2012). Body size was estimated from these wing lengths using the equation (R^2 = 0.92; n = 75, p<0.001; Nasci 1990):

$$M = -0.140 + 0.029L^3 \quad (3)$$

Here, M is dry mass (mg) at emergence and L is wing length (mm).

An allometric relationship (R^2 = 0.46; n = 57, p<0.001; Colless & Chellapah 1960) was then used to estimate lifetime fecundity (F) from M:

$$\log(F) = 4.24 + 0.99 \log(M) \quad (4)$$

The Colless and Chellapah (1960) data are from mosquitoes reared at 26ºC, so mass-dependent fecundity (F) was corrected to each of our experimental temperatures (F_{T_j}'s, with

the index j ranging over the set of our experimental temperatures) using the equation (Gillooly et al. 2001, Dell et al. 2011):

$$F_{T_j} = e^{4.24} M^{0.99} e^{-\frac{E}{k}\left[\frac{1}{T_j} - \frac{1}{299.15}\right]}. \quad (5)$$

Here, the scaling constant ($e^{4.24}$), and exponent (0.99) are from eqn. 4, E is the average activation energy of heterotrophic respiration in eukaryotes (0.65 eV), k is Boltzmann's constant (8.62 x 10^{-5} eV K^{-1}), 299.15 (26ºC) is the reference temperature in Kelvin (the temperature at which the original study was conducted; Colless & Chellapah 1960), and T_j (also in Kelvin) is the jth experimental temperature the rate is standardised to. Each F_{T_j} was then multiplied by 0.5 (assuming a 1:1 male-to-female offspring ratio) and divided by lifespan to obtain the temperature-specific individual daily fecundity.

Parameter sensitivity

We used the delta method to approximate 95% confidence intervals (CIs) for our fitness calculations (Bowles et al. 2015, Caswell 1989, Skalski et al. 2007) to account for how uncertainty in survival and fecundity estimates is propagated through to the r_{max} estimate. This method requires the standard errors of the survival and fecundity element estimates. For survival, we used the standard errors estimated by the Kaplan-Meier survival function. For fecundity, we used the standard errors of the mean daily egg production rates for each treatment. However, since the R^2 for eqn. 4 is low (0.46), as an additional sensitivity analysis, we also calculated fitness using the upper and lower 95% CI's of the exponent (0.99 ± 0.28; eqn. 4) for the scaling of lifetime fecundity with mass.

Elasticity analysis

Elasticities were used to quantify the proportional contributions of individual life history traits to r_{max}. Elasticity, e_{ij}, measures the proportional effect on λ of an infinitesimal change in an element of **A** (eqn. 1) with all other elements held constant (the partial derivative) (Caswell et al. 1984, de Kroon et al. 1986). This partial derivative of λ with respect to each element of **A** is, $s_{ij} = \partial\lambda/\partial a_{ij} = v_i w_j$ with the dot product $\langle \mathbf{w}, \mathbf{v} \rangle = 1$. Here, **w** is the dominant right eigenvector (the stage distribution vector of **A**), **v** is the dominant left eigenvector (the reproductive value vector of **A**), and a_{ij} is the $i \times j^{th}$ element of **A**. Elasticities can then be calculated using the relationship: $e_{ij} = a_{ij}/\lambda \times s_{ij}$. Multiplying an elasticity by λ gives the absolute contribution of its corresponding a_{ij} to λ (Caswell 1986, de Kroon et al. 1986).

Absolute contributions for juvenile survival and fecundity elements were summed and changed proportionally to quantify the sensitivity of r_{max} to these traits.

Statistical analyses

All analyses were conducted using R (R Core Team 2018). In the first instance, to assess how temperature, resource supply, their interaction (whether low-resource supply treatments exhibited different thermal responses) and replicate influenced trait performance we fitted linear regression models. Model diagnostics and Shapiro-Wilk (1965) normality tests were used to assess data normality. Data for development, juvenile mortality rate, lifespan, wing length and fecundity were nonlinear, positive and right skewed. Therefore, for these traits we used full factorial generalized linear models (GLM) with gamma distributions and identity link functions (predictor effects were considered additive) to determine the significance of each predictor on the thermal response of each of these traits. Count data for cumulative juvenile mortality were modeled using a Poisson GLM.

The best model in each case was obtained by dropping terms from the full model (consisting of the trait its fixed effect predictors) sequentially using the Akaike Information Criterion (AIC). Goodness-of-fit of the GLMs was assessed using model deviance/d.f. scores and model residuals.

RESULTS

Except for juvenile mortality rate, all trait responses varied significantly with temperature and resource supply, with a significant interaction between the two environmental variables (Table 1, Fig. 1). Thus, the realised effect of temperature on trait responses was consistently and significantly mediated by resource supply.

Development time varied significantly with the interaction between temperature and resource supply (ANOVA; $F_{2,0.75} = 24.40$, $p<0.001$; Table 1); whereas development time decreased both at warmer temperatures and under high-resource supply, the rate of decrease with temperature was greater under low-resource supply than under high-resource supply. Under low-resource supply, development time decreased by 15.48 days as temperatures increased from 22 to 32°C, whereas under high-resource supply, it decreased by 6.38 days across this range (Table 2, Fig. 1a).

Juvenile mortality rate significantly increased with temperature (ANOVA; $F_{1,\ 26.80} = 20.04$, $p<0.001$; Table 1) and resource supply ($F_{1,\ 7.19} = 7.19$, $p<0.05$). Mortality rate was higher

under high-resource supply than under low-resource supply, but the resource level gradients did not differ significantly (interaction: $F_{1,\ 0.47}$ = 0.35, p>0.61). Under high-resource supply mortality rate increased by 0.31 day^{-1} as temperatures increased from 22 to 32°C; whereas under low-resource supply it increased by 0.25 day^{-1} (Table 2, Fig 1b).

Cumulative juvenile mortality varied significantly with the interaction between temperature and resource supply (ANOVA; χ^2=26.39, p<0.001; Table 1). Under low-resource supply, cumulative mortality decreased as temperatures increased from 22 to 26°C and increased from 26 to 32°C (Fig. 1c). Under high-resource supply, it increased linearly with temperature.

Lifespan varied significantly with the interaction between temperature and resource supply (ANOVA; $F_{2,\ 2.51}$ = 15.34, p<0.001; Table 1). Although lifespan decreased both at warmer temperatures and under low-resource supply, the rate of decrease with temperature was greater under high-resource supply than under low-resource supply. High-resource supply lifespan decreased by 8.61 days, whereas low-resource supply lifespan decreased by 4.71 days as temperatures increased from 22 to 32°C (Table 2, Fig 1d).

The interaction between temperature and resource supply resulted in significant variation in size at maturity (wing length) between resource levels (ANOVA; $F_{1,0.03}$ = 4.50, p=0.01; Table 1). Size decreased both at warmer temperatures and under low-resource supply, though the rate of decrease with temperature was greater under high-resource supply than under low-resource supply. Under low-resource supply, length decreased by 0.37 mm as temperatures increased from 22 to 32°C, while under high-resource supply, length decreased by 0.54 mm (Table 2, Fig 1e).

Predicted fecundity varied significantly with the temperature × resource supply (ANOVA; $F_{2,\ 2.58}$ = 6.99, p<0.01; Table 1). However, only the variation between resource levels at 26°C was significant (Fig. 1f). Fecundity under high-resource supply increased by 7.75 eggs/female/day as temperatures increased from 22 to 32°C; whereas under low-resource supply it increased by 6.05 eggs/female/day (Table 2).

Population fitness (r_{max})

Resource limitation depressed r_{max} to negative values at all temperatures, with a unimodal relationship of r_{max} with temperature (Fig. 2, Table 2). Low-resource supply r_{max} increased from –0.11 at 22°C to –0.05 at 26°C and then decreased acutely to –0.40 at 32°C. In contrast,

under high-resource supply, r_{max} was always positive and increased monotonically with temperature from 0.13 at 22ºC to maximal growth (0.22) at 32ºC.

Elasticity analysis

Juvenile survival was the most important contributor to r_{max} (Fig. 3). For example, under low-resource supply at 32ºC, a 0.25 proportional increase in juvenile survival would halve the rate of decline from –0.40 to –0.20 (Fig. 3a). In contrast, for the same treatment, a proportional increase of the same magnitude for fecundity would increase r_{max} from –0.40 to –0.39 (Fig. 3b). This highlights how the temperature dependence of r_{max} derives mainly from how resource supply level impacts juvenile mortality and development, which determine the number of reproducing individuals and the timing of reproduction, respectively. Fecundity, on the other hand, has a relatively negligible effect on r_{max}, which suggests that the carry-over effect of reduced size at maturity on r_{max} is relatively weak.

DISCUSSION

Our results show that the temperature dependence of population-level fitness and its component life history traits can be significantly modulated by resource supply. When adult lifespan and juvenile development time were expressed as rates (adult mortality and juvenile development rate, respectively), all traits under high-resource supply met EMT expectations by being positive and increasing nonlinearly with temperature (Fig. 1a and d) (Dell et al. 2011). This result is consistent with previous studies that have used laboratory-derived trait responses to temperature to estimate *Ae. aegypti* fitness and R_0; these studies report similar responses of traits to our high-resource supply responses (e.g. Iwamura et al. 2020, Ryan et al. 2019). For example, in Mordecai et al. (2017), juvenile *Ae. aegypti* development rate increased from approximately 0.07 day^{-1} at 22ºC to 0.14 day^{-1} at 32ºC. In the present study, development rate (Fig. 1a, Table 2) increased by a similar margin (~0.08 to ~0.16 day^{-1}) across the same temperature range.

In contrast, under low-resource supply, although trait thermal responses qualitatively met EMT predictions, they deviated markedly from the results of previous laboratory experiments. For example, in the present study under low resource supply, juvenile development rate was ~0.03 day^{-1} at 22ºC, which is 57% less than the rate (~0.07 day^{-1}) used at this temperature in Mordecai et al. (2017) to predict R_0. Similarly, under low-resource supply at 32ºC, we found juvenile development rate was ~0.05 day^{-1}; whereas in Mordecai et al. (2017) it was 64% greater (~0.14 day^{-1}). Juvenile survival proportions under low-resource

supply also differed markedly from the high-resource supply proportions used in Mordecai et al. (2017). In the present study, survival was 0.51 at 22°C, 0.64 at 26°C and 0.22 at 32°C; whereas, in Mordecai et al. (2017) it was approximately 0.83 between 20-22°C, 0.76 at 25°C, and 0.77 between 30-34°C.

These differences between the temperature dependence of traits under low- versus high-resource supply resulted in a marked divergence of the temperature dependence of r_{max} (Fig. 2) between the two treatments, which was negative throughout and unimodal (declining steeply from 26 to 32°C) under low-resource supply, and positive and increasing under high-resource supply. This indicates that population fitness becomes increasingly constrained by resource limitation as temperatures increase. Although resource limitation decreased juvenile mortality rate (Fig. 1b), the elasticity analysis shows that the primary mechanism underlying this is increased cumulative juvenile mortality, which decreased population-level fertility and, ultimately, fitness (Figs. 1c and 3a). The effect of resource limitation on fitness was further compounded by the increase in juvenile development time (Fig. 1a), which delayed the onset of reproduction.

The effects of resource supply on adult traits (size at emergence, adult lifespan and fecundity) were weak compared to its effects on juvenile traits (Fig. 3). For example, under high-resource supply, adult lifespan and body size were higher at 32°C than at 26°C, yet fitness at 32°C was predicted to be 41% higher (Fig. 2). This is because high-resource supply and increased temperature minimised cumulative juvenile mortality and optimised development rate. This allowed faster recruitment at 32°C, leading to increased fitness as greater numbers of individuals could contribute to growth through reproductive output sooner than for other treatments. This finding is consistent with general studies of ectotherm fitness (Huey & Berrigan 2001), including mosquitoes (Dye 1984). Therefore, projections of vector abundance and disease transmission that assume high-resource supply are likely to underestimate the effect of temperature on development time and juvenile survival, and overestimate effects of temperature on lifespan and fecundity.

Cumulative juvenile mortality increased significantly with temperature, and it was generally greater under low-resource supply (Fig. 1c, Tables 1 and 2). This is probably because somatic maintenance cost increases as metabolic rate increases (Kooijman 1988, 2000); if the amount of resource available cannot satisfy basal requirements, mortality will increase. This explains

why the highest level of mortality occurred at 32°C and under low-resource supply, where the energy supply-demand deficit was likely largest.

Development time at both resource supply levels decreased non-linearly with temperature, though it decreased more steeply with temperature under low-resource supply than under high-resource supply (Table 1, Fig. 1a). Qualitatively, this result supports development cost theory, which posits that while metabolic rate increases approximately exponentially with temperature (Brown et al. 2004), development cost is expected to be U-shaped (Marshall et al. 2020), ultimately resulting in a U-shaped temperature dependence of development time. Although our temperature range was not wide enough to determine whether development time is U-shaped in *Ae. aegypti*, our results suggest the relationship is, at least, L-shaped. Development time was highest at 22°C for both resource supply levels. However, high-resource supply possibly minimised development cost at 22°C, which reduced high-resource supply development time (by 67%) relative to low-resource supply at this temperature. At both resource supply levels, the steepest declines in development time occurred as temperatures increased from 22 to 26°C, likely because this change in temperature increased metabolic rate at the cost of development (thus reducing development cost).

Size at emergence decreased significantly with temperature for both resource supply levels (Table 1, Fig. 1e), consistent with the size-temperature rule (Atkinson 1994, Pettersen et al. 2019). Resource supply drove significant intercept variation in the size-temperature relationship, which reflects how high-resource supply allowed larvae to accumulate greater energy reserves and grow to become larger adults than their less well-fed conspecifics that were exposed to the same temperature. Size decreased more steeply with temperature under high-resource supply than under low-resource supply. Wing length decreased by ~0.20 mm at both low- and high resource supply as temperatures increased from 22 to 26°C (Table 2). However, as temperatures increased from 26 to 32°C, wing length decreased by ~0.17 and ~0.34 mm under low- and high-resource supply, respectively. For size at emergence, the decline with temperature under high resource supply may reflect the optimal (or approaching optimal) attainable size at each temperature.

Like size at emergence, adult lifespan decreased more acutely with temperature under high-resource supply than under low-resource supply (Table 1, Fig. 1d). This derived from the difference in lifespan between resource supply levels at 22°C. As temperatures increased from 26 to 32°C, lifespans declined to a similar extent at both resource supply levels. Under

low-resource supply, lifespan decreased by ~3.69 days, whereas under high-resource supply it decreased by ~3.96 days (Table 2). However, as temperatures increased from 22 to 26ºC, lifespan decreased by ~1.02 days under low-resource supply and by ~4.65 days under high-resource supply. This relatively flatter decline under low-resource supply may reflect how larvae respond to cooler temperatures when resources are limited. Cooler temperatures prolong development by slowing underlying rate processes (Angilletta et al. 2004). These processes may have been slowed further by metabolic down-regulation in response to resource limitation, which is predicted to delay development, but increase survival, as individuals invest available energy in maintenance (Moore & Whitacre, 1972, Storey & Storey 1990). Under high-resource supply, lifespan declined linearly, which may reflect how higher levels of resource supply allow temperature to optimise trait responses. For lifespan, the decline with temperature under high resource supply may reflect the optimal (or approaching optimal) attainable lifespan at each temperature.

We did not measure the effect of temperature directly on fecundity but used the size-scaling of this trait to estimate this effect. This is because most of the effect of resource limitation on juveniles is expected to affect adult mosquitoes indirectly, by reducing size at emergence, with few direct carryover effects (Briegel 1990, Steinwascher 1982). Predicted fecundity increased nonlinearly with temperature, significantly mediated by resource supply levels (Fig 1f, Table 1). Across both resource levels, these predicted fecundity values are somewhat lower than those reported in past studies. For example, in Mordecai et al. (2017), *Ae. aegypti* fecundity increased from approximately 3.58 to 11.20 eggs/female/day as temperatures increased from 22 to 32ºC compared to an increase from 1.71 to 9.46 eggs/female/day under high-resource supply and 1.79 to 7.84 eggs/female/day under low supply, across the same temperature range. This difference likely arises from the fact that our size-scaling based predictions ignore additional effects on fecundity, such as adult food supply. However, even substantial underestimation of fecundity by our size-scaling predictions would not affect our main conclusions, because predicted fitness was relatively insensitive to this trait (Fig. 3b).

Although we have not considered the temperature dependence of resource supply itself (supply was held constant across temperatures in our experiments), in nature, the availability of resources may in fact be temperature-dependent. This is because microbial growth rates increase with temperature to some optimum, which may increase the concentration of food in the environment (Craine, Fierer, & McLauchlan 2010; Cross et al. 2015, Smith et al. 2019). For example, *Anopheles* (Chouaia et al. 2012) and *Aedes* (Souza et al. 2019) mosquitoes can

be reared exclusively on cultures of *Asaia* bacteria. The temperature dependence of resource supply is an interesting and potentially important avenue of investigation that would further elucidate how the interaction between temperature and resource availability affects the fitness of mosquitoes.

Organisms experience significant resource limitation over space and time in nature. This is particularly true for insects such as mosquitoes, which have juvenile stages restricted to small, ephemeral aquatic habitats that are susceptible to resource fluctuations (Arrivillaga & Barrera 2004, Barrera et al. 2006, Subra & Mouchet 1984, Walsh et al. 2011). Overall, our results provide compelling evidence for the importance of resource availability in larval habitats in *Ae. aegypti* and other mosquito vectors in mediating the effect of climatic warming on their population growth and therefore, disease transmission. More generally, considering the effect of resource availability is also likely to be important for further advancing Ecological Metabolic Theory, and improving its utility for understanding the responses of holometabolous insects to environmental change.

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Trait	Predictor	χ^2	df	*F* value	p-value
Cumulative juvenile mortality	**Temperature**	**131.54**	**2**	**-**	**<0.001 *****
R^2 = 0.54	**RS**	**7.92**	**1**	**-**	**<0.01 ****
	Temperature: RS	**26.39**	**2**	**-**	**<0.001 *****
Juvenile mortality rate	**Temperature**	**28.06**	**2**	**9.61**	**<0.001 *****
R^2 = 0.23	**RS**	**8.45**	**1**	**5.79**	**0.02 ***
	Temperature: RS	1.43	2	0.49	0.61
	Residuals	157.67	108		
Development time	**Temperature**	**9.78**	**2**	**319.08**	**<0.001 *****
R^2 = 0.96	**RS**	**50.43**	**1**	**3292.46**	**<0.001 *****
	Temperature: RS	**0.75**	**2**	**24.40**	**<0.001 *****
	Residuals	2.30	150		
Lifespan	**Temperature**	**34.23**	**2**	**209.76**	**<0.001 *****
R^2 = 0.73	**RS**	**2.83**	**1**	**34.57**	**<0.001 *****
	Temperature: RS	**2.51**	**2**	**15.34**	**<0.001 *****
	Residuals	12.30	150		
Body size	**Temperature**	**0.66**	**2**	**112.92**	**<0.001 *****
R^2 = 0.78	**RS**	**0.92**	**1**	**315.53**	**<0.001 *****
	Temperature: RS	**0.03**	**2**	**4.50**	**0.01 ***
	Residuals	0.42	143		
Fecundity rate	**Temperature**	**64.48**	**2**	**175.04**	**<0.001 *****
R^2 = 0.79	**RS**	**0.84**	**1**	**4.56**	**0.03 ***
	Temperature: RS	**2.58**	**2**	**6.99**	**<0.01 ****
	Residuals	26.34	143		

Table 1 | Type II Analysis of Variance results from GLMs fitted to the responses of life history traits to temperature and resource levels. Significant effects are shown in boldface type. * ⇒ p<0.05; ** ⇒ p<0.01; *** ⇒ p<0.001. Each pseudo R^2 (= residual deviance/null deviance) approximates how much variance the model was able to capture.

Trait	Temperature (ºC)	Mean ± 95% Confidence intervals	
		Low-resource supply	High-resource supply
Cumulative juvenile mortality (number of individuals)	22	10.60 ± 3.19	4.50 ± 2.05
	26	7.58 ± 3.21	11.40 ± 4.17
	32	22.13 ± 4.88	17.00 ± 2.48
Juvenile mortality rate (day^{-1})	22	0.10 ± 0.06	0.16 ± 0.08
	26	0.13 ± 0.13	0.33 ± 0.10
	32	0.34 ± 0.04	0.47 ± 0.04
Development time (days)	22	36.48 ± 1.24	12.19 ± 0.39
	26	27.86 ± 1.51	8.53 ± 0.25
	32	21.00 ± 4.73	5.81 ± 0.19
Lifespan (days)	22	6.61 ± 0.95	11.35 ± 0.69
	26	5.59 ± 0.70	6.70 ± 0.45
	32	1.90 ± 0.53	2.74 ± 0.39
Wing length (mm)	22	2.65 ± 0.10	3.13 ± 0.03
	26	2.45 ± 0.07	2.93 ± 0.04
	32	2.28 ± 0.10	2.59 ± 0.03
Fecundity (eggs/female/day)	22	1.79 ± 0.57	1.71 ± 0.11
	26	1.97 ± 0.24	3.16 ± 0.21
	32	7.84 ± 3.42	9.49 ± 2.01
Population-level fitness (r_{max})	22	–0.11 ± 0.02	0.13 ± 0.02
	26	–0.05 ± 0.03	0.15 ± 0.03
	32	–0.40 ± 0.05	0.22 ± 0.04

Table 2 | Comparison of the effect of resource supply on the temperature dependence of fitness and its component traits. For individual traits, the significance of the pairwise comparisons between resource supply levels are shown in Fig. 1. The numbers of individuals that survived to adulthood (*n*) in each treatment were: 22ºC under low-resource supply *n* = 23, under high-resource supply *n* = 37; 26ºC under low-resource supply *n* = 29, under high-resource supply *n* = 30; 32ºC under low-resource supply *n* = 10, under high-resource supply *n* = 27.

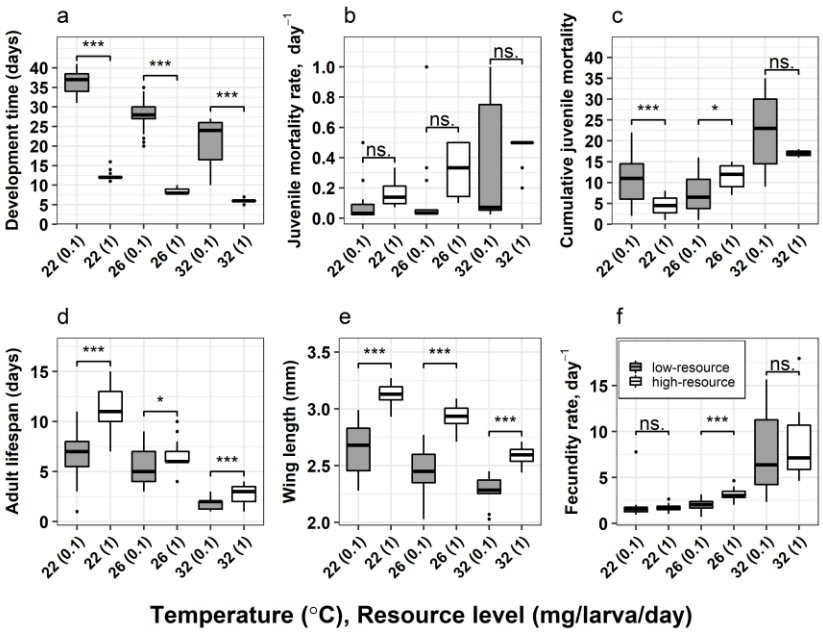

Fig. 1 | The combined effect of temperature and resource supply level on *Ae. aegypti* life history traits. Fecundity data were estimated using eqns. 3, 4 and 5. p-values denote significance levels of the pairwise comparisons of the means for the resource supply levels at each temperature (GLM). * ⇒ *p* value<0.05; *** ⇒ *p* value<0.001; ns. ⇒ nonsignificant. The resulting ANOVAs of the GLMs for each trait are presented in Table 1. The interaction between temperature and resource supply was significant in all cases except for juvenile mortality.

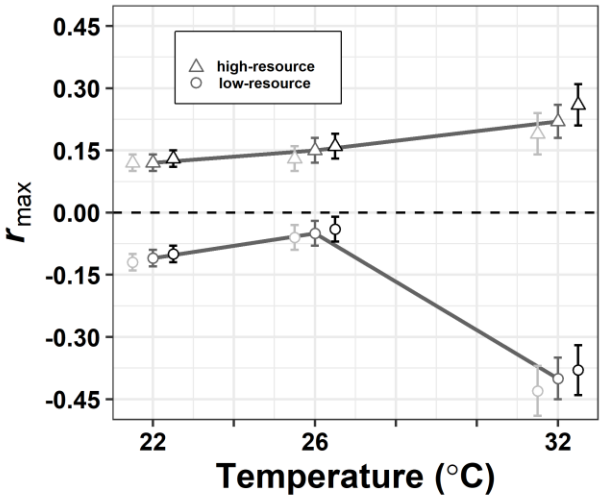

Fig 2 | Population-level *Ae. aegypti* fitness (r_{max}) by resource supply (0.1 (low) or 1 mg/larva/day (high)) across temperatures. Fitness estimates for each treatment, with 95% confidence intervals (CI). The three data points for each treatment represent r_{max} estimated using the 95% CI bounds (±0.28) of the exponent for the scaling of lifetime fecundity with mass (eqn. 4). The lightest greyscale hue estimates derive from the lower 95% CI (0.99–0.28), the midrange hue estimates with trend lines derive from the slope (0.99) and the darkest hue derive from the upper 95% CI (0.99+0.28).

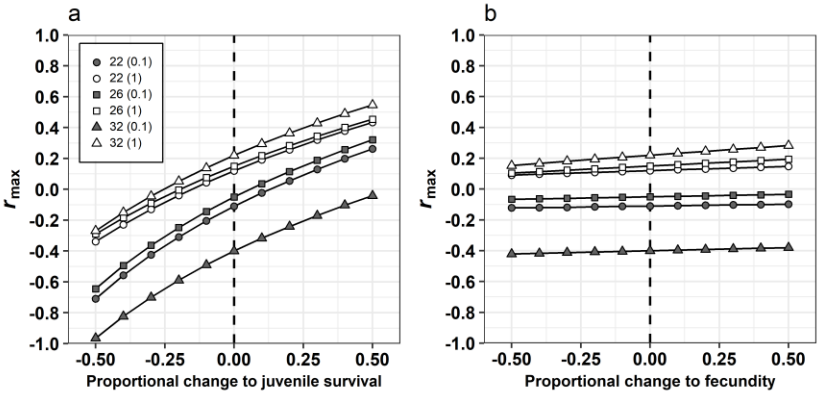

Fig. 3 | Sensitivity of r_{max} to proportional changes in juvenile survival (a) and fecundity (b) for each *Ae. aegypti* population. Juvenile survival was the most important contributor to r_{max}, as relatively small changes in the summed matrix elements for this trait would result in substantial changes in r_{max}. Sensitivity of r_{max} to fecundity was much weaker compared to sensitivity to juvenile traits. Dashed vertical lines in a and b denote r_{max} at zero as represented by the midrange grey hue estimates in Fig. 2. Open symbols denote high-resource supply (1 mg/larva/day); closed symbols denote low-resource supply (0.1 mg/larva/day).