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

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ABSTRACT

Laboratory-derived temperature dependencies of life history traits are increasingly being used to make mechanistic predictions for how climatic warming will affect vector-borne disease dynamics by affecting abundance dynamics of the vector population. These temperature-trait relationships are typically estimated from populations reared on optimal resource supply, even though natural populations of vectors are expected to experience variation in resource supply, including intermittent resource limitation.

Using laboratory experiments on the mosquito *Aedes aegypti*, a principal arbovirus vector, combined with stage-structured population projection modelling, we show that low-resource supply significantly depresses the vector's maximal population growth rate across the entire temperature range (22–32°C) and causes it to peak at a lower temperature than at high-resource supply. This effect is primarily driven by an increase in juvenile mortality and development time, combined with an exaggerated decrease in size of adults with temperature at low-resource supply. 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. Our results provide compelling evidence for future studies to consider resource supply when predicting the effects of climate and habitat change on disease vectors.

INTRODUCTION

The global public health burden of some vector-borne diseases has increased substantially in recent decades [1,2]. The geographical distribution and abundance of vectors is strongly linked to transmission patterns of these diseases [3,4]. There is growing concern that climate and land-use change, coupled with rapid globalization, may result in shifts in both the distributions of vector species and the diseases they transmit [5]. 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 [6–8].

Ecological Metabolic Theory (EMT, including the Metabolic Theory of Ecology (MTE) and Dynamic Energy Budget (DEB) theory) links body size and environmental temperature through metabolic rate to individual-level trait performance and population-level fitness [9–11]. For example, the biological rates (e.g. metabolic, development, mortality) of ectotherms increase approximately exponentially with temperature up to some optimum before declining back to zero at a thermal maximum to affect population growth in a similar way [9,12,13]. While this core EMT prediction is well-supported, models linking metabolic rates to population-level fitness generally assume that resource supply is not a limiting factor [10,14]. Recent efforts to incorporate the effects of temperature and resource availability have focused on individual traits [15], or, when estimating population growth rates, have assumed that mortality is independent of resource availability [16].

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 [11,17]. 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 [15].

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 [18–21]. The classical EMT framework has recently provided important contributions in this area [22–24], including vector-borne diseases [19,20]. 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, Mordecai et al. [19,20] recently used a MTE trait-based framework to predict the temperature-dependence of the basic reproduction number (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, [25], which also applies to disease vectors, such as mosquitoes [26]. 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 [26,27]. Reduced development time, due to increased temperature, can increase population-level fitness by decreasing generation time [28], but

cooler temperatures yield larger, more fecund and longer-living females, which are all traits that generally increase fitness [27,29,30]. 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 [31]. However, smaller females may bite more frequently, which can increase transmission probability [32]. 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 [25,33].

Studies on the effects of resource availability on mosquito traits generally report a positive association between food level and juvenile development and survival [34–36], as well as adult body size, nutritional reserves and fecundity. 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 [37–39]. 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 [40–42], 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; [43]). We show that these factors can each act alone and interact with each other 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^{-1} day^{-1} (high-resource supply). These experimental temperatures span the range of average annual temperatures [44] that this strain of *Ae. aegypti* is likely to experience in the wild (F16-19 originating from Fort Meyer, FL; [45]). Our low-resource supply level was chosen because it is a level of limitation often experienced by wild populations, and 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 [40,41]. The high-resource supply level corresponds to the upper mid-range of the high-resource supply levels used in Arrivillaga & Barrera [40] and Barrera et al. [41], and is consistent with the levels of resource supply commonly used in laboratory studies on this species [35,46].

Batches of approximately 300 *Ae. aegypti* 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. Rearing tubs were cleaned and refilled with fresh tap water daily. 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 [47], 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) [47]. 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 [10,29,48]. Negative $r_{\max}$ values indicate decline and positive ones, growth. The projection matrices were built and analysed using the `popbio` R package [49,50].

Parameterisation

Immature development time and immature and adult survival proportions

Matrix survival elements (the sub-diagonal of the matrix $\mathbf{A}$; eqn. 1) were populated with continuous survival proportions estimated using the Kaplan-Meier survival function in the `survival` R package [49,51]. 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 proportions. 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 [34,52].

Fecundity (the first row of $\mathbf{A}$; eqn. 1)

Allometric relationships between fecundity and size are commonly used in predictions of population growth in *Aedes* mosquitoes [53,54]. Here, we estimated fecundity using temperature and resource supply-dependent scaling between wing length and fecundity [46]. 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 [55]. Wings (one per female) were removed, mounted onto glass

slides, photographed using a dissecting microscope and then measured with ImageJ software [56].

Our analysis of the dataset indicated that the scaling between size and fecundity changes significantly with temperature but not resource supply (Fig. S1). So, to estimate lifetime fecundity (F in eqn. 3) from wing length for mosquitoes that we reared at 22 and 32°C at high- and low-resource supply, we used the scaling coefficients from the Farjana & Tuno (50; n = 264, R^2 = 0.87, p<0.001; eqn. 2) dataset at their at 20 and 30°C, respectively. For mosquitoes that we reared at 26°C, there is no corresponding temperature treatment in the Farjana & Tuno (50) dataset, so we used the scaling coefficients from the Briegel dataset at 27°C (56; n = 206, R^2 = 0.77, p<0.001; eqn. 2). Lifetime fecundity (F) was then divided by lifespan and multiplied by 0.5 (assuming a 1:1 male-to-female offspring ratio) to obtain temperature-specific individual daily fecundity. Later, we show that this level of variation in the scaling of fecundity does not change our results qualitatively.

$$\begin{aligned} &22°\text{C}, F = 0.93 + 3.16 \log(L) \\ &26°\text{C}, F = 0.40 + 3.80 \log(L) \\ &32°\text{C}, F = 0.26 + 4.08 \log(L) \end{aligned} \qquad (2)$$

Parameter sensitivity

We used the delta method to approximate 95% confidence intervals (CIs) for our fitness calculations [47,57] 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. As additional sensitivity analyses, we recalculated fitness using the upper and lower 95% CIs of the exponents (Figs. 3, S1) for the scaling of lifetime fecundity with wing length. The standard error for the scaling exponent at 27°C is not provided in Briegel [52], though the model's R^2 is satisfactory (0.77). Thus, to determine the sensitivity of $r_{\max}$ to uncertainty in fecundity estimates at 26°C, we assumed a similar 95% CI (± 0.25) to those determined through our analysis of the Farjana & Tuno [46] dataset at 20 and 30°C.

Elasticity analysis

Elasticities were used to quantify the proportional contributions of individual life history traits to $r_{\max}$. Elasticities can provide valuable insights into the sensitivity of population growth to hypothetical environmental perturbations during different life stages. Elasticity, e_{ij}, measures the proportional effect on λ of an infinitesimal change in an element of $\mathbf{A}$ (eqn. 1) with all other elements held constant (the partial derivative) [58,59]. This partial derivative of λ, with respect to each element of $\mathbf{A}$, is $s_{ij} = \partial\lambda/\partial a_{ij} = v_i w_j$ with the dot product $\langle \mathbf{w}, \mathbf{v} \rangle = 1$. Here, $\mathbf{w}$ is the dominant right eigenvector (the stage distribution vector of $\mathbf{A}$), $\mathbf{v}$ is the dominant left eigenvector (the reproductive value vector of $\mathbf{A}$), and a_{ij} is the $i{\times}j^{\text{th}}$ element of $\mathbf{A}$. 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 [58,59]. 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 [49]. In the first instance, to assess how temperature, resource supply, their interaction (whether low-resource supply treatments exhibited different thermal responses) and replicate influenced development time, lifespan and wing length, we fitted linear regression models. Model diagnostics and Shapiro-Wilk [60] tests were used to assess data normality. These data were nonlinear, positive and right skewed. Therefore, 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. Replicate was included in these GLMs as a fixed effect. Goodness-of-fit was assessed using model deviance/d.f. scores and model residuals.

We investigated the effect of temperature and resource supply on juvenile mortality rate by fitting a set of candidate distributions (exponential, log-logistic, Gompertz and Weibull) to the survival data with R package `flexsurv`. The Gompertz survival function was the best fit to these data according to the Akaike Information Criterion (AIC) (Table S3). The final mortality model was obtained by dropping terms from the full model (consisting of temperature × resource supply + replicate as fixed effect predictors). If removing a term did not improve model fit (ΔAIC > –2), it was removed from the full model (Table S3). For each treatment, maximum likelihood methods executed in `flexsurv` estimated mortality parameters (and their 95% CIs) of the Gompertz model, $\mu_x = ae^{bx}$, where (a) is the baseline morality rate, and (b) is the change in mortality rate with time (i.e. the slope of the mortality trajectory). These parameter estimates were then used to determine the significance of the effects of temperature and resource supply on juvenile mortality.

RESULTS

All trait responses varied significantly with temperature and resource supply, with a significant interaction between the two environmental variables (Tables S1, S2; Figs. 1, 2). Thus, the realised effect of temperature on trait responses was consistently and significantly mediated by resource supply.

Baseline juvenile mortality rates, a, were significantly lower at low-resource supply than at high-resource supply as temperatures increased from 22 to 32°C (non-overlapping 95% CIs at 26 and 32°C; Fig 1c). Mortality rate trajectories, b, were significantly lower at high-resource supply than at low-resource supply as temperatures increased from 22 to 32°C (non-overlapping 95% CIs at 26 and 32°C; Fig 1d).

Development time varied significantly with the interaction between temperature and resource supply (ANOVA; $F_{2,0.75} = 24.11$, $p<0.001$; Table S1). Whereas development time decreased both at warmer temperatures and at high-resource supply, the rate of decrease with temperature was greater at low-resource supply than at high-resource supply. At low-resource supply, development time decreased by 17.01 days as temperatures increased from 22 to 32°C, whereas at high-resource supply, it decreased by 6.38 days across this range (Table S2, Fig. 2a).

Lifespan varied significantly with the interaction between temperature and resource supply (ANOVA; $F_{2,\ 2.41} = 15.34$, $p<0.001$; Table S1). Although lifespan decreased both at warmer temperatures and at low-resource supply, the rate of decrease with temperature was greater at high-resource supply than at low-resource supply. High-resource supply lifespan decreased

by 8.89 days, whereas low-resource supply lifespan decreased by 4.71 days as temperatures increased from 22 to 32°C (Table S2, Fig 2b).

The interaction between temperature and resource supply resulted in significant variation in size at maturity (wing length) between resource levels (ANOVA; $F_{2,0.03} = 4.36$, p=0.01; Table S1). Size decreased both at warmer temperatures and at low-resource supply, though the rate of decrease with temperature was greater at high-resource supply than at low-resource supply. At low-resource supply, length decreased by 0.37 mm as temperatures increased from 22 to 32°C, while at high-resource supply, length decreased by 0.54 mm (Table S2, Fig 2c).

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. 3, Table S2). Low-resource supply r_{max} increased from –0.09 at 22°C to –0.03 at 26°C and then decreased acutely to –0.38 at 32°C. In contrast, at high-resource supply, r_{max} was always positive and increased monotonically with temperature from 0.17 at 22°C to maximal growth (0.28) at 32°C.

Elasticity analysis

Juvenile survival was the most important contributor to r_{max} (Fig. 4). For example, at low-resource supply at 32°C, a 0.5 proportional increase in juvenile survival would almost halve the rate of decline from –0.384 to –0.204 (Fig. 4a). In contrast, for the same treatment, a proportional increase of the same magnitude for adult survival would increase r_{max} from –0.384 to –0.379 (Fig. 3b), and fecundity would increase r_{max} from –0.384 to –0.376 (Fig. 3c). This underlines 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 and adult survival, on the other hand, have relatively negligible effects 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 at high-resource supply met EMT expectations by being positive and increasing nonlinearly with temperature (Fig. 2a, c) [61]. 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. For example, in Mordecai et al.'s [20] temperature-dependent R_0 predictions, juvenile *Ae. aegypti* development rate increased from approximately 0.07 day^{-1} at 22°C to 0.14 day^{-1} at 32°C. In the present study, development rate (Fig. 1a, Table S2) increased by a similar margin (~0.08 to ~0.17 day^{-1}) across the same temperature range.

In contrast, at 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, at low-resource supply, juvenile development rate was ~0.03 day^{-1} at 22°C, which is 57% less than the rate (~0.07 day^{-1}) used at this temperature in Mordecai et al. [20] to predict R_0. Similarly, at low-resource supply at 32°C, we found juvenile development rate was ~0.05 day^{-1}; whereas in Mordecai et al. [20] it was 64%

greater (~0.14 day^{-1}). Juvenile survival proportions at low-resource supply also differed markedly from the high-resource supply proportions used in Mordecai et al. [20]. In the present study, survival was 0.51 at 22°C, 0.64 at 26°C and 0.22 at 32°C (Fig. 1a); whereas in Mordecai et al. [20] it was approximately 0.83 between 20-22°C, 0.76 at 25°C, and 0.72 at 32°C.

These differences in juvenile trait responses are likely to substantially alter temperature-dependent R_0 predictions. For example, when the abundance components of Mordecai et al.'s R_0 framework [7] are parameterised with juvenile trait responses at our low-resource supply, the estimated number of mosquitoes at 32°C decreases by almost one order of magnitude (from ~257.68 to ~28.12). This underlines the importance of considering resource supply when predicting temperature-dependent R_0.

The differences between the temperature-dependence of traits at low- versus high-resource supply resulted in a marked divergence of the temperature-dependence of r_{max} (Fig. 3) between the two treatments. At low-resource supply, fitness was negative throughout and unimodal (declining steeply from 26 to 32°C). This indicates that population fitness becomes increasingly constrained by resource limitation as temperatures increase. Fitness at high-resource supply was positive, increasing and linear. This absence of unimodality suggests that the temperature at which fitness peaks (T_{pk}) may be higher than 32°C when resources are abundant. However, the effects of temperature and resource availability across a broader upper range of temperatures would be required to verify this.

The elasticity analysis shows that the primary mechanism underlying the divergent trends of of r_{max} across resource supply levels is decreased juvenile survival, which decreased population-level fertility and, ultimately, fitness (Figs. 1, 3). As temperatures increased from 22 to 32°C, baseline juvenile mortality rates were significantly lower at low-resource supply than at high-resource supply (Fig. 1c), but, at high-resource supply, rate trajectories (Fig. 1d) were negative and significantly lower than at low-resource supply as temperatures increased across this range. 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.

Development time at both resource supply levels decreased nonlinearly with temperature, though it decreased more steeply with temperature at low-resource supply than at high-resource supply (Table S2, Fig. 1a). 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).

Juvenile survival decreased significantly with temperature, and it was significantly lower at low-resource supply (Fig. 1). This is probably because somatic maintenance cost increases as metabolic rate increases [11,17]; 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 at low-resource supply, where the energy supply-demand deficit was likely largest. The Gompertz-shaped juvenile survival curves observed at 22 and 26°C at low-resource supply (Fig. 1a) may well arise from the amount of resource being enough for somatic maintenance but insufficient for development. This could be a key line of future investigation because it points to the importance of understanding how resource availability combines with temperature and other environmental factors to affect natural mosquito

populations. For example, the negative effects of resource limitation on population growth through increased juvenile development time and mortality may be exacerbated, as individuals remain in the vulnerable juvenile stages for longer, which may increase predation threat [62]. If resource availability increases with climatic warming, the negative effects of predation on population growth could be offset by increased development and recruitment rates [63]. Alternatively, population growth could be dampened, if climate change reduces the quantity of food available to ectotherms [15,64].

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. 4). For example, at high-resource supply, adult lifespan and body size were higher at 26°C than at 32°C, yet fitness at 32°C was predicted to be 39% higher (Fig. 3). This is because high-resource supply and increased temperature minimised 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 [65], including mosquitoes [37]. 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.

Size at emergence decreased significantly with temperature for both resource supply levels (Table S1, Fig. 1c), consistent with the size-temperature rule [25]. 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 at high-resource supply than at 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 S2). However, as temperatures increased from 26 to 32°C, wing length decreased by ~0.17 and ~0.34 mm at low- and high-resource supply, respectively. For size at emergence, the decline with temperature at 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 at high-resource supply than at low-resource supply (Table S1, Fig. 1b). 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. At low-resource supply, lifespan decreased by ~3.69 days, whereas at high-resource supply it decreased by ~4.24 days (Table S2). However, as temperatures increased from 22 to 26ºC, lifespan decreased by ~1.02 days at low-resource supply and by ~4.65 days at high-resource supply. This relatively flatter decline at low-resource supply may reflect how larvae respond to cooler temperatures when resources are limited. Cooler temperatures prolong development by slowing underlying rate processes [66]. 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 [67,68]. At 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 at 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 carry over effects [52,69]. Predicted fecundity increased nonlinearly with temperature, mediated by resource supply levels (Fig 1d, Table S1). Across both resource levels, these fecundity estimates are similar to those reported in past studies. For example, in Mordecai et al. [20], *Ae. aegypti* fecundity increased from approximately 3.58 to 11.20 eggs female^{-1} day^{-1} as temperatures increased from 22 to 32ºC compared to an increase from 4.29 to 14.17 eggs female^{-1} day^{-1} at high-resource supply and 5.05 to 12.25 eggs female^{-1} day^{-1} at low supply, across the same temperature range. Any differences likely arise from the fact that our size-scaling-based predictions ignore additional effects on fecundity, such as adult food supply. However, even substantial under- or overestimation of fecundity by our size-scaling predictions and the use of starved adult lifespans, would not affect our main conclusions because predicted fitness was relatively insensitive to these traits (Figs. 3, 4).

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 [8,70,71]. For example, *Anopheles* [72] and *Aedes* [73] 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.

We note that experimenting with more resource levels would not change our qualitative results, which we have shown to be robust using thorough sensitivity analyses. Indeed, the two resource levels we have chosen represent extremes, and it is reasonable to conclude that mosquito population fitness in the field fluctuates, with resource fluctuations, between radically different temperature responses as we have found here (Fig. 3). One avenue for future work is to find more accurate methods to estimate effective temperature-dependent fitness values in the field, accounting for resource fluctuations.

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 [40–42,74] 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 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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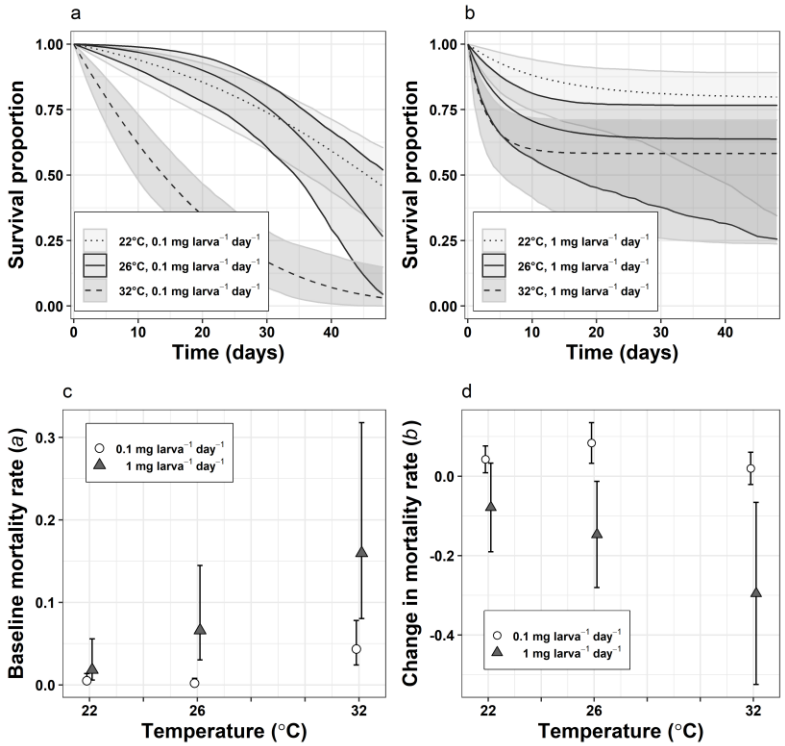

Fig. 1 | The effect of resource supply on the temperature-dependence of juvenile survival across time (days) with 95% confidence bounds. Survival curves at **(a)** low- and **(b)** high- resource supply by temperature. **c,** Baseline mortality rates, *a*, by resource supply level across temperatures with 95% CIs. Mortality rates were significantly lower at low-resource supply than at high-resource supply as temperatures increased from 22 to 32°C (95% CIs at 26 and 32°C do not overlap). **d,** Change in mortality rate trajectories, *b*, by resource supply level across temperatures with 95% CIs**.** Rate trajectories were significantly lower at high-resource supply than at low-resource supply as temperatures increased from 22ºC (95% CIs at 26 and 32°C do not overlap).

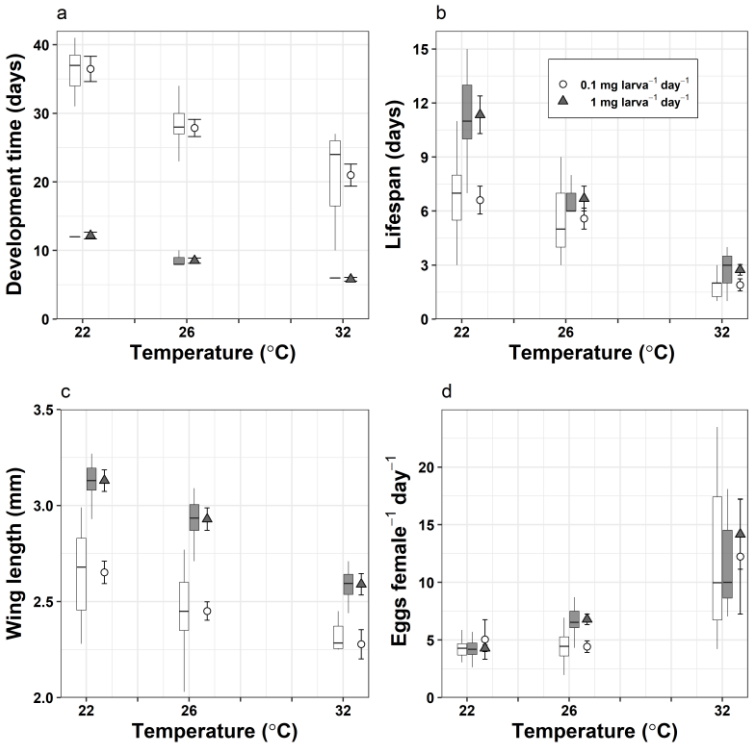

Fig. 2 | The combined effect of temperature and resource supply level on *Ae. aegypti* life history traits. a-c, Resource supply significantly modulated the effect of temperature on all directly measured traits, except adult lifespan at 26°C (**b**). Symbols denote the GLM-estimated means with 95% CIs (Table S2) for the resource supply levels at each temperature (circles are low-resource supply treatments; triangles are high-resource supply treatments). The resulting ANOVAs of the GLMs for each trait are presented in Table S1. **d,** Predicted fecundity increased significantly with temperature at both resource levels (non-overlapping 95% CIs). The extent to which fecundity increased with temperature and resource level was only significant at 26°C. The numbers of females that survived to adulthood (*n*) in each treatment were: 22°C at low-resource supply $n = 23$, at high-resource supply $n = 37$; 26°C at low-resource supply $n = 29$, at high-resource supply $n = 30$; 32°C at low-resource supply $n = 10$, at high-resource supply $n = 27$.

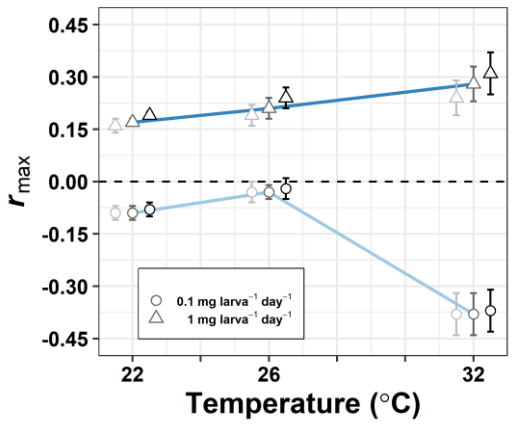

Fig 3. | Population-level *Ae. aegypti* fitness (r_{max}) by resource supply (0.1 (low) or 1 mg larva^{-1} day^{-1} (high)) across temperatures. Fitness estimates for each treatment, with 95% confidence intervals (CI). The three data points for each treatment represent r_{max} estimated using the 95% CI bounds of the exponents for the scaling of lifetime fecundity with wing length (eqn. 2, Fig. S1). The lightest greyscale hue estimates derive from the lower 95% CIs, the midrange hue estimates with trend lines derive from the slopes and the darkest hue derive from the upper 95% CIs.

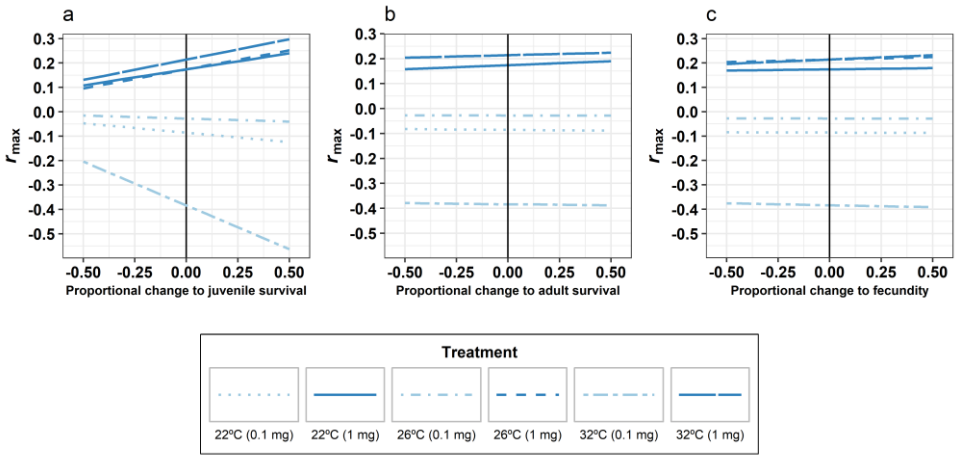

Fig. 4 | Sensitivity of r_{max} to proportional changes in juvenile survival (a) adult survival (b) and fecundity (c) for each *Ae. aegypti* population. Juvenile survival was the most important contributor to r_{max}, as relatively small changes in the summed matrix elements for this trait would result in relatively large changes in r_{max}. Sensitivity of r_{max} to adult traits was much weaker compared to sensitivity to juvenile traits. Solid black vertical lines denote r_{max} at zero as represented by the midrange grey hue estimates in Fig. 3. Dark blue lines denote high-resource supply (1 mg larva^{-1} day^{-1}); light blue lines denote low-resource supply (0.1 mg larva^{-1} day^{-1}).

Supplementary Information

Table S1 | 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	Predictor	χ^2	df	*F* value	p-value
Juvenile development time	**Temperature**	**9.74**	**2**	**314.64**	**<0.001 *****
R^2 = 0.96	**RS**	**50.30**	**1**	**3251.01**	**<0.001 *****
	Temperature: RS	**0.75**	**2**	**24.11**	**<0.001 *****
	Replicate	0.01	2	0.18	0.83
	Residuals	2.30	148		
Lifespan	**Temperature**	**34.54**	**2**	**209.76**	**<0.001 *****
R^2 = 0.74	**RS**	**3.18**	**1**	**34.57**	**<0.001 *****
	Temperature: RS	**2.41**	**2**	**15.34**	**<0.001 *****
	Replicate	0.40	2	2.47	0.08
	Residuals	11.94	148		
Body size	**Temperature**	**0.65**	**2**	**111.58**	**<0.001 *****
R^2 = 0.79	**RS**	**0.92**	**1**	**314.28**	**<0.001 *****
	Temperature: RS	**0.03**	**2**	**4.36**	**0.01 ***
	Replicate	0.003	2	0.48	0.62
	Residuals	0.41	141		

Table S2 | Comparison of the effect of resource supply on the temperature-dependence of fitness and its component traits. The means with 95% CIs for development time, lifespan and wing were estimated by the GLMs (Table 1). For fecundity, these were estimated using the `Rmisc` package in R. For r_{max}, 95% CIs were approximated using the method described in [57].

Trait	Temperature (°C)	Mean ± 95% Confidence intervals	
		Low-resource supply	High-resource supply
Development time (days)	22	36.45 ± 1.78	12.19 ± 0.47
	26	27.86 ± 1.22	8.53 ± 0.37
	32	19.47 ± 1.53	5.81 ± 0.26
Lifespan (days)	22	6.61 ± 0.72	11.35 ± 0.99
	26	5.59 ± 0.54	6.70 ± 0.64
	32	1.90 ± 0.38	2.46 ± 0.28
Wing length (mm)	22	2.65 ± 0.06	3.13 ± 0.06
	26	2.45 ± 0.05	2.93 ± 0.06
	32	2.28 ± 0.07	2.59 ± 0.06
Fecundity (eggs female^{-1} day^{-1})	22	5.05 ± 1.71	4.29 ± 0.28
	26	4.42 ± 0.50	6.79 ± 0.46
	32	12.25 ± 5.00	14.17 ± 3.03
Population-level fitness (r_{max})	22	–0.09 ± 0.02	0.17 ± 0.01
	26	–0.03 ± 0.02	0.21 ± 0.03
	32	–0.38 ± 0.06	0.28 ± 0.05

Table S3 | Simplification of the Gompertz juvenile survival model. The full model includes the effects of temperature × resource supply and replicate on mortality. The interaction model without replicate won because it had the lowest AIC. ΔAICs were calculated as differences from the interaction model.

Model terms	Model name	AIC	ΔAIC	df
Temperature × RS	**Interaction**	**1050.85**	**0**	**7**
Temperature × RS + replicate	Full	1053.05	+2.2	9
Temperature + RS	No interaction	1053.50	+2.7	5
Temperature	Temperature only	1055.99	+5.1	4
Resource	Resource only	1110.30	+59.5	3
None	Null	1108.70	+57.9	2

Sensitivity of r_{max} to uncertainty in predicted fecundity

As an additional sensitivity analysis, we recalculated fitness using the upper and lower 95% CIs of the exponents for the scaling of lifetime fecundity with wing length (eqn. 2). These are shown in Fig. S1. The standard error for the scaling exponent at 27°C was not provided in Briegel [52] but the model's R^2 is quite high (0.77). Thus, to determine the sensitivity of r_{max} to uncertainty in fecundity estimates at 26°C, we assumed a similar 95% CI (± 0.25) to that of the Farjana et al. [46] dataset at 20 and 30°C.

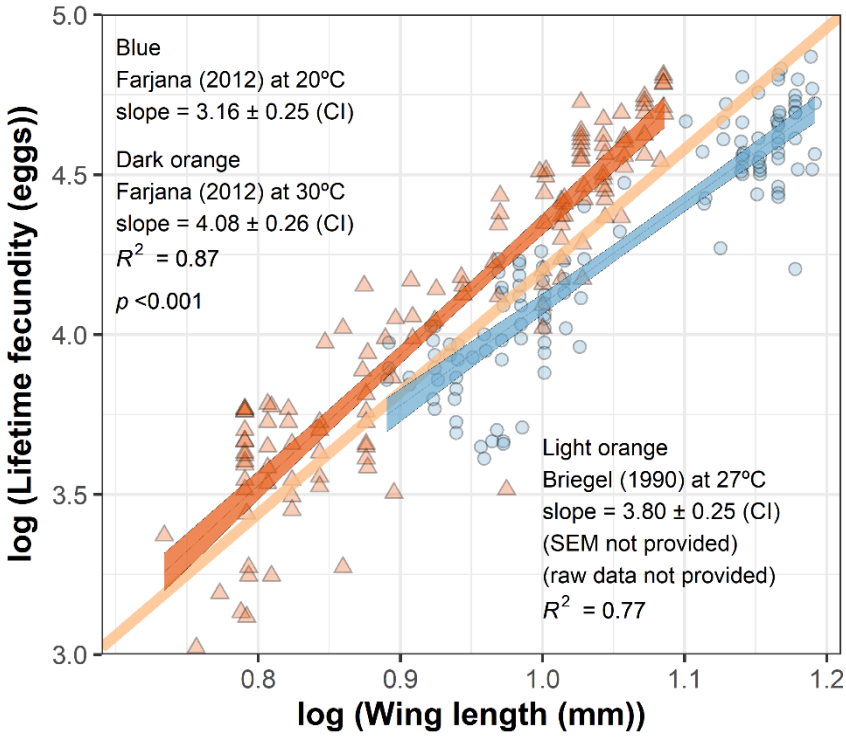

Fig. S1 | a, Analysis of the Farjana et al. [46] dataset shows that the scaling of wing length and fecundity in *Ae. Aegypti* is temperature-dependent. The scaling exponents (slopes) for both resource supply levels are significantly higher at 30°C than at 20°C. However, the effect of resource supply on fecundity is non-significant at the temperature level (not shown). The standard error for the scaling exponent at 27°C is not shown because it is not provided in [52], so for 26°C, we assumed a similar 95% CI to those in Farjana et al. ([46]; 3.80 ± 0.25). Despite these assumptions relating to fecundity, our r_{max} calculations are robust to uncertainty/variation in the underlying scaling and temperature dependences (Figs. 3 and 4).